

EFFECTS OF HUMAN ACTIVITY ON ADELIE PENGUIN *Pygoscelis adeliae* BREEDING SUCCESS

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Abstract

Adelie penguin *Pygoscelis adeliae* colonies were exposed to two forms of human activity currently occurring in Antarctica: nest checking for scientific purposes and recreational visits (disturbance treatments). Hatching success and chick survival at these colonies were compared to that at an undisturbed (control) colony. Six colonies were used — three larger (mean of 70 nests) and three smaller (mean of 44 nests). Treatments (nest checking, recreational visits and control) were each replicated at one colony of each size. For both larger and smaller colonies, hatching success and chick survival were highest at control colonies and lowest at colonies subjected to recreational visits. These differences were statistically significant between smaller colonies where hatching success was 35% lower in the colony subjected to nest checking (compared to the control colony) and 47% lower in the colony subjected to recreational visits. For chick survival these reductions were 72% and 80% respectively. No significant difference was found in breeding success (hatching success or chick survival) between the two disturbance treatments (nest checking and recreational visits) in either size class. Disturbance treatment and colony size both influenced hatching success and chick survival significantly, but there was no statistical interaction between these parameters. Penguins bred either in the centre of a colony or at its periphery had no significant influence upon their breeding success.

Keywords: breeding success, scientific disturbance, recreational disturbance, adelie penguins, experimental designs.

INTRODUCTION

The breeding success of seabirds is affected by numerous factors, including food availability, weather and the physical condition, and the breeding and foraging proficiency of both members of a breeding pair. Human activity can also influence seabird breeding success, as has been shown for various species of gull *Larus* spp. (Hunt, 1972; Hand, 1980; Fetterolf, 1983), double-crested cormorants *Phalacrocorax auritus*, southern fulmars

Fulmars glacialis, black guillemots *Cephus grylle*, least terns *Sterna albifrons* and auklets *Aethia pusilla* (Ellison & Cleary, 1978; Ollason & Dunnet, 1980; Cairns, 1980; Brubeck *et al.*, 1981; Piatt *et al.*, 1990).

In Antarctica, scientific and recreational activities are increasing (Enzenbacher, 1992) and have the potential to affect seabirds breeding there. Anecdotal evidence suggests that south polar skuas *Catharacta macrormicki* (Johnston, 1971), giant petrels *Macronectes giganteus* (Harris, 1991), chinstrap *Pygoscelis antarctica* and gentoo *P. papua* penguins (Muller-Schwarze, 1984) have all suffered declines in the size of local populations due to the regular presence of humans.

Adelie penguins *Pygoscelis adeliae* are the most abundant penguin breeding in the high Antarctic. They reproduce during the austral summer in dense colonies on ice-free areas of coast, and as such, are readily accessible to people. Adelie penguins are often considered to be relatively immune to human disturbance because they do not always display the overt behavioural responses generally associated with distress (Tenaza, 1971; Oelke, 1975). There is evidence, however, that recreational visits (Thomson, 1977; Wilson *et al.*, 1990; Woehler, 1990) and activities associated with scientific research (Young, 1990) have contributed to the decline of local breeding populations over time periods from 12 to 28 years. These reports, however, use anecdotal evidence collected with little or no control over disturbance stimuli, thus making it difficult to determine cause-and-effect relationships. Some studies have examined the effect of disturbance associated with scientific research by comparing reproductive performance at disturbed colonies with that at undisturbed ones (Davis, 1982). The objective of those studies was to determine causes of egg and chick mortality, and although attempts were made to quantify the effect of investigator disturbance on breeding success, the aim was not specifically to examine the impacts of a range of human activities on the reproductive performance of adelie penguins.

Consequently, despite having a general understanding of the effects of human disturbance on adelie penguins, management agencies remain constrained by a lack of specific and scientifically rigorous information.

Experiments designed to quantify the effects on breeding success of specific types and intensities of human activity could provide information for the management of human behaviour around adelic penguin colonies. The aim of this study was to quantify the effects of two types of human activity on adelic penguin breeding success; nest checking for scientific purposes and recreational visits (either by commercial tourists or off-duty station personnel).

