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Leopard seal predation rates at penguin colonies of different size

DAVID G. AINLEY[1]*, GRANT BALLARD[2], BRIAN J. KARL[3] and KATIE M. DUGGER[4]

[1]*H.T. Harvey and Associates, 3150 Almaden Expressway, Suite 145, San Jose, CA 95118 USA*
[2]*PRBO Conservation Science, 4990 Shoreline Highway, Stinson Beach, CA 94970, USA*
[3]*Landcare Research New Zealand, Private Bag 6, Nelson, New Zealand*
[4]*Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803, USA*
**dainley@penguinscience.com*

Abstract: In a study designed to elucidate the factors that might differentially affect the well being and biology of Adélie penguins (*Pygoscelis adeliae*) that breed in colonies of different size, we investigated the predation rates on penguins by leopard seals (*Hydrurga leptonyx*) over a period of six years. The study colonies varied in size across the full range for this penguin species, contrasting with previous studies in which data were gathered only at very large colonies, and only in single years. The number of seals present varied directly with the amount of penguin traffic in the areas near the beach, where most predation takes place. Seals were present persistently only when penguin traffic exceeded about 250 penguins per hour. Predation rates also varied with penguin traffic in a curvilinear fashion, leveling off where traffic exceeded about 1200 penguins per hour. With respect to predation, it appears to be advantageous for Adélie penguins to nest in very small or very large colonies. At large colonies, the number of penguins moving to and from the colony 'swamp' the seals' predatory efforts, thus reducing the chances that an individual penguin will be taken. Small colonies are of little interest to the seals.

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Key words: Adélie penguin, colony size, *Hydrurga leptonyx*, predator swamping, *Pygoscelis adeliae*

Introduction

The predation of Adélie penguins (*Pygoscelis adeliae*) by leopard seals (*Hydrurga leptonyx*) has attracted much attention among penguin biologists, beginning with the anecdotal observations of the early explorers (e.g. Levick 1914) to the quantified estimates of seal hunting tactics, kill rates and the factors that affect them in more recent years (Kooyman 1965, Penney & Lowry 1967, Müller-Schwarze & Müller-Schwarze 1975, Rogers & Bryden 1995, Court 1996). As summarized by Hall-Aspland & Rogers (2004), the Adélie penguin is the primary prey of leopard seals in those coastal waters of Antarctica near large penguin colonies; otherwise the diet of leopard seals is "perhaps the most catholic of any seal" (Kooyman 1981, p. 269). Penguin kill rates near to colonies can be significant, estimated at up to 5% of the breeding population (Penney & Lowry 1967), making the act of breeding, and doing so successfully, a seemingly hazardous proposition (Ainley *et al*. 1983). A penguin that fails to breed, or which loses its eggs soon after laying, does not have to swim many times through the line of seals that spread along a colony landing beach, nor is it pressured by waiting mates or chicks to deal with hazardous conditions if it chooses otherwise. Due to an ability to build up fat reserves upon which it lives while at the colony, a non-breeder has to pass through a seal line only 2–4 times during the summer, whereas a penguin that eventually provisions chicks must make the crossing 20–30 times per season.

We began a study of Adélie penguin natural history patterns as a function of colony size in an attempt to determine the factors responsible for the gradual growth in most colonies of this species in the Ross Sea, with especially high rates of increase at small colonies (Taylor & Wilson 1990). One part of this effort was the quantification of seal predation rates at colonies of different size. Most observations of leopard seals have been made at large Adélie penguin colonies – in fact, three have been conducted at Cape Crozier, one of our study colonies (Kooyman 1965, Penney & Lowry 1967, Müller-Schwarze & Müller-Schwarze 1975). Our intent was not to repeat these studies, all of which described various environmental factors that affect seal kill rate at high latitude colonies – tide height, wave height, water clarity, and the amount and type of ice can affect predation rate, and can vary on a within- and between-day basis. Research by others has shown that Adélie penguins at the high latitude of our study, during summer, exhibit no consistent circadian pattern to their arrivals and departures (Müller-Schwarze 1968, Davis 1995), and the same is true for leopard seal predation (references above), unlike patterns at much lower latitudes where there is a predictable diel periodicity to penguin traffic (cf. Wilson *et al.* 1993) and to seal predation (T. Rogers, personal communication 2004).

