

AVIAN PREDATION AT A SOUTHERN ROCKHOPPER PENGUIN COLONY ON STATEN
ISLAND, ARGENTINA

Marcela Liljeström

A Thesis Submitted to the
University North Carolina Wilmington in Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

Department of Biology and Marine Biology

University of North Carolina Wilmington

2005

Approved by

Advisor Committee

Dr. Mark Galizio, Dr. Michael McCartney and Dr. Adrián Schiavini

Dr. Steve Emslie
Chair

Accepted by

Dr. Robert Roer
Dean, Graduate School

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ABSTRACT

The association between avian predation on Southern Rockhopper Penguins (*Eudyptes chrysocome chrysocome*) and subcolony size was examined during the chick-rearing period. In addition, activities of various predator and scavenger species at these subcolonies was documented and quantified for the first time. Subcolonies ranging from 69 to 1520 nests were observed for 461 and 386 hr, respectively, during December 2003 and 2004. Striated Caracaras (*Phalacrocorax australis*) were the most common predator/scavenger in all subcolonies except for two in which Kelp Gulls (*Larus dominicanus*) and Dolphin Gulls (*Larus scoresbii*) were dominant. The greatest numbers of predation and attempted predation events were observed on the functional and geometric edge of the subcolony. Kelp Gulls were only observed approaching central nests from the air. Striated Caracaras were mostly observed approaching nests on the geometric and functional edge from peripheral and central tussocks, respectively. In both years nest success was correlated with subcolony size. Small subcolonies in which predation was observed had a proportionally higher predation rate (predation rate per nest) than larger subcolonies with similar absolute predation rates, suggesting that if predation does occur, subcolonies may lower their predation risk by a dilution effect, once they have reached some minimum size. Subcolonies can also have zero or low predation risk when surrounded by larger subcolonies or when part of the territory of a Striated Caracara. Within each subcolony, nests in central locations of large subcolonies or those on the geometric edge of embankments seem to be the most protected from predation.

ACKNOWLEDGMENTS

I would like to thank my committee and advisor for their assistance and suggestions during the thesis writing. I am especially grateful to Dr. Dargan Frierson from the Statistics Department at UNCW for his patience and help with the statistical analyses. Special thanks to Soledad Albanese, Carlos Cabrera, Christine Calleri, Carolina Gargiulo, Fernanda Malacrida, and Marcelo Turus, who assisted in the field and put up with endless observation hours under difficult weather conditions. “La Colina de la Vida” will long be remembered by all of us. I would also like to thank Jonathan Meiburg and Andrea Raya Rey for sharing their observations on Striated Caracaras and Rockhopper Penguins at Staten Island. The National Geographic Society provided financial support for the field work, and the Argentinean Navy and the “Ushuaia” tour vessel provided transportation to and from Staten Island. Finally, special thanks go to my family and friends from Argentina for their support and encouragement along the way.

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INTRODUCTION

Among the proposed advantages of coloniality, reduced probability of predation is the most widely studied. Animals living in colonies may lower rates of nest predation in several ways: 1) by early detection of predators (given that group vigilance increases with the number of individuals present), 2) by deterring predators through group mobbing and defense, 3) through the “encounter effect” (decreasing the probability of detection by a predator), and/or 4) by dilution of predation risk (“dilution effect”) either through synchronized reproduction, thus swamping the ability of predators to exploit them, or by clustering nests to create the “selfish herd effect” (see reviews in Wittenberger and Hunt 1985, Brown and Brown 2001). Hamilton’s selfish herd model predicts that, if a predator always takes the prey item closest to it, prey will seek to minimize the distance between themselves and their neighbors, and maximize the number of neighbors (Hamilton 1971).

Several studies have shown lower predation at higher densities of prey or in larger colonies (Spear 1993, Anderson and Hodum 1993, Hernández-Matías et al. 2003). Conversely, other studies have shown an opposite trend (Stokes and Boersma 2000). The “selfish herd” concept has been extended to predict the center as the optimal location for a nest in a colony. Because peripheral nests have neighbors only on one side, individuals breeding at the edge of a colony should suffer higher losses due to predation than individuals breeding near the center (Tenaza 1971). In support of this concept, several authors have reported higher predation rates on colony edges than on the center (Taylor 1962, Tenaza 1971, Spear 1993, Emslie et al. 1995, Yorio and Quintana 1997), though others have shown the reverse (Bellinato and Bogliani 1995, Brunton 1997) or even no differences in chick mortality between edge and central nests (Barbosa et al. 1997).

Colonial breeding is most common among marine birds; of some 260 species, 98% nest in colonies (Lack 1968). Effects of predators on colonial seabirds have been widely investigated (see review by Wittenberger and Hunt, 1985). In penguins, impacts and activities of predators have been studied in the Gentoo (*Pygoscelis papua*) and Adélie Penguins (Tenaza 1971, Davis 1982, Ainley et al. 1983, Young 1994, Emslie et al. 1995), King Penguin (*Aptenodytes patagonicus*) (Hunter 1991, Le Bohec et al. 2003) and Chinstrap Penguin (*Pygoscelis antarctica*) (Barbosa et al. 1997). These studies have provided contradictory results, indicating the complexity of the predator-prey relationship.

Rockhopper Penguins (*Eudyptes chrysocome*) breed on sub-Antarctic and temperate islands throughout the southern ocean (Williams 1995). Over the past years, the population has undergone considerable declines at most of the islands where they nest (Woehler and Croxall 1997). The reasons for these trends are largely unknown, but some have been attributed to a drop in sea surface temperatures, starvation prior to molt, and human activities such as commercial fishing and pollution (see Pütz et al. 2002). This overall population decline has resulted in the classification of Rockhopper Penguins as a vulnerable species, according to the International Union for the Conservation of Nature (IUCN; Birdlife International 2000).

The southern subspecies (*Eudyptes chrysocome chrysocome*) breeds on the coasts of southern South America and the Falkland (Malvinas) Islands, in approximately 52 locations (Schiavini 2000). Staten Island (Isla de los Estados), east of the Tierra del Fuego archipelago, has two of the three known breeding colonies for Argentina and, in contrast to the widespread population decline, the population here appears to be stable or increasing with a total of 173,000 nests (27.3 % of the breeding population; Schiavini 2000).

Previous observations suggest that the Striated Caracara (*Phalacrocorax australis*) is an important predator at Rockhopper Penguin colonies on Staten Island (J. Meiburg pers. comm., ML pers. obs.). The IUCN lists the Striated Caracara as Near-Threatened due to its small numbers and restricted range (Birdlife International 2005). Its distribution includes isolated shores and islands off southern South America (Narosky and Yzurieta 1987).

Here, I present data on the occurrence and impact of predator-scavengers associated with Rockhopper Penguins on Staten Island to test the hypothesis that breeding in larger subcolonies offers more protection to chicks against aerial predators than smaller ones. If so, I predict that large subcolonies will experience less predation per individual than smaller ones and that predation risk and nest predation will decrease with subcolony size. Additional objectives were to document and quantify the activities of various predator and scavenger species associated with Rockhopper Penguin subcolonies, evaluate seasonal and annual variation in these activities, and analyze the predator- scavenger's impact, through predation, on subcolonies of different sizes during the chick rearing period. This information was used to determine if reduced predation is an important advantage of colonial breeding in Rockhopper Penguins.

METHODS

Study Area

The study was conducted at Bahía Franklin, Staten Island (54° 50' S, 64° 40.5' W), Argentina (Fig. 1), where the largest colony of Southern Rockhopper Penguins on the island (167,000 breeding pairs in 102 subcolonies) is located (Schiavini 2000). Within colonies, penguins form distinct nest aggregations or subcolonies that are easily identifiable on the ground

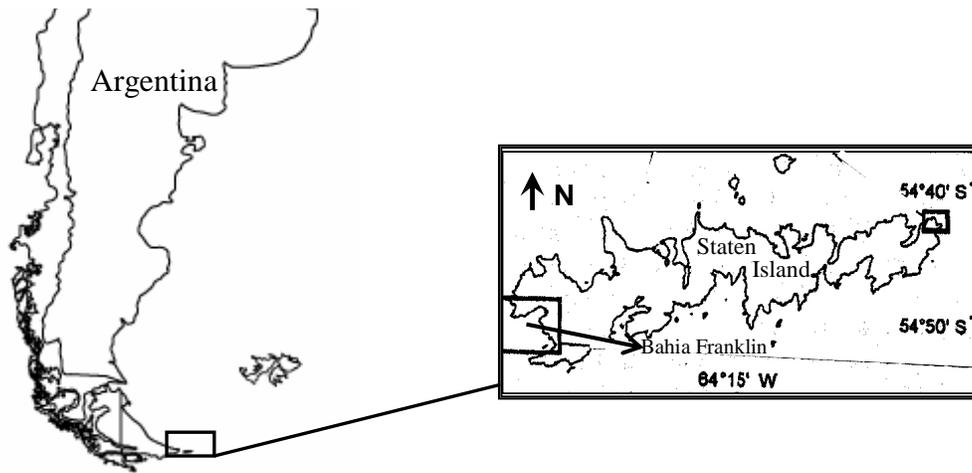


FIG. 1. Location of the two Rockhopper Penguin colonies (open squares) on Staten Island, Argentina.

or from aerial photos by differences in soil and vegetation modified by the bird's activities (Fig. 2). Nests are distributed mainly on areas of tussock grass (*Poa flabellata*) which are found surrounding the subcolonies (peripheral tussocks) and often scattered in the center (central tussocks) as well.

Rockhopper Penguins arrive at the colony in late September, lay eggs in late October and hatch chicks in late November (A. Raya Rey pers. comm.). The chick rearing period includes the brooding or guard stage which extends from the end of November to mid December, and the crèche stage which extends until the end of January/beginning of February. During the brooding stage chicks are guarded at the nest mostly by the male. As chicks get older they are left unguarded and form crèches (A. Raya Rey pers. comm.).

Eight subcolonies ranging from 69 to 1520 nests and nine subcolonies ranging from 72 to 1682 nests were observed during 7-30 December 2003 and 8-25 December 2004, respectively (Table 1). Logistic constraints on visiting the colony prevented additional observations outside of these time periods. Study subcolonies were chosen because of their relatively easy access from the camp site, their near circular shape and their different sizes spread throughout the area (Fig. 3). The size of each subcolony was estimated as the mean total number of occupied nests (either by adults and chicks/eggs or by adults only), determined from repeated counts by different observers during the first observation day. Subcolonies were observed for 3 hr periods alternating periodically between 08:00-20:00 each day, by the author and three trained field assistants.

Nest location was classified as geometric edge, functional edge or central. Those nests in the most external ring of the subcolony and not completely surrounded by other nests were considered as "geometric edge"; nests at least one nest away from the periphery of the subcolony



FIG. 2. Aerial photo looking over part of the Rockhopper Penguin colony at Bahía Franklin. The subcolonies show up as lighter colored patches with easily identifiable limits, one of the subcolonies is circled in red. (Photo by A. Schiavini, November 1998).