METHODS

Study site

The study was conducted near Rookery Lake (68°29'S; 78°06'E), in the Vestfold Hills, Antarctica. Field work was carried out between 10 November 1993 and 18 January 1994. The site contained roughly 6445 breeding pairs of adelic penguin (Woehler *et al.*, 1989) and approximately 15 breeding pairs of south polar skua (M. Giese, unpublished data). Penguin colonies ranged in size from 20 to over 300 pairs, but most were small and discrete, containing fewer than 80 breeding pairs.

In this study a 'colony' is a group of penguins breeding as a geographically continuous unit (after Penney, 1968), while a 'rookery' describes a number of discrete colonies located within one larger area. Penguins in this rookery were not visited or otherwise disturbed in the summer preceding this study and, to my knowledge, birds were exposed to minimal human disturbance even before this.

Experimental treatments

The primary objective of the experiment was to compare breeding success at colonies subjected to different types and intensities of human activity within one breeding season. To achieve this, six colonies were exposed to three experimental treatments, with each treatment replicated over two colonies. These included two disturbance treatments; nest checking and recreational visits, and one control treatment of no disturbance.

Colonies exposed to nest checking were visited every second day for approximately 15 min. Disturbance stimuli during each visit involved one person standing 10 m from the perimeter of the colony while a second person moved around and sometimes into the colony, using a pole to lift birds slightly off their nests if nest contents were not readily visible (as described by Davis, 1982). Investigators spoke to each other only for the purposes of recording data. This procedure is commonly used by scientists studying adelic penguins and is the technique recommended by the Commission for the Conservation of Antarctic Marine Living Resources for recording breeding success in adelic penguins (CCAMLR, 1992). The impact of these procedures, however, has not been studied quantitatively.

Colonies exposed to recreational activity were visited no fewer than twice and no more than four times every day by two people. Each visit lasted 10 min, during which time investigators walked slowly around the colony, 5 m from its edge, talking quietly, crouching, kneeling and taking photographs. This regime resembled the

visitation intensity and activity of tourist groups visiting penguin colonies on the Antarctic Peninsula and some sub-Antarctic islands (R. Leddingham, pers. comm.). Control colonies were visited by two people every second day but were approached no closer than 30 m.

Colony selection

All colonies were within 100 m of the hard-rock coast, had slopes of less than 5°, were round to ovoid in shape and had a north-easterly aspect. Colonies were all located within a single rookery in an attempt to control for environmental conditions known to affect breeding success (e.g. sea-ice movements and weather).

Attempts were also made to select colonies of approximately the same size (between 60 and 70 breeding pairs each). However, heterogeneity of colony size dictated that three colonies were slightly smaller (mean 44, SD = 5 nests) and three were slightly larger (mean 70, SD = 6 nests). Although this difference was significant ($t = 5.407$, d.f. = 4, $p < 0.05$), it had no effect on the proportion of peripheral to central nesting birds between colonies ($t = 0.36$, d.f. = 4, $p > 0.05$). This was probably due to subtle differences in colony shape and differences in the nesting density at each colony. Peripheral nests were those that had no other active nests between them and the edge of the colony at the commencement of incubation (Spurr, 1973).

Procedures common to all colonies

Prior to being exposed to any of the three experimental treatments, birds were subjected to general disturbances associated with mapping colonies and marking and weighing adults. Individual nests were assigned a number from colony maps and photographs taken at the beginning of incubation. Day one of incubation was the first day a single adult was alone on the nest after it had been occupied previously by a pair. At this time, the incubating bird at each nest was marked on the breast with *Nyanzol-D* branding dye, thus enabling recognition of one member of each breeding pair throughout the season.

To verify the assumption that there was no significant difference in the general body condition of birds between colonies, a sample of 10 birds from each colony was weighed. These birds were the first 10 individuals to relieve their mates from the first incubation shift. Mean weights per colony ranged from 4.66, SD = 0.4 kg to 4.97, SD = 0.4 kg ($n = 60$). One-way ANOVA revealed no significant difference in average body weight between colonies prior to the experiment ($F_{5,54} = 0.92$, $p > 0.05$).