We predicted that

1) predation would be infrequent at small colonies, which have low rates of penguin traffic, and

2) where penguin traffic was sufficient, predation rate

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Table I. A summary of observations of leopard seals and their predation rates on Adélie penguins at three colonies of differing size on Ross Island, 1996–2003. Means are given with the standard error. Estimated percent of breeders taken is a relative number for comparative purposes, calculated as kills per seal per hour * max number of seals seen per day * number of hours in the (approximately) 91 day (2184 hr) breeding season (1 November to 31 January) / colony size (total individuals); adjusted for the proportion of the entire landing beach under observation.

Year	Colony	Colony size (pairs)	observation (days)	Hours	Mean no. penguins	Mean no. seals seen hr^{-1}	No. kills hr^{-1}	Max no. seals d^{-1}	Kills seal hr^{-1}	Estimated % breeders taken
1996	West Crozier	99 500	26 Dec–21 Jan (9)	11.0	1128	2.09 ± 0.86	0.73 ± 0.38	4	0.25 ± 0.12	1.6%
1997	West Crozier	133 000	19 Dec–19 Jan (26)	33.8	1,747	0.59 ± 0.16	0.21 ± 0.13	4	0.15 ± 0.07	0.7
	North Bird	32 700	23 Dec–17 Jan (23)	41.8	973	0.81 ± 0.24	0.12 ± 0.06	1	0.13 ± 0.06	2.2
	Royds	3900	14 Dec–22 Jan (37)	62.7	295	0.00	0.00	0	0	0
1998	West Crozier	107 700	15 Dec–23 Jan (31)	46.4	2492	1.22 ± 0.30	0.26 ± 0.11	4	0.19 ± 0.09	1.2
	North Bird	25 400	22–31 Dec (11)	10.8	673	0.00	0.00	0	0	0
	Royds	3400	19–23 Jan (5)	5.0	74	0.00	0.00	0	0	N/A[1]
1999	West Crozier	119 400	14 Dec–11 Jan (20)	23.1	1962	0.73 ± 0.20	0.61 ± 0.19	4	0.48 ± 0.14	2.6
	North Bird	25 000	15 Dec–16 Jan (20)	20.5	574	0.10 ± 0.07	0.00	1	0	0
	Royds	3600	14–25 Jan (8)	5.7	150	0.33 ± 0.21	0.50 ± 0.50	1	0.43 ± 0.46	N/A[1]
2000	West Crozier	118 800	13 Dec–22 Jan (37)	51.2	2772	2.06 ± 0.28	0.50 ± 0.11	7	0.17 ± 0.04	1.6
2003	Royds	2000	11 Nov–26 Jan (58)	118.1	203	0.02 ± 0.01	0.02 ± 0.01	1	0.02 ± 0.01	1.1

[1]Numbers not tallied for colony-seasons that had < 10 h of observation (see text).

would increase linearly with rate of traffic but only to a certain threshold, beyond which predation rate would level off.

The results of observations, gathered over a period of six years at three neighbouring colonies in the Ross Sea, Antarctica, are presented in this paper.

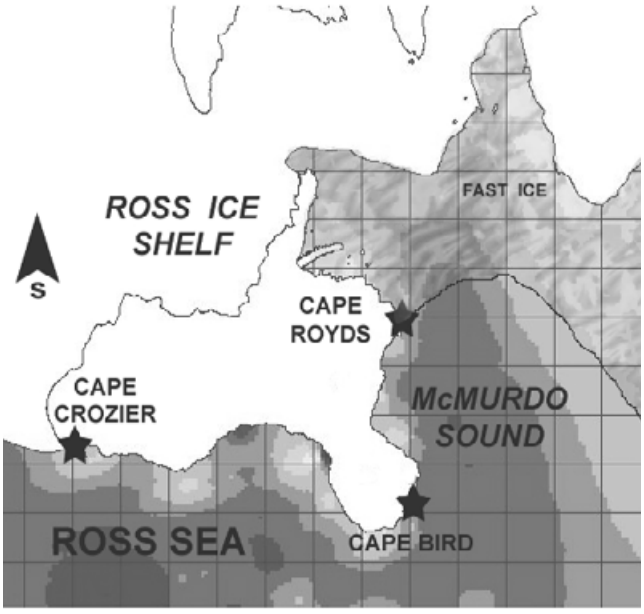

Fig. 1. Ross Island showing locations of the three Adélie penguin colonies where leopard seal observations were made, 1996–2003. The grid is 10 km; bathymetric contour intervals are 100 m.