TABLE 1. Mean number of nests in study subcolonies (SC1-9) during December 2003 and 2004. SC9 was only observed in 2004.

year	SC1	SC2	SC3	SC4	SC5	SC6	SC7	SC8	SC9
2003	69	506	929	1520	440	122	574	179	-
2004	72	473	978	1660	386	132	361	145	1682

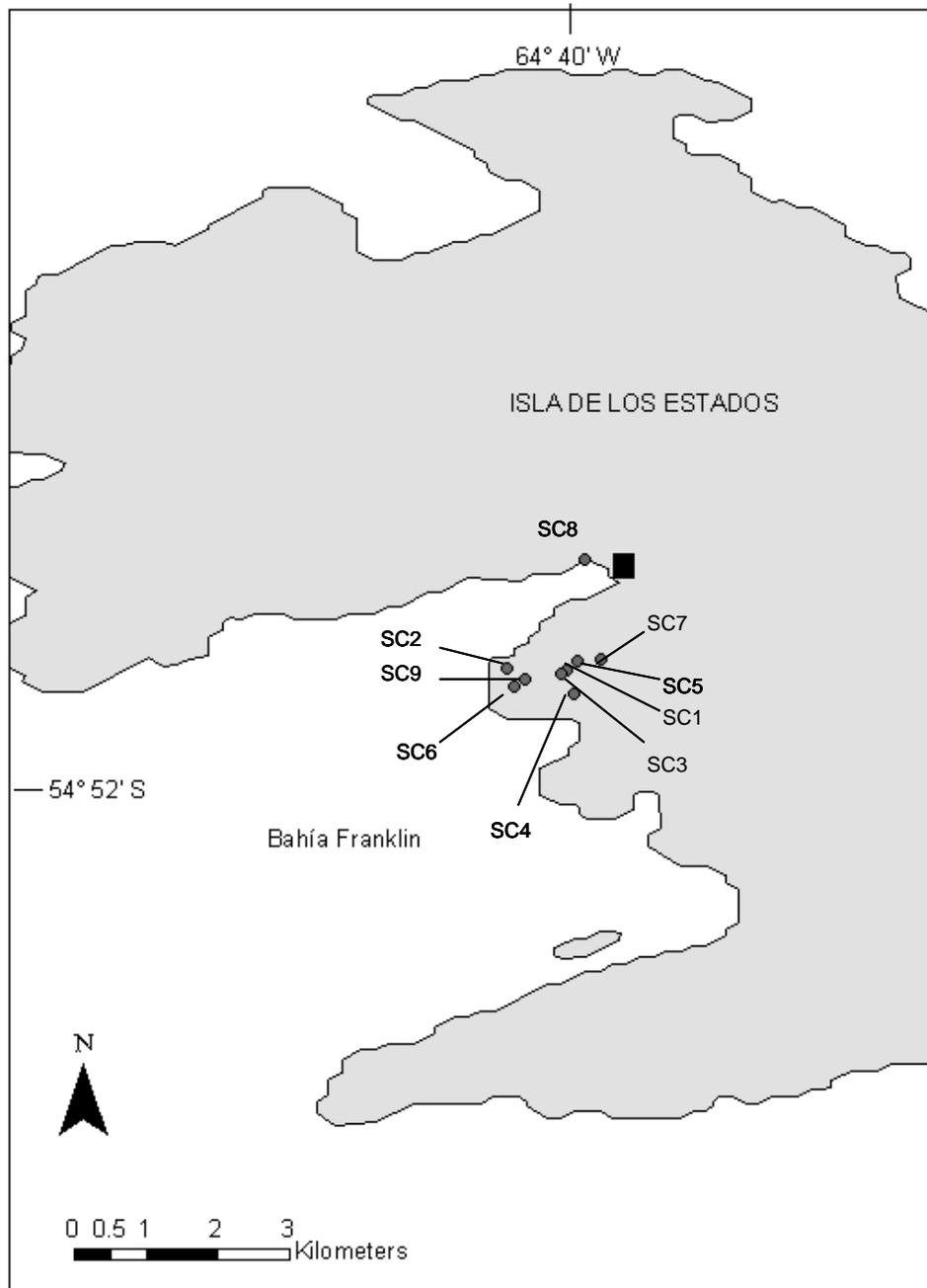


FIG. 3. Location of the study subcolonies (SC 1-9, black circles) and camp site (black square) at Bahía Franklin.

and next to a tussock were considered as “functional edge”; and “central” nests were those at least one nest away from the edge of the subcolony and not next to a tussock. Study subcolonies < 200 nests only had geometric edge and central locations because no central tussocks were present. Nests on the geometric edge can be accessed from a peripheral tussock, from the ground or from the air while nests on the functional edge can be accessed from a central tussock or from the air, and central nests can be accessed only from the air. Although nests with a functional edge or central location could potentially be accessed from the ground, this seems unlikely since little free ground space occurs between nests, making it difficult for a predator to land within the subcolony. This functional definition allows study of the vulnerability of a nest to an aerial predator’s attack.

Nest Observations

During each observation period species and activity of predators and scavengers were recorded. Following the classification of Emslie et al. (1995), activities were classified as searches, attempted predation, predation, scavenging and stored food retrieval. Searches were recorded either when birds flew low (2 -11 m above the penguins) and circled slowly over the subcolony (“search from air”), approached the subcolony near the edges on the ground (“search from ground”) or when they stood on tussocks in the center or in the periphery of the subcolony (“search from central or peripheral tussock”, respectively). Attempted predation occurred when birds took and lost or attempted to take a chick and predation when a bird successfully took a chick from the colony. It also was noted if attempts were from the air, from the ground, or from a central/peripheral tussock. Scavenging was recorded when a predator fed on food remains in or next to the colony; stored food retrieval was when predators took food remains stored in

central or peripheral tussocks back to their nests. For predation and attempted predation events, penguins behavior and nest location within the subcolony also was recorded.

Activity rates were calculated as the number of events recorded per hour of observation. To evaluate annual and seasonal variations in predator's activities, these rates were determined for each species and analyzed by year, subcolony, time of day (divided into four- 3 hr time periods) and time of season (divided into 2-day intervals that included between 28-53 hr of observations each and during which each subcolony had been observed at least twice). Rate categories included total activities (searches, predation, attempts and scavenging) and searches either by each species or for all species together. Predation and attempted predation events were rare and were only observed for Striated Caracaras and Kelp Gulls (*Larus dominicanus*), thus they were pooled and analyzed for both species together. Because predation rates may vary in different weather conditions (Young 1994), and in 2003 it was observed that activity rates seemed to vary with wind speed, wind speeds were recorded during all observations in 2004.

Hypotheses Testing

The encounter effect hypothesis, which predicts that the probability of encountering a group is independent of group size, was tested using methods similar to Uetz and Hieber (1994). An encounter was considered to occur each time a predator or a scavenger arrived at the subcolony and searched for vulnerable or dead prey. Observed encounter rates (search rates by all species together) at each subcolony were compared to the expected values obtained by multiplying the encounter rate for the smallest subcolony by the size of each subcolony.

The impact of predation as a function of subcolony size was analyzed by using observed activity events at each subcolony to calculate the following measures: predation rate as the total number of predation events by all predators per hr, relative predation rate as the predation rate divided by subcolony size, individual attack rate as the total number of attacks (predation and attempted predation events by all predators) per hr divided by subcolony size, and individual predation risk as the number of predation events by all predators divided by search events by all predators divided by subcolony size. A double log plot of individual predation risk versus group size yields a slope of -1, a result to be expected assuming a dilution effect with the probability of attack per individual being inversely related to group size (Inman and Krebs 1987). Thus, the predictions of the dilution effect hypothesis (a decrease of each individual's probability of being captured by being in a group) were tested by comparing the slope of the relationship between the observed individual predation risk and subcolony size to the expected slope of - 1 (Uetz and Hieber 1994).

A second approach to comparing the strategies of large vs. small subcolonies from the viewpoint of the prey consisted of monitoring a sample of nests in each subcolony (except for subcolonies < 140 nests, where all nests were monitored). Since the study was restricted to the chick-rearing period, the only breeding variable recorded was the number of chicks surviving at each nest during this period. At each subcolony, nests along a radial transect were plotted on a map and monitored every 3 days in 2003 and every other day in 2004 until the crèche period. Nest monitoring was completed by one observer with 8x10 binoculars from outside each subcolony to minimize disturbances. The cause of chick death was listed as predation based on observed predator attacks (which happened only once) or when chicks were missing from the nest; if chicks were found dead next to the nest it was assumed that they had died by other causes

because during observed predation events chicks were always taken away from the nest by the predator.

Nest monitoring data was used to estimate nest success (number of nests that had at least one chick divided by the total number of nests on the transect), chick mortality (number of chicks lost to predation or other causes divided by the total number of chicks on the transect) and nest predation (number of nests that suffered chick predation divided by the total number of nests on the transect that had a chick). For subcolonies < 140 nests, denominators in the above indices were calculated using whole subcolony totals. These indices were estimated for each subcolony and for the different nest locations within each subcolony (in the latter case they were calculated with respect to the total number of nests/chicks on that nest location in the transect).

The effect of breeding in the geometric edge/functional edge/center of large subcolonies or breeding in the functional edge/center of small subcolonies was compared by testing differences in the three breeding variables between these different nest locations. Subcolonies were classified as 'large' when > 200 nests (all of which also had central tussocks) or as 'small' when < 200 nests (none had central tussocks).

Statistical Analyses

Two-way ANOVAs without replication were used to analyze diurnal patterns in total activity rates (with predator and time period as the main effects and predator mean activity rate as a single replicate) and patterns in predation and attempted predation rates (with year and time period as the main effects and predation and attempted predation rate as a single replicate).

Wilcoxon test was used to examine seasonal variations in activity rates. The correlations of

activity rates, wind speed, and subcolony size were tested using Spearman's correlation coefficient. Exact Chi-square tests were used to examine the proportion of observed predation and attempted predation events and nest success, nest predation and chick mortality obtained from transects for different nest locations. Effects of subcolony size, year and presence of central tussocks on the occurrence of predation were examined by means of logistic regression with predation outcome (no predation event observed or at least one predation event observed) as a binary dependent variable. Logistic regression was also applied to quantify the relationships between subcolony size and nest success, chick mortality and nest predation. Results from both years were pooled when appropriate. A significance level of $P < 0.05$ was used for all statistical tests. All analyses were completed using SAS 9.1 and JMPIN 3.2.6 software.

RESULTS

A total of 461 and 386 hr of observation were completed during the study periods of 2003 and 2004, respectively. Approximately equal numbers of observations were made in each of the four time periods and similar numbers of observation periods were obtained for all subcolonies each year (although there were some differences due to bad weather conditions).

Predator/Scavengers Using Rockhopper Penguin Subcolonies

The predator/scavenger community associated with Rockhopper Penguin subcolonies at Staten Island included Striated Caracaras, Kelp Gulls, Dolphin Gulls (*Larus scoresbii*), Turkey Vultures (*Cathartes aura*), Southern Giant Petrels (*Macronectes giganteus*), Chilean Skuas (*Catharacta chilensis*) and Crested Caracaras (*Polyborus plancus*). In both years almost 50% of the total activity events at all subcolonies combined were by Striated Caracaras (Fig. 4). Kelp

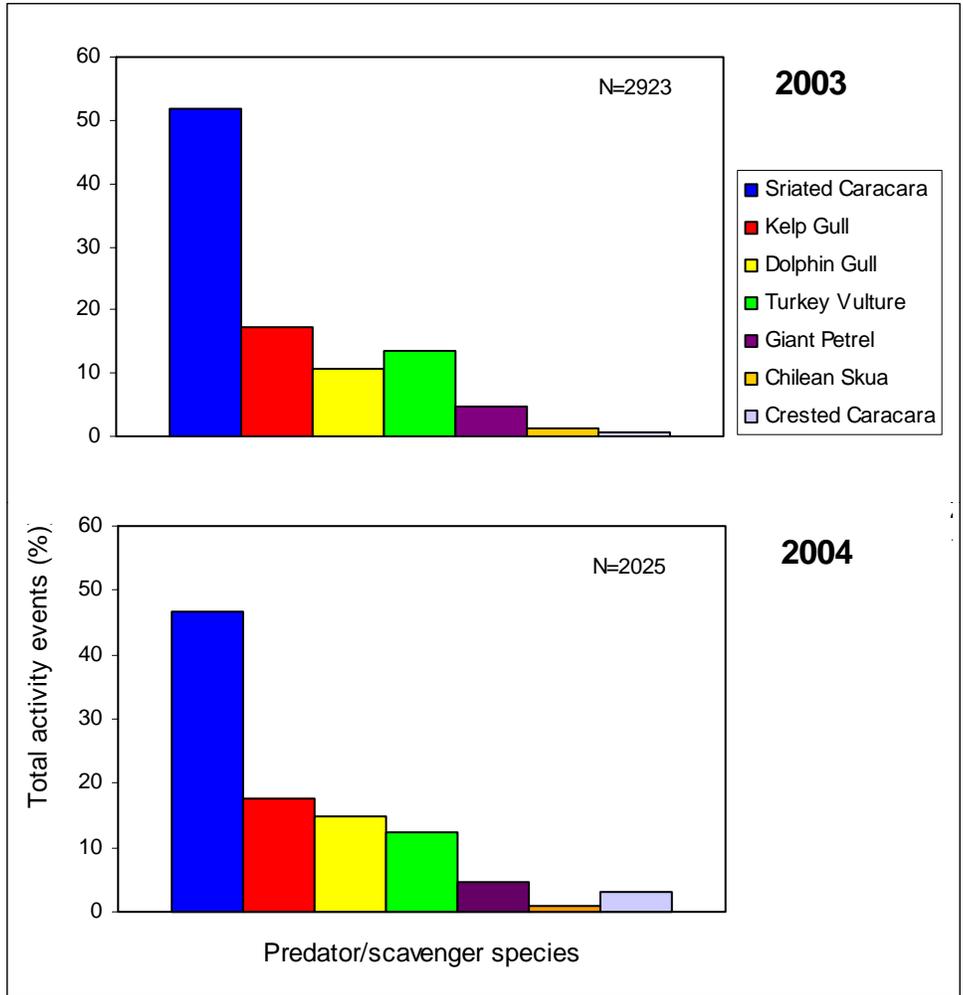


FIG. 4. Percent of total activity events (searches, predation, attempts and scavenging) by predator/scavenger species at all subcolonies combined during 2003 and 2004.