Methods

Study area

The three study colonies were located on Ross Island (*c*. 77ºS, 166–169ºE) (Fig. 1). The number of penguins nesting at these colonies ranged over three orders of magnitude, approximately representing the entire range in colony size for this species (see Woehler 1993): Cape Crozier, west portion (99 000 to 133 000 nesting pairs); Cape Bird, North portion (25 000 to 33 000); and Cape Royds (2000 to 3900; Table I). Colony size was determined by aerial photography (Taylor & Wilson 1990, Landcare Research NZ, unpublished data).

Observation points remained the same throughout the study. From each, either a large portion of or the entire landing beach at each colony could be easily seen. At Cape Crozier West, the landing beach stretches ~1.5 km; from the observation point at about 115 m high about two-thirds of it was in good view. At Cape Bird North, the landing beach stretches ~1 km, and from the observation point at about 50 m high, about 40% was in view. At Cape Royds, the main landing beach is about 100 m long and entirely in view from the observation point at about 15 m elevation.

Observation protocols

In most years, our presence at these colonies coincided with the chick period (mid December to late January). After 2000, we began to arrive a month earlier. We identify 'seasons' by the initial year; e.g. 1996 represents the November 1996 to February 1997 season. During our presence, on any given day, observers logged data for

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periods that were usually one hour in duration. There was extensive overlap in observers one season to the next: four observers participated in all years, five for three seasons, and only three for a single season. New observers spent a few sessions with experienced observers before being allowed to record results alone. On many days different persons contributed one or more observation periods, sometimes sequentially but usually, by intent, spacing the effort through the day. Daylight was continuous; most observations fell within the period from about 09h00 to 20h00 (GMT +12:00). As the observation points were exposed, rarely did we conduct observations during severely inclement weather.

During observation periods, observers scanned the landing beach continuously, and, at 5 min intervals tallied the number of penguins that they had seen diving in or jumping out of the water. Using 5 min intervals made the tallying easier. Since penguins travel in flocks, with the flocks entering the water being much larger than those exiting the water, this exercise involved estimating/counting flock size. The departing flocks build in numbers over time as penguins wait for one individual to make the first plunge, after which they all go in a rush. Therefore, departing flocks were "pre-counted." The observation effort was most intense at the largest colony (Crozier); however, the arrival and departure of flocks was not continuous and thus the tallying was manageable. At the same time, observers watched for leopard seals which, unless hauled out asleep on an ice floe, generally positioned themselves next to the beach ice foot or just beyond the breaking waves; the 'high-risk zone' for the penguins includes the waters within 10–20 m of the beach or ice foot (Penney & Lowry 1967, Müller-Schwarze & Müller-Schwarze 1975). Leopard seals were much more easily seen if they were chasing or catching penguins because of copious splashing, and circling South Polar skuas (*Stercorarius maccormicki*) looking for scraps. Therefore, keeping track of penguins provided the opportunity to keep track of seals, enhanced by frequent scanning using 8x or 10x binoculars. The binoculars also allowed observers to separate leopard from Weddell seals (*Leptonychotes weddelli*). Observers tallied seals seen, chases seen, and kills made during the 5 min intervals. A seal seen in the same location during more than one interval was considered to be the same seal. Observers also noted other things, such as territorial encounters between leopard seals.

Data analysis

We summarized the data into hour-long intervals, because seal observations among 5 min intervals were not independent. Locating a hunting seal in one 5 min interval increased the likelihood of finding it in subsequent intervals, so this procedure helped us to address autocorrelation and to avoid pseudo-replication. We did not use colony-seasons when we had < 10 h of observation, which was the case in one season for Bird and two seasons for Royds. At Royds, in particular, predation was so infrequent that including < 10 h observations would be inappropriate in attempting to quantify predation rate (see Results).

We modelled the effect of the number of penguins at risk to predation (mean number of penguins diving into or jumping out of the water per hour) on the mean number of seals observed per hour and the mean number of kills per seal per hour for each colony-season (Table I). We also investigated the effect of total predation rate (kills per hour) on the number of penguins in the water, as we wondered if penguins would begin to stay out of the water or avoid a beach approach at certain predation levels (Table I). All data were normally distributed and plots of variance-to-mean ratios of all variables suggested variances were homogeneous (i.e. variances were not proportional to means). Our hypotheses were straightforward and involved only single-factor models, so we used normal regression (Proc REG; SAS Institute 1997) to investigate the relationship between the number of seals and predation rates. In addition to linear relationships, we hypothesized the potential for non-linear relationships between kill rate and penguin traffic, which might better reflect the maximum rates at which seals could harvest penguins. To test this hypothesis, we ran models that included the pseudo-threshold ($Y= \alpha + \beta * \ln (X + 0.05)$) and quadratic ($Y= \alpha + \beta X + \beta X^2$) structure on the independent variable. Residual plots suggested that errors were independent and normally distributed, indicating that model assumptions were not violated. The best structure (linear, pseudo-threshold, quadratic) for each independent variable was chosen based on the model with the highest adjusted r^2. All models and effects were considered significant at $\alpha < 0.05$.

Results

During 1996, some preliminary observations to work out the protocols were made at the largest colony (Cape Crozier); the following season observations began at all three colonies. The effort proceeded as planned for three seasons (Table I), but thereafter the amount of fast ice began to vary differently adjacent to these colonies, due in part to the grounding of some very large icebergs in the vicinity and, in the case of Cape Crozier, growth of the Ross Ice Shelf. When there was extensive fast ice, the coming and going of penguins moved too far away for easy viewing. Therefore, we were unable to make observations at any colony in 2001 and 2002. In 2003 we were able to conduct our effort only at Cape Royds. At Cape Crozier, the fast ice moved the penguin landing (no longer a beach, having become a fast ice edge) from shallow to deep water. This situation exposed the leopard seals to potential killer whale (*Orcinus orca*) predation. Killer whales were frequently

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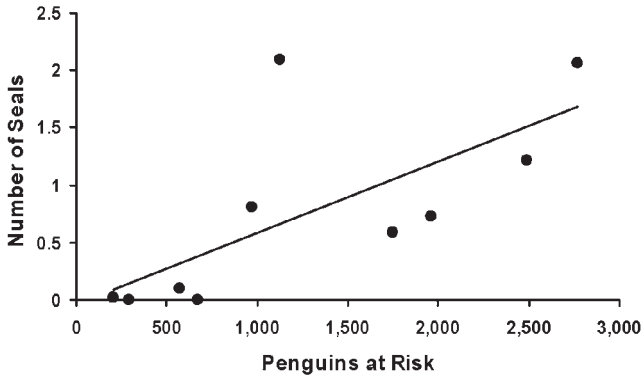

Fig. 2. Mean number of seals seen per hour relative to the number of penguins at risk (number diving into or leaving the water per hour of observation). Shown here are data for all colony-seasons in which at least 10 hours of observations were made (adj r^2 = 0.43, $P < 0.023$).

seen in the vicinity, though they were not observed hunting seals at Cape Crozier, and the type 'C' whales most commonly observed from Crozier are thought to eat mostly fish (Pitman & Ensor 2003, Ballard & Ainley 2005). The seal-eating type 'B' killer whales have been observed in the waters around Ross Island, especially in McMurdo Sound (DGA personal observation). In fact, with the landing in deep water, we saw little evidence of leopard seals at Cape Crozier after 2000, even during extensive observations designed to record any mammals present within binocular range of the colony. Even at a distance of > 2 km a leopard seal kill of a penguin is obvious owing to the dozens of hovering skuas that are quickly attracted.

The average number of seals seen per observation period per colony-season varied as a function of the number of penguins at risk: the sum of those diving into or exiting the water (Fig. 2; adj $r^2 = 0.43$, $P < 0.023$). The within-season pattern was similar. This was evident at Cape Crozier, especially in 2000, when we had more biologists present than usual and, thus, could devote more time to the leopard seal watches (Fig. 3). Rarely did we observe a leopard seal at the smallest colony (Cape Royds), where few penguins come and go (Table I). In fact, we saw only one seal on four different days in the four years of observation there. Three of those days occurred in 2003, two days of which were consecutive and, thus, probably involved the same individual.

In contrast, the total number of seals seen per season at the large colony (Cape Crozier) ranged from 16 to 99 during the five seasons of observations. At Cape Bird, a medium-sized colony, numbers of seals observed were intermediate between Royds and Crozier, i.e. up to 35 observations per season. At Crozier, along the section of the beach being viewed, we interpreted our sightings to represent a maximum of four seals being present at any one time in all years except 2000. We knew that seals were also positioned along the stretch of beach not included in our study because we could see them from other locations. Previous studies noted up to six seals working the *entire* length of beach at any one time. On numerous occasions, we witnessed what appeared to be territorial behaviour, where one seal would rush at another if it approached too closely. The result was a regular spacing of the seals along the beach (see also Penney & Lowry 1967). At Bird we regularly saw one seal along the study section of the beach (noted also by Court 1996).