Gulls, Dolphin Gulls and Turkey Vultures were the second most common species with 10-20 % of the total activity events. Chilean Skuas, Giant Petrels and Crested Caracaras were rarely seen and accounted for less than 5% of the total activity events. Striated Caracaras were the most active predators in both years at all subcolonies except for subcolonies 8 (SC8) and 2 (SC2) where Kelp Gulls and Dolphin Gulls dominated, respectively (Fig. 5). SC8 was the most isolated from the other subcolonies (Fig. 3), the most exposed to the wind, the closest to the water, and bordered a 10-15 m cliff on which Kelp Gulls nest. Subcolonies SC1, SC3, SC5, and SC7 and subcolonies SC2, SC6 and SC9 were in close proximity to each other (Fig. 3) in an area generally occupied by groups of adult/juvenile Striated Caracaras, Turkey Vultures and Crested Caracaras. SC4 was about 400 m away from these last subcolonies and, instead, was part of the feeding territory of a breeding pair of Striated Caracaras who would chase away any other Striated Caracaras trying to approach the subcolony. The percent of total activities by Striated Caracaras in consecutive years did not decrease significantly at SC 1, SC3, SC7 and SC8 (X^2 test, all $P > 0.05$ and $df = 1$); but did so by 10-20 % at SC2, SC 5 and SC6 (X^2 test, all $P < 0.05$ and $df = 1$). SC4 experienced a significant decrease of about 30% in Striated Caracara's activities from 2003 to 2004 ($X^2 = 82.831$, $P < 0.001$, $df = 1$). In 2003 this subcolony was occupied by a very active single adult breeding pair of Striated Caracaras, whose nest with three chicks was next to the subcolony. In 2004 their nest was in the same location, but had only one chick and one egg which disappeared between 12-14 December. Subsequently, activities of the breeding pair at SC4 decreased considerably compared to previous days and to 2003.

In both years, considering all subcolonies together, searching was the predominant predator-scavenger activity recorded. For Kelp Gulls, Dolphin Gulls and Turkey Vultures, as well as for the less common species (which were not analyzed), searching from the air was the

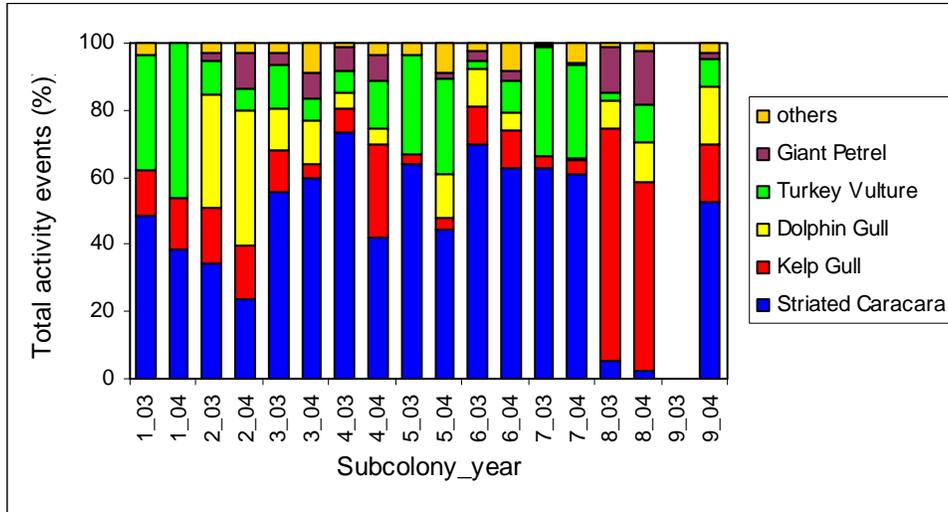


FIG. 5. Percent of total activity events (searches, predation, attempts and scavenging) at each subcolony in 2003 and 2004 for each predator/scavenger species (1_03: SC 1 in 2003, etc). 'Others' includes Crested Caracara and Chilean Skua. (SC 9 was only observed in 2004).

predominant activity, accounting for over 85 % of their total activities (Fig. 6). Only in SC8 were Kelp Gulls occasionally observed searching from periphery tussocks. This subcolony had only a few, very short tussocks compared to the rest of the subcolonies. For Striated Caracaras, searches from the air and from peripheral tussocks were the most predominant activity accounting for 30-50 % of their total activities, followed by searches from central tussocks which comprised ~ 10 % of the total activities (Fig. 6). Striated Caracaras spent much of their time perched on peripheral tussocks, possibly searching for dead or unattended chicks. Generally, they would spend several minutes searching from a single or several peripheral tussocks before moving to a central or peripheral tussock for their predation attempt. Average time spent on a tussock before their attempt was 5 min, but some were observed remaining up to 25 min and even 55 min on one occasion. Predation and attempted predation events were rare and were only observed for Kelp Gulls (four attempts and one predation) and Striated Caracaras (32 attempts and 34 predations).

Temporal Variation in Activity Rates

Total activity rates for Striated Caracaras were highest in the afternoon (time period 3, 14:00-17:00) however, there was no significant diurnal pattern in total activity rates for any of the species (2003: $F_{3,18} = 1.35$, $P = 0.29$; 2004: $F_{3,18} = 0.57$, $P = 0.64$; Fig. 7). There was, however, a significant species effect (2003: $F_{6,18} = 53.57$, $P < 0.001$; 2004: $F_{6,18} = 51.12$, $P < 0.001$). In both years Striated Caracaras had a higher total activity rate than all other species (Tukey comparisons, minimum significant difference: 0.7043 in 2003 and 0.5352 in 2004, both years $P < 0.05$). Overall predation and attempted predation rate was higher in 2004 (0.119 events/hr) than in 2003 (0.054 events/hr). Predation and attempted predation rate did not vary

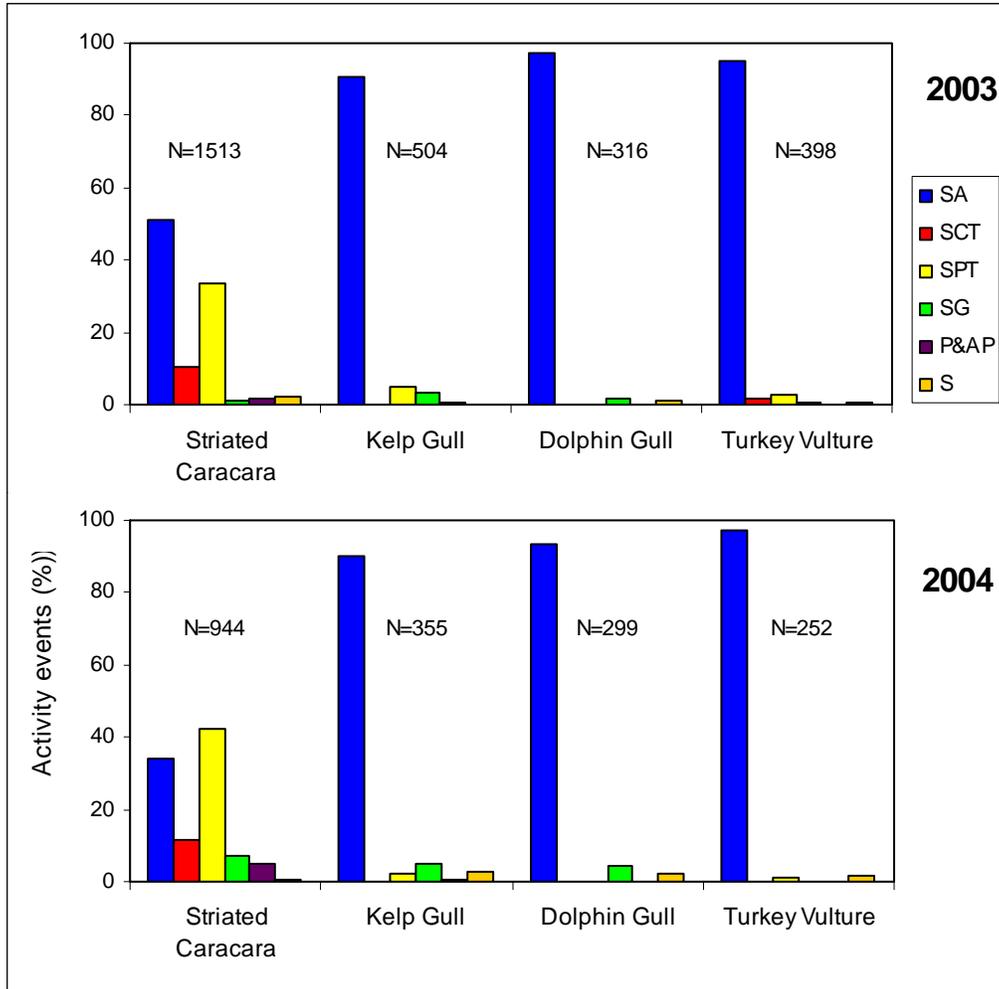


FIG. 6. Relative importance of different activities of the four most common predator/scavenger species on the penguin subcolonies during 2003 and 2004 (SA: search from air, SCT: search from central tussock, SPT: search from peripheral tussock, SG: search from ground, P&AP: predation and attempted predation, S: scavenging).

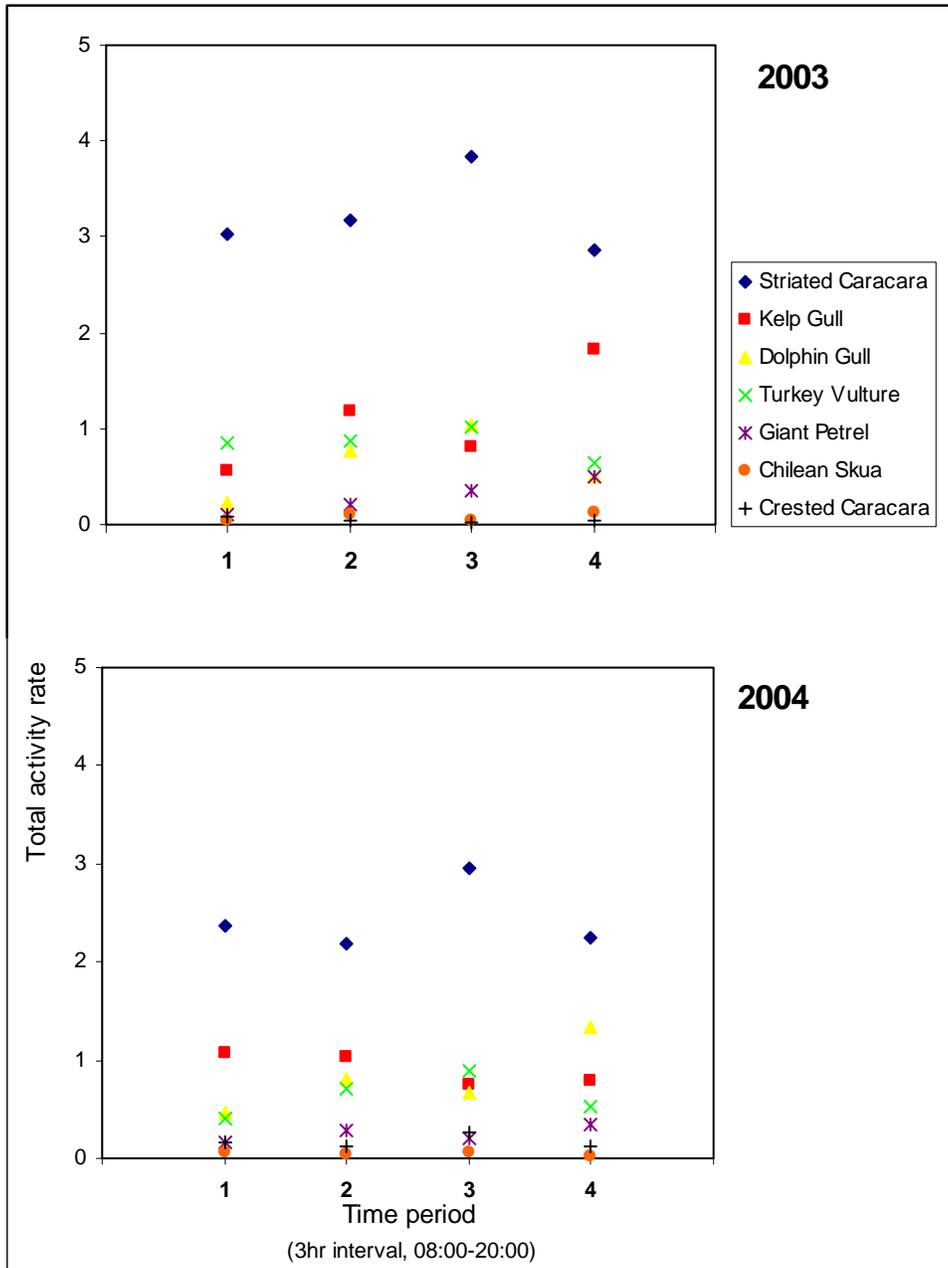


FIG. 7. Total activity rates (searches, predation, attempts and scavenging events/hr) of predator/scavengers with time of day. Each time period represents a 3hr interval between 08:00-20:00.

throughout the day ($F_{3,3} = 3.13$, $P = 0.19$), but there was a significant year effect ($F_{1,3} = 18.87$, $P = 0.022$).

Total activity rates by Striated Caracaras and Turkey Vultures showed no significant seasonal variation in either year (Wilcoxon test, both years $P > 0.05$; Fig. 8). However, total activity rates by Kelp Gulls and Dolphin Gulls were higher during the last week of the study, once penguin crèches had formed, than during the first weeks. This increase throughout the season was only significant for Dolphin Gulls (Wilcoxon test, 2003: $P = 0.22$ for Kelp Gulls, $P = 0.042$ for Dolphin Gulls; 2004: $P = 0.053$ for Kelp Gulls, $P = 0.035$ for Dolphin Gulls; Fig. 8). Early in the breeding season activity by gulls was low. Later in the season, as crèches formed and both penguin parents were foraging, the open ground space between nests increased and the number of gulls also increased. Gulls continually searched the subcolonies from the air, on occasion landing and walking inside the subcolony attempting to take unattended small chicks, dead chicks or abandoned eggs. Even though scavenging rates were too low for statistical analysis, scavenging events by gulls were not observed until after 24 December in 2003 ($n = 4$) and 18 December in 2004 ($n = 15$).

In 2003 total predation and attempted predation rate by Striated Caracaras and Kelp Gulls was not correlated with time of season ($r = -0.2044$, $P = 0.36$; Fig. 9); however, in 2004 it showed a significant negative correlation ($r = -0.5192$, $P = 0.027$; Fig. 9). When pooled for years, predation and attempted predation rate was also negatively correlated with time of season ($r = -0.3462$, $P = 0.029$), possibly because as the breeding season advanced, chicks got heavier and larger making it more difficult for predators to kill them.

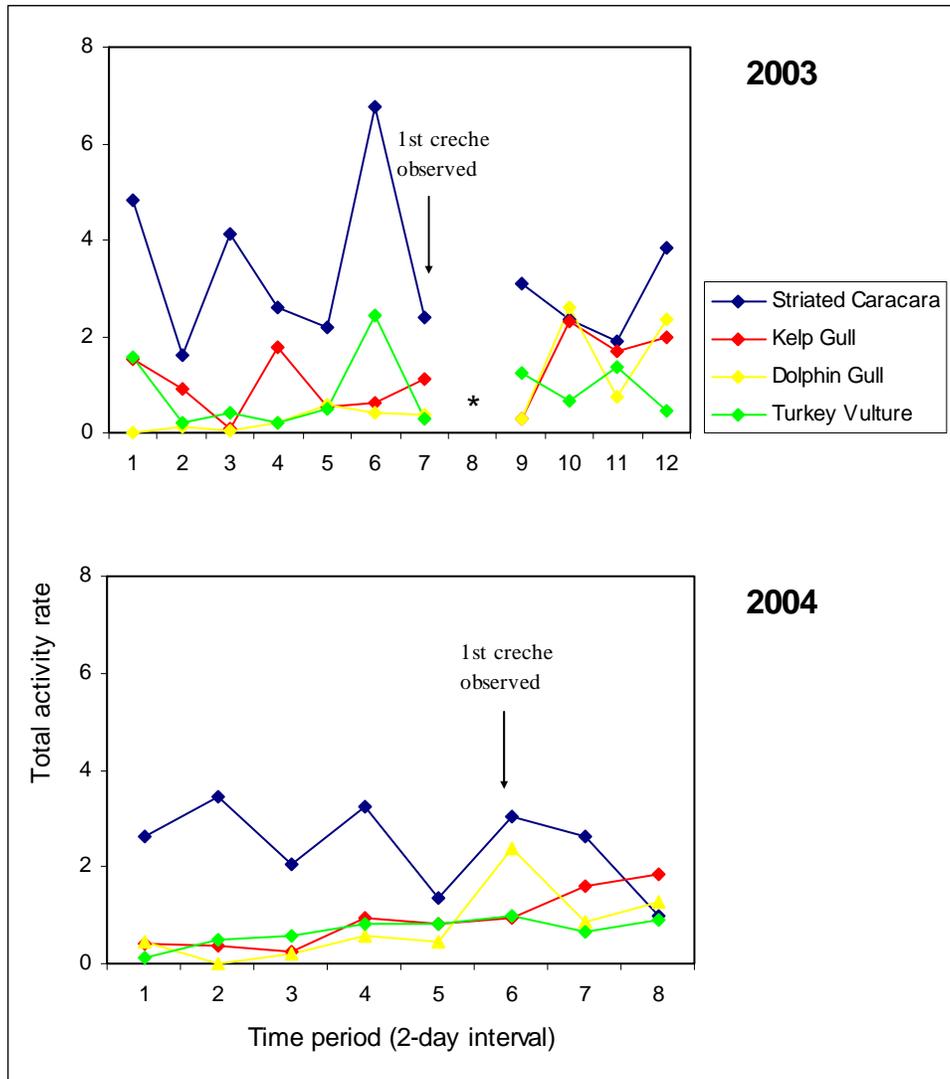


FIG. 8. Total activity rate (searches, predation, attempts and scavenging events/hr) of the four most common predator/scavenger species with time of season, divided into 12 (7-30 December in 2003) and 9 (8-25 December in 2004) two-day intervals.

*: bad weather conditions prevented observations during time period 8 in 2003.

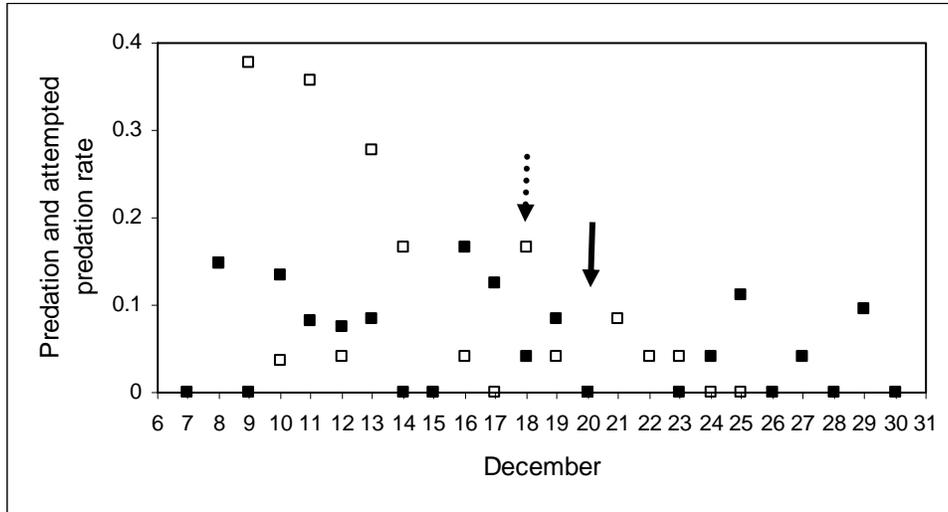


FIG. 9. Daily predation and attempted predation rates (predation and attempt events/hr) by Striated Caracaras and Kelp Gulls on Southern Rockhopper Penguin chicks during 2003 and 2004. Filled squares: 2003, open squares: 2004. Solid arrow: 1st crèche observed in 2003, dashed arrow: 1st crèche observed in 2004.

Weather and Activity Rates

Total activity rate by Kelp Gulls correlated with wind speed up to 27 km/h ($r = 0.7303$, $P < 0.001$, $n = 20$; Fig.10) and decreased for wind speeds over 29 km/hr. Total activity rate by Giant Petrels was also positively correlated with wind speed ($r = 0.4256$, $P = 0.043$, $n = 23$), but not for other species (Turkey Vulture: $r = 0.0054$, $P = 0.98$; Dolphin Gull: $r = 0.158$, $P = 0.47$; Chilean Skua: $r = 0.2146$, $P = 0.32$; Crested Caracara: $r = 0.0535$, $P = 0.80$). Young (1994) found variation in predation rates in relation to weather, higher predation rates by South Polar Skuas (*Catharacta maccormicki*) on windy or stormy days when adult Adélie penguins may be distracted, thus facilitating prey capture. However for Striated Caracaras and Kelp Gulls on Staten Island, total predation and attempted predation rate was not correlated with wind speed ($r = -0.0692$, $P = 0.75$, $n = 23$).

Predation and Nest Location

Predation and attempted predation events on penguin chicks were rarely observed for Striated Caracaras and Kelp Gulls (Table 2). In both years, the main predator was the Striated Caracara, which accounted for 93 % ($n = 71$) of observed predations and attempts on Rockhopper Penguin chicks. In 2003 predation and attempted predation events were higher on the functional edge of the subcolony, but not significantly so (exact $X^2_2 = 3.92$, $P = 0.17$; Fig. 11). In 2004, these events varied significantly with nest location (exact $X^2_2 = 13.087$, $P = 0.002$; Fig. 11).

Highest predation and attempted predation events were observed on the functional and geometric edge of the subcolony. In both years there was a significant association between the predator's method of approach and the nest location (2003: exact $X^2_6 = 50$, $P < 0.001$; 2004:

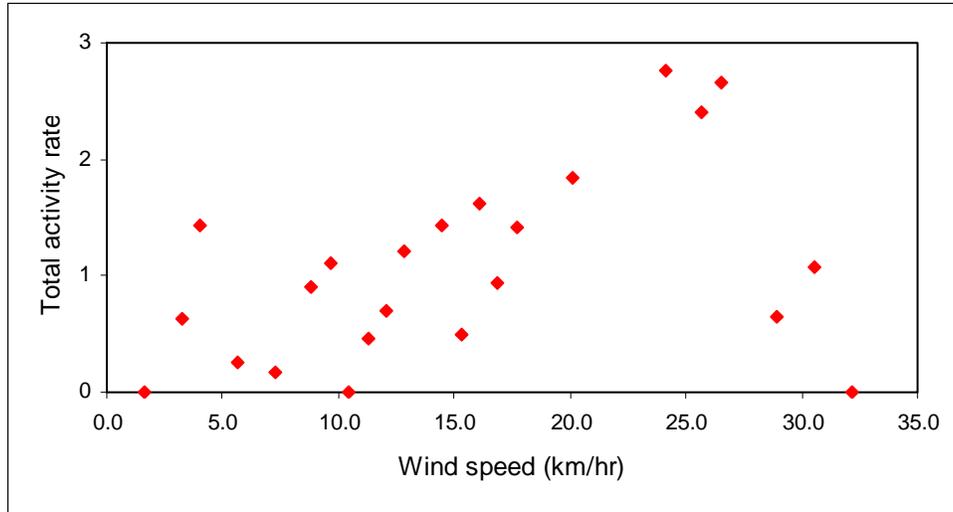


FIG. 10. Total activity rate (searches, predation, attempts and scavenging events/hr) by Kelp Gulls for wind speeds observed during 8-25 December 2004.

TABLE 2. Predation (P) and attempted predation (AP) events on Rockhopper Penguin chicks by Striated Caracaras and Kelp Gulls at study subcolonies during 2003 and 2004. Species counts not indicated as P or AP include both types of events.