In 2000, fast ice was beginning to build up in front of the Cape Crozier colony. In that year, the number of leopard seals jumped to seven, which included what we interpreted to be leopard seals foraging on fish. These seals dove under the fast ice, often from leads a distance back from the ice edge, staying submerged for periods of 5–10 min. They reappeared, taking and expelling several loud breaths, then dove again, and did this continuously for several hours. We never saw them chasing or eating penguins when in this behaviour mode (see also Rogers & Cato 2002, for discussion of such behaviour). Such behaviour contrasted with this species' usual 'penguin-hunting mode,' in which they lay motionless at an ice edge or just beyond the beach

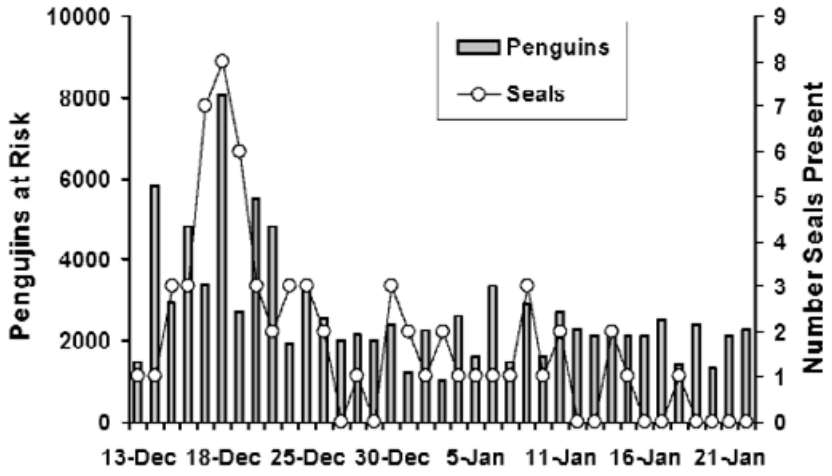

Fig. 3. Seasonal change in number of leopard seals present relative to the number of penguins at risk (number diving into or leaving the water per hour of observation); Cape Crozier 2000–01.

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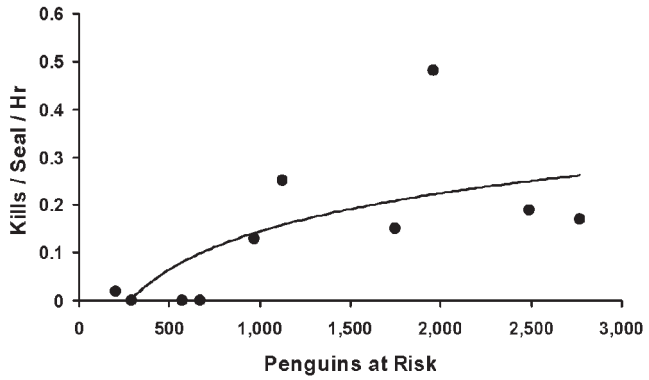

Fig. 4. Mean number of penguins killed per seal per hour relative to the number of penguins at risk (number diving into or leaving the water per hour of observation). Shown here are all colony-seasons for which at least 10 hours of observations were made (adj $r^2 = 0.39$, $P < 0.031$).

wave wash with just their nostrils protruding above the water surface.

The average number of penguin kills per seal per hour also varied as a function of penguins at risk, but in a log-linear fashion (adj $r^2 = 0.39$, $P < 0.031$; Fig. 4). The rate reached an asymptote when penguin traffic reached about 1200 swimming penguins and thereafter did not increase in spite of a continued increase in traffic. Interestingly, when we modelled mean number of penguins at risk as a function of total kill rate (unadjusted by number of seals present), penguin numbers increased with kill rate to a point; then it appeared that at the highest kill rates fewer penguins exposed themselves to the risk of being eaten (adj $r^2 = 0.87$, $P = 0.0003$; Fig. 5).

Discussion

Quantified observations of leopard seal predation have been made previously only during single seasons at very large Adélie penguin colonies (exceeding 100 000 pairs): Cape Crozier (Kooyman 1965, Penney & Lowry 1967, Müller-Schwarze & Müller-Schwarze 1975) and Magnetic Island, Prydz Bay (Rogers & Bryden 1995). Over an entire summer breeding season, these authors estimated that the seals took 1.4–5.0% of the penguins at Cape Crozier, and 2.7% of the penguins at Magnetic Island. These estimates were based on the daily rate of penguin kills, the length of the nesting season, and the size of the penguin breeding population. These authors showed that the effectiveness by which leopard seals captured penguins varied with conditions, and described rules that penguins needed to follow to avoid being taken by a seal.

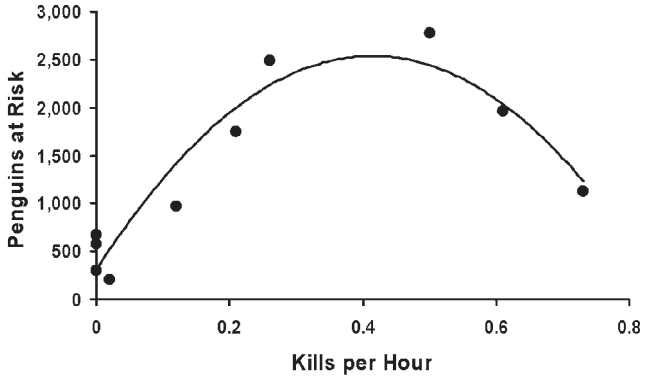

Fig. 5. The change in the total numbers of penguins at risk as a function of total predation rate (adj $r^2 = 0.87$, $P = 0.003$). All colony-seasons having at least 10 hr of observation were included.

Our study confirms that leopard seals are not readily attracted to small colonies where few penguins come and go (see also Ainley 2002). On the basis of our data, it appears that sustained penguin traffic of more than about 250 penguins per hour in the high-risk zone, just off the landing beach, is required to interest a leopard seal on a regular basis. Small Cape Royds, which varies annually in size from 2000 to 4000 breeding pairs, rarely exhibited a traffic rate higher than this. More seals are attracted with more penguin traffic on both a within-season and colony-specific basis. Phenological patterns in the leopard seal's activity must also be important because, at least as shown at Cape Crozier, penguin traffic can remain high while seal predation slackens during the late summer (see also Müller-Schwarze & Müller-Schwarze 1975).

We observed, by way of our inter-colony comparison, that leopard seal kills per hour per seal reached saturation (levelled off) at a penguin traffic level of about 1200 penguins swimming in the high-risk zone per hour. This saturation was probably due to:

1) the territoriality of seals, which prevents additional seals from foraging (thus, curtailing the linear relationship between number of penguins and number of seals),

2) an increased reluctance of penguins to expose themselves to predation when kill rates became high, and

3) the fact that seals kill penguins no faster than they can handle or consume them.

Leopard seals can effectively catch a penguin only by using stealth: a wait and rush tactic. Once they catch one, regardless of their massive jaws, they take dainty bites to consume it (Penney & Lowry 1967, Müller-Schwarze & Müller-Schwarze 1975). There are periods when single seals kill numbers of penguins in rapid succession, but these appear to be exceptional (reviewed in Ainley 2002) or occur during particularly risky (for penguins) conditions (above citations; also T. Rogers, personal communication 2004).

Owing to the apparent saturation in the kill rate, it appears

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that predation by leopard seals would have its greatest relative impact at medium-sized penguin colonies, assuming seal densities per kilometre of penguin landing area were comparable. At larger colonies, the greater numbers of penguins appear to effectively 'swamp' the predator. Therefore, in regard to predation, there appears to be a benefit to Adélie penguins who nest in large colonies: a lower chance of being taken by a leopard seal. Owing to the seals' disinterest, reduced predation by seals appears to be an advantage to nesting in tiny colonies as well. However, to assess whether or not leopard seals take more than 1.4–5% of penguins at medium-sized Cape Bird, i.e. the predation impact measured by others at Crozier, would require a team of observers of a size far beyond our capability, owing to the very long total landing beach there (several kilometres). In the case of Royds, considering the two seasons in which sufficient observations were made, about 0.6% (range 0–1.1%) of the population may have been eaten, although when a seal does show up its effect can be important (2003). In contrast, at the large Crozier colony, the percent of the population taken, average 1.6% (range 0.7–2.6%), was only triple the average at Royds, even though the colony is up to 35 times larger (Table I).

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