* SC9 was only observed in 2004.

subcolony	year	mean number of nests	Striated Caracara	Kelp Gull	total P & AP events	P & AP rate (events/hr)
SC1	2003	69	0	0	0	0
	2004	72	0	0	0	0
SC2	2003	506	0	0	0	0
	2004	473	0	0	0	0
SC3	2003	929	0	0	0	0
	2004	978	1P	0	1	0.024
SC4	2003	1520	7	0	7	0.095
	2004	1660	0	0	0	0
SC5	2003	440	1P	0	1	0.018
	2004	386	0	0	0	0
SC6	2003	122	3	0	3	0.058
	2004	132	1AP	0	1	0.031
SC7	2003	574	10	0	10	0.167
	2004	361	12	0	12	0.182
SC8	2003	179	0	4AP	4	0.078
	2004	145	0	0	0	0
SC9	2003*	-	-	-	-	-
	2004	1682	31	1P	32	0.464
Total	2003	4461	21	4	25	0.054
	2004	7571	45	1	46	0.119

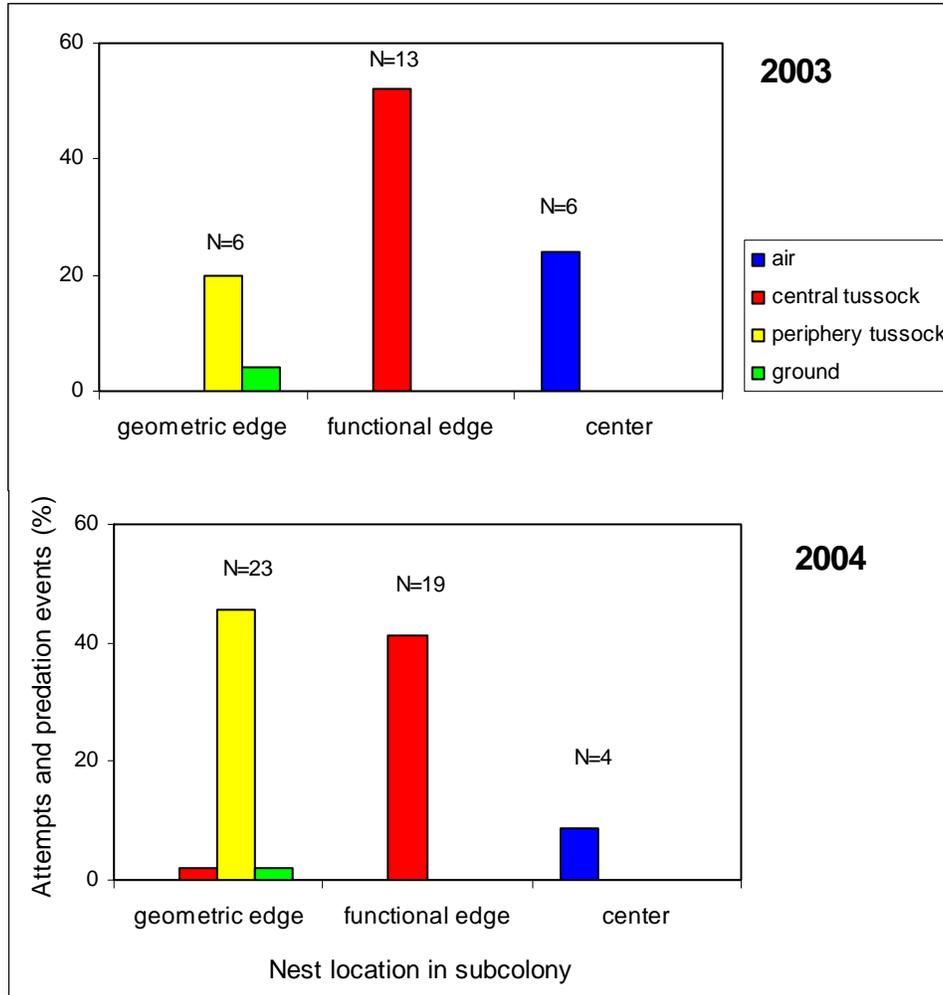


FIG. 11. Percent of total predation and attempted predation events (n=25 in 2003, n=46 in 2004) on Rockhopper penguin chicks by Striated Caracaras and Kelp Gulls during 2003 and 2004. Events were recorded from the air, from central or peripheral tussocks or from the ground on nests on the geometric edge, functional edge or center of the subcolonies (see Methods for definitions of nest location).

exact $X^2_6 = 87.8$, $P < 0.001$; Fig.11). Predation and attempted predation events from peripheral and central tussocks were associated with nests on the geometric and functional edges, respectively; events from the air were associated with central nests; and those from the ground (which were very rare) were associated with nests on the functional edge. Kelp Gulls were only observed approaching from the air. Striated Caracaras, on the other hand, were observed in all four methods of approach, but they used peripheral or central tussocks more frequently. Normally, they would land on a tussock and remain as long as it took the adult penguins to habituate to their presence or become distracted. Occasionally, penguins from nests near that tussock would chase the attacking bird away.

During 78.2 % ($n = 36$) of the predation and attempted predation events on chicks, penguins showed increased vocalizations and aggression against the predator; for 10.9 % of the events ($n = 5$) there was no response from the parent while the remaining 10.9 % were events on solitary chicks (during crèche formation). When successful, the Striated Caracara would hop to the ground and take the chick away in its bill. Typically, if the bird was a breeding adult with a nest next to the subcolony (as in SC4 in 2003) it would kill its prey on a central or peripheral tussock and cache parts of it in tussocks within the subcolony. Later that day, the bird would retrieve the stored food from the tussocks and feed it to its own chicks. If the bird was a juvenile or an adult with no conspicuous nest nearby, it would fly to a nearby tussock, consume the prey and leave.

Activity Rates and Subcolony Size

Total activity rate by all species and searches, predation and attempted predation rate (SPAP rate) considered collectively by Striated Caracaras, Kelp Gulls and Dolphin Gulls (the

three most common species) were pooled for 2003 and 2004 as ANCOVA analysis revealed no significant year effect (total act. rate: $P = 0.38$; SPAP rate: $P = 0.35$) and no significant year x subcolony size interaction (total act. rate: $P = 0.98$; SPAP rate: $P = 0.92$). Subcolony size was positively correlated with total activity rate by all species ($r = 0.7132$, $P = 0.001$, $n = 17$) as well as with SPAP rate by Striated Caracaras, Kelp Gulls and Dolphin Gulls ($r = 0.6569$, $P = 0.004$, $n = 17$). Total relative activity rate, instead, was negatively correlated with subcolony size however not significantly so ($r = -0.473$, $P = 0.055$, $n = 17$). Relative SPAP rate showed the same trend ($r = -0.3407$, $P = 0.18$, $n = 17$).

Encounter rate (search rate by all species) was positively correlated with subcolony size ($r = 0.7132$, $P = 0.001$, $n = 17$). The observed slope of 0.00353 ± 0.00287 (95 % confidence limits) was significantly different from the expected slope of 0.00778 ($t = 3.163$, $P = 0.006$; Fig. 12), thus supporting the encounter effect hypothesis. The rate of encounter increased at a lower rate than expected when subcolony size increased.

Individual attack rate, based on predation and attempt events per hr per nest (Fig. 13) for subcolonies where attacks were observed, was not correlated with subcolony size ($r = -0.5$, $P = 0.17$, $n = 9$). The attack rate may not necessarily be diluted by being in a larger subcolony because, once the subcolony is detected, predators may attempt to prey on more than one nest or on the same nest more than once. On a few occasions the same Striated Caracara was observed either attempting to take different chicks or consecutively attempting to take the same chick twice. Also, Striated Caracaras were observed returning to the same nest throughout the day (though in this case it was not certain if it was the same Striated Caracara or not).

The occurrence of predation events was not significantly different either for subcolony size (Wald X^2 : 0.2966 , $P = 0.59$), for year (Wald X^2 : 0.7512 , $P = 0.39$) or for the presence of

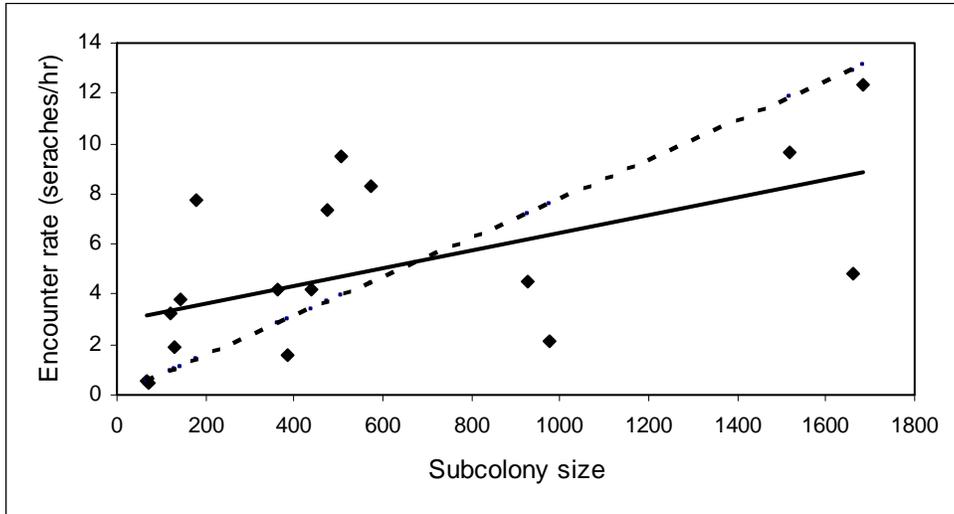


FIG. 12. Encounter rate of all predator/scavenger species together on Rockhopper Penguin subcolonies in 2003 and 2004. Dashed line represents expected encounter rates based on the predictions that encounter rate is proportionate to subcolony size (no encounter effect). Solid line represents linear fit of observed encounter rates.

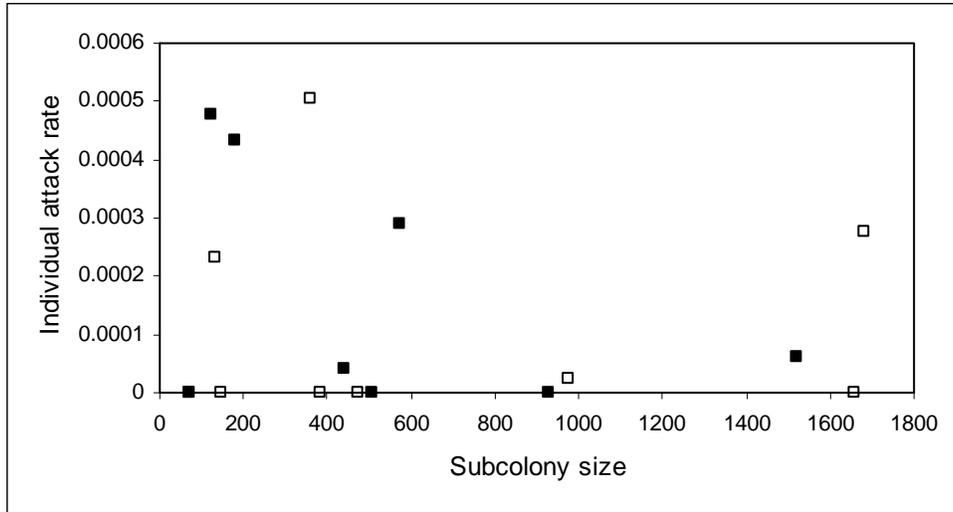


FIG. 13. Individual attack rate (predation and attempt events per hr per nest) by Striated Caracaras and Kelp Gulls on Southern Rockhopper Penguin chicks. Filled squares: 2003, open squares: 2004.

central tussocks (criteria chosen for the classification in large or small subcolonies) (Wald X^2 : 0.8043, $P = 0.37$). Neither predation rate nor relative predation rate were correlated with subcolony size (predation rate: $r = 0.4089$; relative predation rate: $r = 0.236$; both $P > 0.1$ and $n = 17$; Fig. 14). Predation events were rare, and in several small as well as large subcolonies no predation events were observed. Subcolonies > 200 nests with a low predation rate (< 0.05 events/hr and different to zero) had also a low relative predation rate (< 0.0001 events/hr; Fig. 14). However, for the three subcolonies > 200 nests with predation rates > 0.05 events/hr, predation rates were proportionally lower for the larger subcolonies (the largest subcolony with the highest predation rate has the lowest relative predation rate; Fig. 14).

For subcolonies < 200 nests, predation events were observed in only one of them (Table 2). Even though this subcolony had a low predation rate (< 0.05 events/hr), this rate was proportionally higher than for larger subcolonies with similar predation rates (< 0.05) and even slightly higher than the largest subcolony with the highest predation rate. However, reanalysis of the data with only those subcolonies in which predation events were observed revealed a negative though nonsignificant correlation of predation rate or relative predation rate with subcolony size (predation rate: $r = 0.4643$; relative predation rate $r = -0.5357$; both: $P = 0.29$ and $n = 7$).

Individual predation risk (predation events per searches per nest) was zero in several subcolonies (regardless their size) in which predation or attempts were not observed (Fig. 15 A). For those subcolonies in which predation and attempts were observed, large subcolonies also experienced reduced individual risk. Individual predation risk decreased with increasing subcolony size, but not significantly so ($r = -0.6786$, $P = 0.09$, $n = 7$; Fig. 15 A). This relationship on a double log plot gives an observed slope of -0.88012 ± 0.95748 (95 %

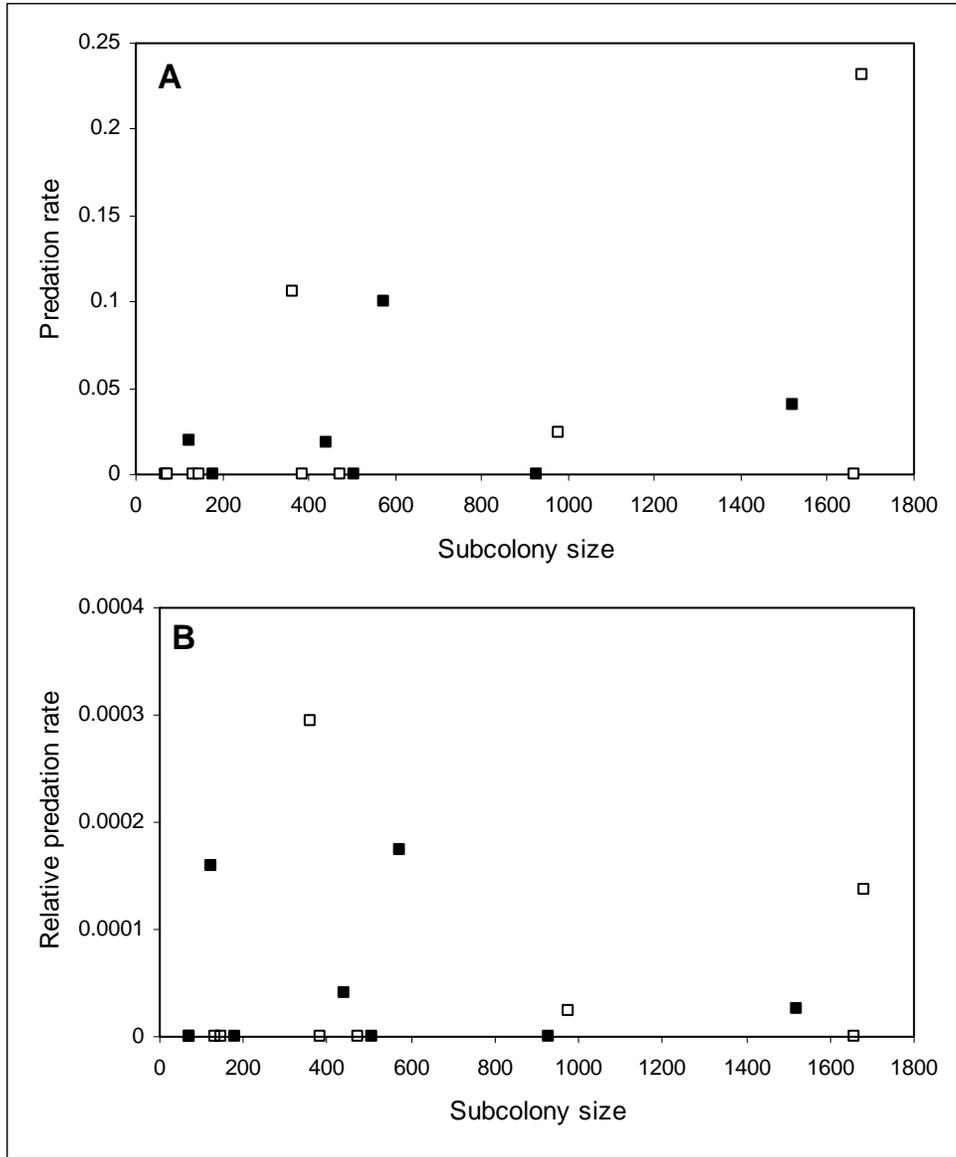


FIG. 14. **A**: Observed predation rate (predation events per hr) and **B**: relative predation rate (predation events per hr per nest) by Striated Caracaras and Kelp Gulls on Southern Rockhopper Penguin chicks. Filled squares: 2003, open squares: 2004.

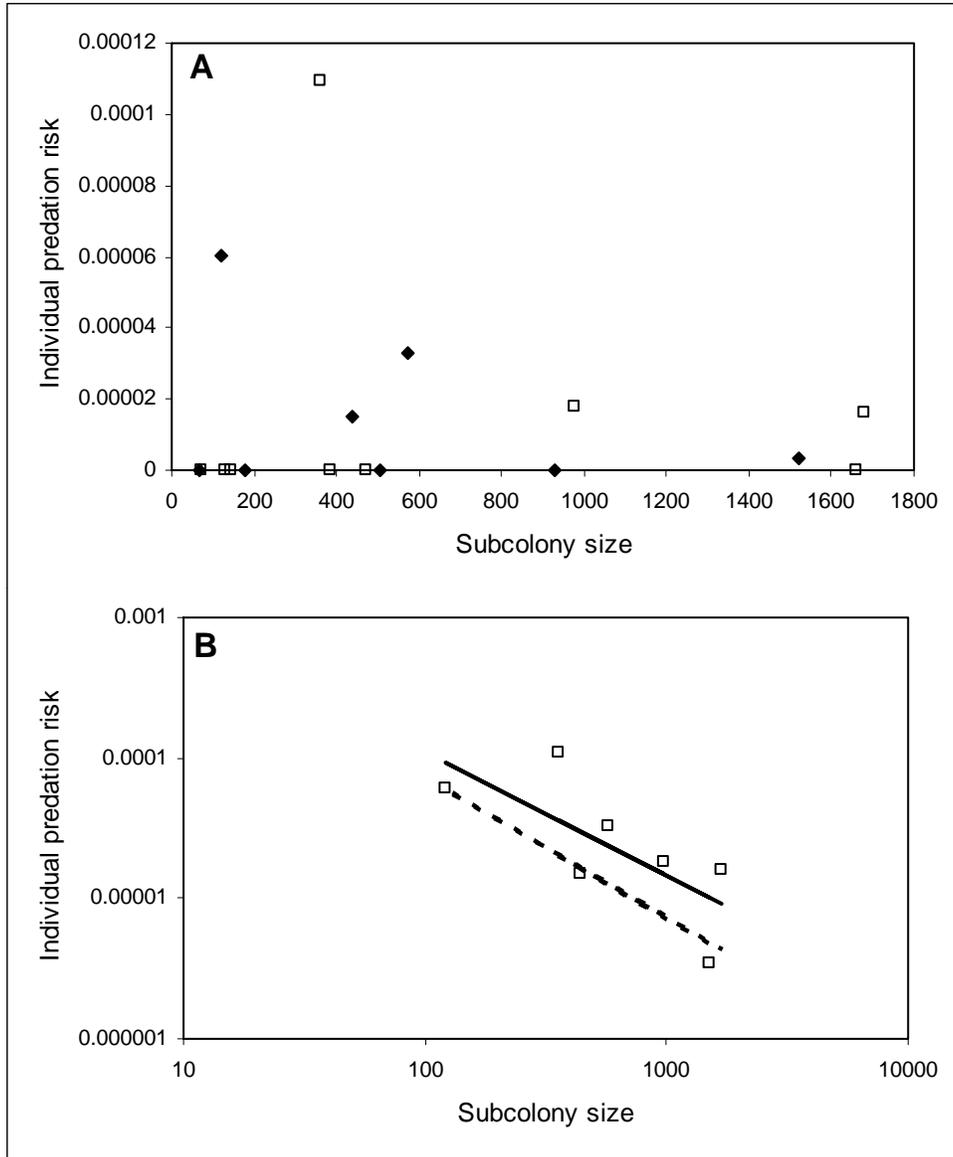


FIG. 15. **A:** Estimated individual predation risk (predation events per searches per nest) Filled squares: 2003, open squares: 2004. **B:** Estimated individual predation risk for subcolonies in which predation events were observed, solid line represents the linear fit for these data ($\log y = -2.1963 - 0.88012 \log x$, $P = 0.06$, $n = 7$). Dashed line: expected values based on numerical dilution (calculated by multiplying predations/searches in the smallest subcolony in which predation was observed by $1/\text{subcolony size}$).

confidence interval; Fig. 15 B), which is not significantly different from the expected slope of -1.00000 , assuming a simple dilution effect in which the probability of predation per nest is inversely related to subcolony size.

Nest Checks: Nest Success, Chick Mortality and Nest Predation

Nest success significantly increased with subcolony size in 2003 and 2004 (Table 3). Logistic regression analyses were used to model the relationship between nest success and subcolony size for 2003 and 2004 (Fig. 16). Small subcolonies had a significantly lower nest success in both years (2003: $X^2_1 = 4.678$, $P = 0.003$; 2004: $X^2_1 = 18.198$, $P < 0.0001$; Table 4); however, there were no differences in chick mortality or nest predation between large and small subcolonies for either year (both years $P > 0.05$; Table 4). In 2003 there were no differences in nest success, chick mortality or nest predation among the different nest locations in large or small subcolonies (Table 4). In 2004 chick mortality and nest predation in large subcolonies were highest in the functional edge (chick mortality: $X^2_2 = 22.481$; nest predation: $X^2_2 = 23.341$; both $P < 0.0001$ for; Table 4). Overall nest success (2003 + 2004) was also lower in small (0.574 %) than in large subcolonies (0.743 %) ($X^2_1 = 15.24$, $P < 0.0001$), and overall chick mortality and nest predation were higher in the functional edge (0.175 % and 0.138 %, respectively) than in the geometric edge (0.088 %, 0.054 %) or center (0.047 %, 0.034 %) of large subcolonies (chick mortality: $X^2_2 = 16.08$, $P < 0.001$; nest predation: $X^2_2 = 13.649$, $P = 0.001$). When effects of subcolony size and nest location were examined using logistic regression, the probability of chick mortality and nest predation was independent of subcolony size in both years (Table 5). However, in 2004 nest location had a significant effect on chick

TABLE 3. Effect of subcolony size on nest success, chick mortality and nest predation in 2003 and 2004.

The parameter estimate gives the estimated coefficient of the fitted logistic regression model.

Variable	df	Parameter Estimate	Standard Error	Wald Chi-Square	P
December 2003					
Nest success					
Intercept	1	1.0193	0.171	35.5468	< 0.0001
Subcolony size	1	0.0009	0.0003	7.3313	0.0088
Chick mortality					
Intercept	1	-2.1478	0.2805	58.65	< 0.0001
Subcolony size	1	-0.0012	0.0006	3.2	0.0738
Nest predation					
Intercept	1	-2.6095	0.3322	61.71	< 0.0001
Subcolony size	1	-0.0008	0.0007	1.51	0.2189
December 2004					
Nest success					
Intercept	1	0.3885	0.1236	9.8822	0.0017
Subcolony size	1	0.0005	0.000153	13.0584	0.0003
Chick mortality					
Intercept	1	-2.3398	0.2529	85.58	< 0.0001
Subcolony size	1	0.0001	0.0003	0.13	0.7171
Nest predation					
Intercept	1	-2.4044	0.2705	79.01	< 0.0001
Subcolony size	1	-0.0002	0.0003	0.4	0.5261

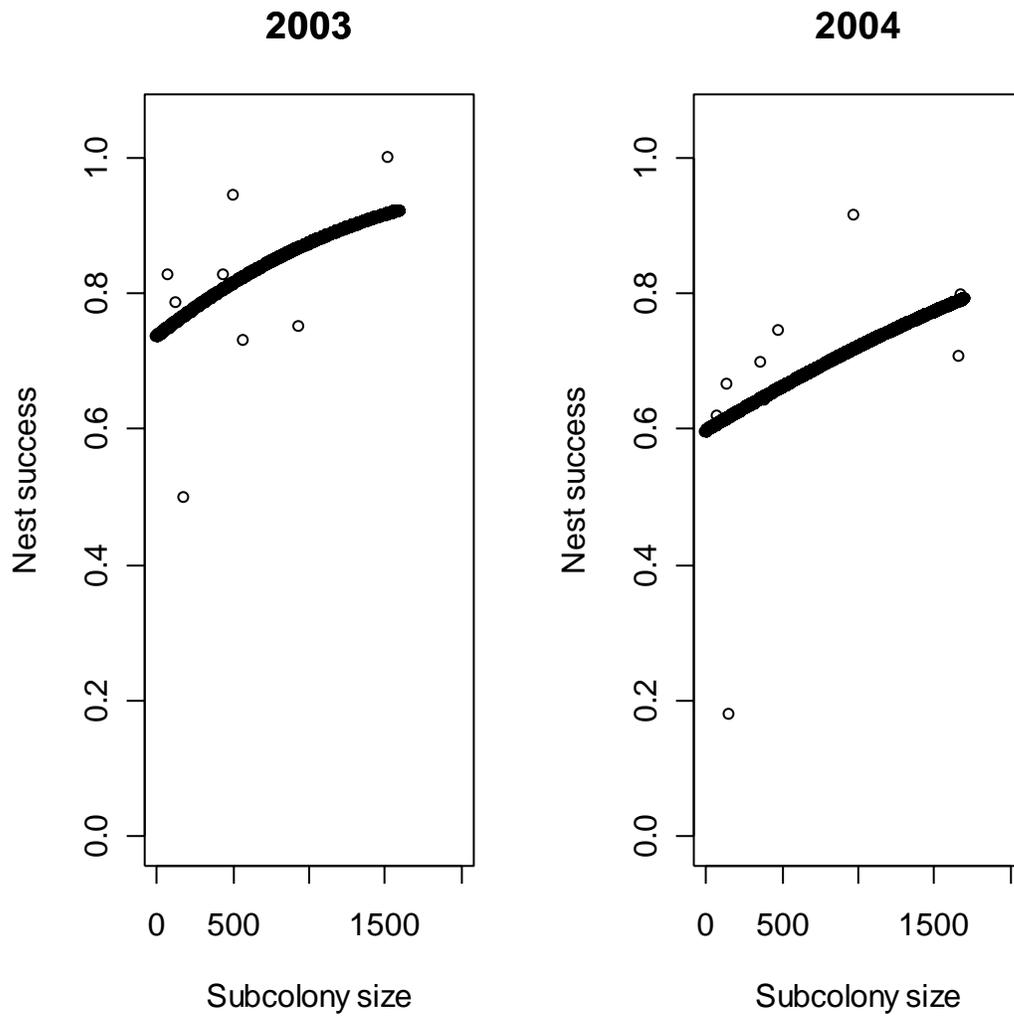


FIG. 16. Logistic regression curve showing the relationship between nest success and subcolony size in 2003 and 2004. Open circles: observed nest success at each subcolony, calculated as the number of nests that had at least 1 chick divided by the total number of nests on the transect. Solid line: estimated probability of nest success.

TABLE 4. Differences in nest success, chick mortality and nest predation between large and small subcolonies and between different nest locations within large or small subcolonies in 2003 and 2004 (n = total number of nests, chicks, and nests with chicks monitored on the transect). Percentage was calculated as the number of nests that produced at least one chick related to the total number of nests at the beginning of nest checks, as the number of chicks lost to predation or other causes related to the total number of chicks at the beginning of nest checks, and as the total number of nests that suffered chick predation related to the total number of nests with chicks at the beginning of nests checks (see Methods).

	Nest success		Chick mortality		Nest predation	
	n	%	n	%	n	%
December 2003						
Large subcolonies	149	85.2	134	5.2	132	4.5
Small subcolonies	221	76.0	185	8.6	182	5.5
X ²	4.678 *		1.362		0.143	
Large subcolonies						
Geometric edge	19	100	21	9.5	21	9.5
Center	80	82.5	69	4.3	68	4.4
Functional edge	47	89.4	44	4.5	43	2.3
X ²	4.499		0.932		1.691	
Small subcolonies						
Geometric edge	84	71.4	67	9.0	66	7.5
Center	137	78.8	118	8.5	116	4.3
X ²	1.566		0.12		0.864	
December 2004						
Large subcolonies	335	74.3	279	10.8	274	7.7
Small subcolonies	242	57.4	149	6.7	148	6.8
X ²	18.198 **		1.872		0.39	
Large subcolonies						
Geometric edge	40	82.5	36	8.3	34	2.9
Center	212	75	167	4.8	167	3.0
Functional edge	83	68.7	76	25	73	20.5
X ²	2.84		22.481 ***		22.341 ***	
Small subcolonies						
Geometric edge	91	57.1	53	1.9	52	1.9
Center	151	57.6	96	9.4	96	9.4
X ²	0.005		3.058		2.973	

* P < 0.05, df = 1; ** P < 0.0001, df = 1; *** P < 0.0001, df = 2

TABLE 5. Effect of subcolony size and nest location on nest success, chick mortality and nest predation in 2003 and 2004. The parameter estimate gives the estimated coefficient of the fitted logistic regression model.

Variable	df	Parameter Estimate	Standard Error	Wald Chi-Square	P
December 2003					
Nest success					
Intercept	1	0.846	0.4192	4.0726	0.0436
Subcolony size	1	0.000947	0.000387	5.9711	0.0145
Location	1	0.1208	0.2425	0.2483	0.6183
Chick mortality					
Intercept	1	-2.008	0.6871	8.5396	0.0035
Subcolony size	1	-0.0011	0.000682	2.6067	0.1064
Location	1	-0.877	0.3958	0.0491	0.8246
Nest predation					
Intercept	1	-1.7848	0.766	5.4296	0.0198
Subcolony size	1	-0.00057	0.000698	0.6774	0.4105
Location	1	-0.53	0.4607	1.3236	0.2499
December 2004					
Nest success					
Intercept	1	0.4651	0.2968	2.4558	0.1171
Subcolony size	1	0.000563	0.000158	12.7419	0.0004
Location	1	-0.0434	0.1529	0.0807	0.7763
Chick mortality					
Intercept	1	-4.877	0.7033	48.0875	< 0.0001
Subcolony size	1	-0.00012	0.000282	0.1955	0.6584
Location	1	1.2515	0.2957	17.9119	< 0.0001
Nest predation					
Intercept	1	-5.4093	0.8155	44.0009	< 0.0001
Subcolony size	1	-0.00052	0.000346	2.227	0.1356
Location	1	1.4787	0.3435	18.5318	< 0.0001

mortality and nest predation; the probabilities of chick mortality and nest predation were highest in the functional edge of the subcolony (Table 5, Fig. 17).

In some of the subcolonies where no predation was observed, there was evidence of chick predation (missing chicks) from the transect nest checks. With the cumulative number of missing chicks on the transect within the nest check period, 'transect -predation rates' can be calculated as preyed chicks per hr. In all but two of the subcolonies in which predation events were not observed, these transect-predation rates were higher than the observed predation rates (which were zero). For subcolonies in which predation events were observed, the transect-predation rate was lower than the observed predation rate. Predation rates obtained from nest checks are not as accurate as direct observations, since missing chicks (assumed to be lost due to predation) might have died from other causes (starvation, other penguins, etc.) and then were scavenged. Moreover, the subset of nests in a transect may not be representative of the entire subcolony. Results suggest that observed predation rates might have been underestimated at some of the subcolonies in which predation events were not observed, especially for those in which predators were frequently seen searching (ex: SC8).

DISCUSSION

Striated Caracaras

Striated Caracaras at Bahía Franklin were the main predators on Rockhopper Penguin chicks. This result agrees with previous observations which indicated that these subcolonies are usually occupied by either a single adult breeding pair of Striated Caracaras or by a "gang" of juveniles, immatures and / or adult nonbreeders; these groups sometimes also included Turkey Vultures and juvenile Crested Caracaras (J. Meiburg, pers. comm.). On a survey conducted on Staten Island during 1995, 37 Striated Caracaras were observed along 196 km of coastline

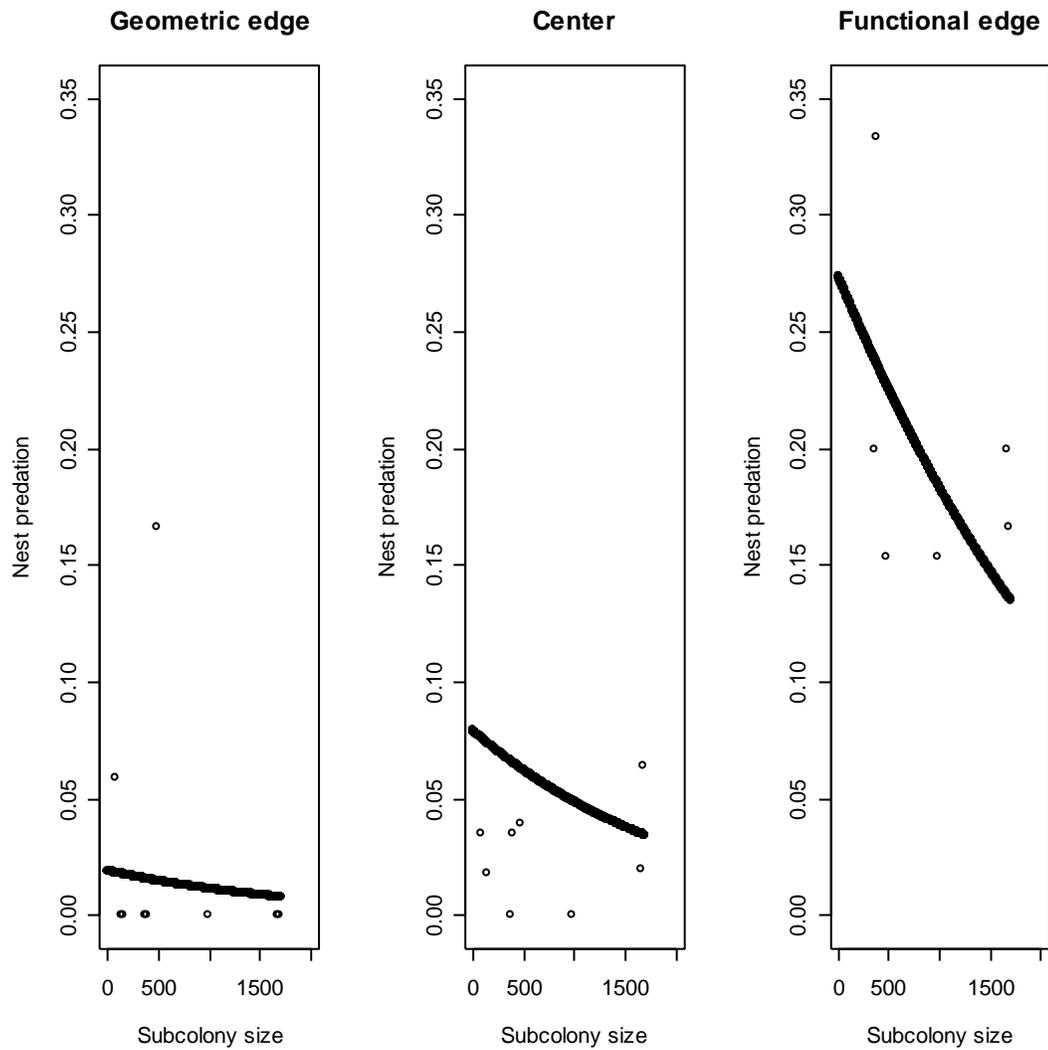


FIG. 17. Logistic regression curve showing the relationship between nest predation and subcolony size on the geometric edge, center and functional edge of subcolonies in 2004. Open circles: observed nest predation at each nest location within each subcolony calculated from the nest checks on each transect. Solid line: estimated probability of nest predation on each location of the subcolony.

surveyed (68% of total coastline but not including Bahía Franklin) and all of them were at or in close proximity to colonies of marine mammals or seabirds (Frere et al. 1999). In another survey conducted in November 2001 at Bahía Franklin, 20 adult Striated Caracara pairs (five of them with nests) and five immature foraging groups were located and their territories mapped (J. Meiburg, pers. comm). All of the territories were within the Rockhopper colony at Bahía Franklin.

As Striated Caracaras hold territories within the Rockhopper Penguin colony and most of the observed predation and attempted predation events on penguin chicks were by this species, it is reasonable to conclude that at Bahía Franklin this predator feeds predominantly on Rockhopper Penguins and has the greatest impact on them. Skua predation is a major cause of egg mortality in Rockhopper penguins on New Island, Falkland Islands (St. Clair and St. Clair 1996). Skuas were also observed taking penguin chicks from their nests, while parents stood beside or near them (St. Clair and St. Clair 1996), and killing lone chicks during the Rockhopper crèche period (Pettingill 1960). The Chilean Skua (*Catharacta chilensis*) has been recorded at Staten Island (Schiavini et al. 1999) and on occasion they have been seen feeding on adult/chick penguin remains in the periphery of the subcolonies or close to their nests (A. Raya Rey, pers. comm.). Also, analysis of regurgitated pellets collected by skua nests during December 1999 showed that penguin remains were the most important item, accounting for 74% of all prey (unpublished data). During this study, skuas were never seen taking penguin chicks or scavenging, and accounted for less than 5 % of the total activity events in all subcolonies for both years. However, further study is needed on their potential impact on Rockhoppers during the incubation period.

Other Predator/Scavengers

Kelp Gulls and Dolphin Gulls were the second most common species observed at the subcolonies. Kelp Gulls were most common at SC8 where, in both years, gull nests with chicks/eggs were present. Kelp Gull activities at penguin colonies have been studied for Adélie Penguins at King George Island (Emslie et al. 1995) and for King Penguins at Marion Island (Hunter 1991). At both sites, Kelp Gulls were observed frequently scavenging but never preying on eggs or chicks. At Punta Leon, Argentina, Kelp Gulls were the main predator on a mixed colony of Royal Terns (*Sterna maxima*) and Cayenne Terns (*Sterna eurygnatha*); they preyed mainly upon tern eggs but were twice observed preying on tern chicks (Yorio and Quintana 1997).

At Staten Island, Kelp Gulls were observed scavenging later in the season and in 2003 they were only observed attempting to take penguin chicks at SC8 on four occasions. However, given the small size of SC8, this resulted in a high individual attack rate. Moreover, this subcolony had the lowest nest success in both years and the highest nest predation in 2004, suggesting that Kelp Gulls might have an important impact here. At Staten Island, Kelp Gulls were always seen approaching central nests and from the air. Instead, at Punta Leon, Gulls approached almost exclusively peripheral tern nests and from the ground (Yorio and Quintana 1997). These alternate methods of approach at different sites may be due to variations in the prey's nest defense behavior and nesting density. At Staten Island the estimated nesting density for Rockhopper Penguins is $102.5 (\pm 29.7)$ nests per 100 m^2 (Schiavini 2000). Instead, at Punta Leon, Royal and Cayenne Terns nest together with a density of 9-11 nests per m^2 (Quintana 1995 in Yorio and Quintana 1997) which, among other factors, appears to result in a low frequency of aerial predation (Yorio and Quintana 1997).

The increase of Kelp Gull activity rate with wind speed might explain their dominance in a place as SC8, the most isolated and exposed to the wind of all study subcolonies. Gulls always approached nests from the air, and higher wind speeds might give them greater maneuverability and speed when approaching the nests and greater lift when searching from the air. Dolphin Gulls, on the other hand, did not have an important impact as predators but they seem to be important scavengers. Not only did their total activity rate increase significantly later in the season; scavenging events were also observed at this time of season and they were seen walking inside the subcolony searching for dead chicks or abandoned eggs, mostly in SC2 and SC9. Dolphin Gulls are mainly specialized scavengers and at Punta Tombo, Argentina, they mainly feed by scavenging on food dropped by other colonial seabirds and on sea lion excrement; and they have also been seen scavenging remains of Magellanic Penguin (*Spheniscus magellanicus*) eggs already preyed upon by other species and stealing cormorant and Kelp Gull eggs (Yorio et al. 1996).

Activity Rate and Subcolony Size

Searches were the most common activity for all species. This result agrees with other studies of South Polar Skuas (*Catharacta maccormicki*) at Adélie Penguin colonies (Young 1994) and Brown Skuas (*Catharacta lonnbergi*) at Adélie and Gentoo Penguin colonies (Emslie et al. 1995). Emslie et al. (1995) suggested that frequent searches by predators might help them locate vulnerable prey or assess prey for later attacks.

Encounter rate (search rate) increased with subcolony size, but at a lower rate than expected, thus supporting the encounter effect hypothesis. The encounter effect favors being in a group by decreasing the probability of detection by a predator and because the detection of larger

three-dimensional groups does not increase proportionally with group size (Vine 1973, Taylor 1977, Uetz and Hieber 1994). If the probability of detection of a group initially increases linearly with group size and then levels off, large groups hunted visually will not be proportionally more conspicuous than small groups (Inman and Krebs 1987). For Rockhopper Penguins the encounter effect may not be very important; the probability of detection may not vary much among subcolonies since most of them are in close proximity to each other. Further studies are needed to better explain the pattern of predator encounter seen at these subcolonies.

Impact of Predation

The effect each species of predator has on a colony depends on the size of the predator in relation to the defending species or risk, and the method of approach by the predator (Brunton 1997). In Least Terns (*Sterna antillarum*) the relationship between colony size and the percentage of nests lost to each type of predator depends on the predator's method of approach, either aerial or from the periphery; small colonies appeared to be more vulnerable to predators with periphery approach, whereas large colonies were more vulnerable to predators approaching from the air (Brunton 1999). Brunton (1997) concluded that the selfish herd hypothesis may be limited to applying only when predators are restricted to approach from the edge due to the type of predator, the effectiveness of the antipredator behavior by the prey species, or the physical characteristics of the nesting site.

The ratio of peripheral to central nests depends on the shape and the size of the subcolony. For any subcolony size, circular shapes have the lowest ratio. Thus, when predation occurs mainly on the edge and given a circular shape, the disadvantage of peripheral nests would be less in larger subcolonies. If predation from the ground is an important method of approach

by the predator then highest levels of predation are more likely to occur on the edge (especially if nest density is high, making it difficult for a predator to land within the colony), giving central nests an advantage against predation since they can only be accessed from the air.

Several studies have reported higher nest predation on the edge of the colonies (Young 1994, Emslie et al. 1995, Yorio and Quintana 1997). In all these studies predators approached almost exclusively from the ground. In Rockhopper Penguin subcolonies at Staten Island, Striated Caracaras attacked preferentially from tussocks. Even though attacks from the ground were rare, peripheral nests would still be more vulnerable to predation than central nests because they can be accessed from peripheral tussocks. The argument given above would still hold true if it was not for the large subcolonies also having tussocks within them (central tussocks). In 2004, predation and attempts were indeed significantly higher on nests on the geometric and functional edge. Thus, being in the center might not be an advantage unless the nest is not next to a central tussock. Also, the proportion of peripheral to central nests does not necessarily decrease with subcolony size; this will depend on how many central tussocks are present. Conversely, and to complicate the interpretation even more, some peripheral nests might be more protected than central nests depending on the topography of the subcolony.

Nest-site topography has been identified as a potential factor, among others, in determining the likelihood that a particular nest will be subject to predation. Weidinger (1998) showed that skua predation on Cape Petrels (*Daption capense*) was lower on nests in vertical parts of cliffs, on narrow ledges and with more sides sheltered by rock walls. Similarly, Double-crested Cormorants (*Phalacrocorax auritus*) and Pelagic Cormorants (*P. pelagicus*) nesting in steeper and more central locations had the lowest predation pressure (Siegel-Causey and Hunt 1981). The landscape at Bahía Franklin presents eroded areas creating embankments up to 1-2

meters high, at the top of which is the ground level with tussocks. These embankments are sometimes found bordering part of the periphery of subcolonies, thus creating a barrier to predators approaching from the edge (it seems unlikely for a Striated Caracara to jump from a tussock onto a nest that is 2 meters below). In these situations, peripheral nests would be as protected as central ones, whereas those on the functional edge would be the most vulnerable to predation.

In 2004, nest checks in large subcolonies revealed a higher nest predation on functional edge nests, suggesting that in certain parts of the subcolonies these nests are indeed the most vulnerable to predation. In small subcolonies, no differences in nest predation between the geometric edge and center were found, probably because Striated Caracaras were rarely seen here. Even though in one of them (SC8) Kelp Gulls were most common and nest predation was higher in the center, predation rate may have been too low to show any significant differences.

The number and kinds of predators and their life history strategies also should be considered when assessing predation impact. Emslie et al. (1995) suggested that differences in reproductive success by penguins of the same species at different locations may be explained, in part, by differences in the number and kind of predators associated with them. A greater number and diversity of predators could result in a greater proportion of prey killed. Striated Caracaras at Staten Island often hold territories that include entire penguin subcolonies. Larger subcolonies offer a greater number and variety of prey, and might attract more predators than smaller ones. Indeed, at SC9, the largest of all subcolonies and apparently not part of a Striated Caracara territory, up to five caracaras were seen simultaneously. Instead, at SC4, a similar sized subcolony and part of a Striated Caracara territory, no more than two caracaras (the breeding pair) were observed because they would always exclude other caracaras from their territory.

Several studies have shown that predators with feeding territories have higher reproductive rate compared with pairs with out feeding territories (Spear 1993, Young 1994). In this study, regardless of the possible benefit for the predator, being part of the territory of a Striated Caracara seems to be beneficial from the view point of the prey. SC4 had a lower proportion of predation rate and a lower predation risk than SC9.

Predation rates increased (though not significantly) with subcolony size, which is consistent with other studies. Hunter (1991) calculated predation rates on King Penguins by collecting carcasses and found that they increased with colony size. Emslie et al. (1995) calculated predation rates on Adélie Penguins from direct observations and found the highest rates at larger colonies. However, breeding in larger colonies can still be adaptive for reducing predation risk as long as predation rates are proportionally lower in larger colonies. In this study, for large subcolonies in which predation occurs over a certain predation rate threshold (0.05 predation events/hr?) the individual predation rate (relative predation rate) was reduced by being in a larger subcolony. Instead, for small subcolonies individual predation rate was high, regardless of low overall predation rates. Davis (1982) found that the number of Adélie chicks lost to predation was greatest at the largest crèche, although the proportion was smallest. Hernández-Matías and Ruiz (2003) found that larger subcolonies of Common Terns had a higher absolute number of predated nests but a lower percentage of nest predation than smaller subcolonies and observed that the probability of predation was negatively related to subcolony size. Thus, higher predation rate in larger colonies does not necessarily mean that the individual predation risk is higher.

In this study, the analysis of the individual predation risk suggests that, for those subcolonies in which predation was observed, there is a dilution effect and that those individuals

seem to reduce their risk of predation by being in larger subcolonies. Some authors have considered that predation has a secondary role in the evolution of coloniality (Ward and Zahavi 1973), others that it may even be a cost for colonial breeders (Clode 1993). However, Wittenberger and Hunt (1985) suggest that as a general rule, the proportion of nests lost to predators will decrease with increasing colony size once the colony is large enough to swamp all local predators. Here, small subcolonies for which predation was observed had a proportionally higher predation rate than larger subcolonies with similar absolute predation rates suggesting that, indeed, the swamping effect of colony size may not take place unless the colony reaches some minimum size.

Differences in breeding success are not always attributable to predation. Factors such as the quality of birds nesting at the edge versus the center of the colony might be involved (Coulson 1968). In Chinstrap Penguins, nests in large subcolonies, whatever their position, were more successful than nests in small ones (Barbosa et al. 1997). For Rockhoppers, in both years, small subcolonies had lower nest success than large ones, but no differences were found in nest predation or chick mortality. For large subcolonies, direct observations suggest that higher nest success may be explained in part by a dilution effect thus reducing the probability of predation per nest.

Lower breeding success in small subcolonies has been explained by the increased proportion of peripheral nests (Tenaza 1971). The lower breeding success of peripheral nests may be due to higher rates of nest predation (Tenaza 1971) or, as in Adélie Penguins, to the presence of older and more experienced birds in the center of the colony and a larger proportion of young and inexperienced birds on the periphery (Ainley et al. 1983). In the present case, low nest success in small subcolonies may be partially attributable to predation and the high

predation risk of small subcolonies. However, predation rates were low or not even observed at several other small subcolonies. At the start day of nest checks, many of the nests were already empty (they just had the breeding penguin pair). Thus, it is possible that these pairs had either lost their eggs during the incubation or their chick earlier in the season, or that they were young or inexperienced breeders. The effects of age-related factors on nest success and the impact of predation during the incubation period remain to be explored.

Results from this study do not completely support the hypothesis that breeding in larger subcolonies offers more protection to chicks against aerial predators than smaller ones. For Rockhopper Penguins at Staten Island, in regard to reducing the probability of predation, size is not all that matters. If predation does occur, subcolonies may lower their predation risk by a dilution effect, once they have reached some minimum size. Subcolonies can also have zero or low predation risk when surrounded by larger subcolonies or when part of the territory of a Striated Caracara. Within each subcolony, nests in central locations of large subcolonies or those on the geometric edge of embankments seem to be the most protected from predation. Consequently, when assessing the impact of predation on Rockhopper Penguins at Staten Island, factors to be considered include: predator species (their methods of approach and territoriality), subcolony size, location of the subcolony (isolated or surrounded by other large subcolonies), nest-site characteristics (presence of central tussocks or embankments), and nest location within each subcolony.

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