Data collection

Every second day, adult attendance (whether a marked or unmarked adult was present) and nest activity (whether each nest appeared to have eggs and/or chicks) were noted for all nests at each colony. Nest activity was determined most accurately for nest check colonies because the nest contents were examined as

part of the experimental treatment. For recreation and control colonies, nest activity was assessed by observing each nest and recording whether or not it was occupied by an incubating or brooding adult, and was therefore active. For colonies subjected to recreational visits, it was possible to verify these records by noting the contents of nests as adults shifted their position in response to human disturbance, thus exposing eggs and/or chicks. Using this method, the activity of most nests in recreation colonies could be determined by the end of the last visit each day. For control colonies, there was no extraneous disturbance stimulating adults to shift. Nest activity was therefore verified by observing colonies with binoculars for longer periods of time (30 min), thus increasing the likelihood of a bird voluntarily shifting on the nest and temporarily exposing nest contents.

Estimates of nest activity from counts of occupied nests proved to be reasonably accurate. Counts of occupied nests were also made at nest check colonies prior to nests being checked. At these colonies, counts were within 1.04 ± 0.10 of the number of nests subsequently found to be active by nest checking ($n = 40$ days of counts).

Analysis

Only those nests whose activity status was verified by nest checking or by observing nest contents as adults shifted were included in the analysis. Breeding success was examined in terms of two parameters: hatching success and chick survival to two weeks. Hatching success was expressed as the number of nests with at least one chick divided by the original number of nests with eggs. Chick survival was the number of nests in which at least one young was raised to two weeks of age divided by the number of nests with eggs. Two weeks of age represented the longest, reliable record of chick survival. This age permits only a conservative estimate of overall nest failure, but chicks in this study were unmarked, making it difficult to determine their fate in the creche and fledging stages. Since colonies were inspected every second day, hatching date could only be estimated to within an accuracy of 48 h. Consequently, the date at which chicks reached two weeks of age was also only estimated to within a 48 h period. In discussing results the term breeding success is sometimes used to denote both hatching success and chick survival.

Two-way contingency table analysis (Statview SE and Graphics, 1987) was used to compare breeding success across experimental treatments within each size class. The statistical power associated with these results (i.e. the probability of correctly rejecting a null hypothesis of no difference in breeding success due to treatment) was calculated using P-C Size Consultant (Dallel, 1990). Power results were subjected to sensitivity analysis using standard power tables (Kraemer & Thiemann, 1989) so that the nature of the critical effect size could be fully understood (i.e. the degree to which each treatment affected breeding

success). Sensitivity analysis examined power under two hypothetical effect sizes: 0.2 and 0.5. These correspond to a 20% and 50% reduction in breeding success due to disturbance treatment, and represent small and medium sized effects respectively (Cohen, 1977).

Two-way contingency table analysis was also used to examine the influence of three independent variables on both hatching success and chick survival. Independent variables were: experimental treatment (nest check, recreation or control), colony size (larger or smaller) and nest position (periphery or centre). This analysis revealed strong effects due to treatment and colony size so the possibility of there being an interaction between these variables was investigated with a likelihood ratio test (JMP Version 2.04, 1989).

Determining causes of egg loss

Three criteria were used to determine the most likely cause of egg loss per nest: the length of the incubation phase for individual nests compared to the colony mean, the pattern and length of the incubation shifts of each breeding adult, and data from the last nest record prior to the nest being found completely empty with no attending adults.

The cause of egg loss was assigned to predation by south polar skuas if the length of the incubation phase was shorter than the mean for the colony (minus two standard deviations), if the pattern and length of adult incubation shifts were normal and if the last nest record showed at least one adult attending an empty nest. The cause of egg loss was assigned to desertion (due to failure of adults to co-ordinate nest attendance), if the length of the incubation phase was within one standard deviation of the mean for the colony and at least one member of the pair experienced an incubation shift much longer or much shorter than normal (suggesting desertion of the mate or premature departure of the incubating bird, respectively). Finally, for desertion to be assigned as the cause of egg loss, the last nest record had to show one adult attending a nest with at least one egg (i.e. an active nest) (see Ainley *et al.*, 1983). Occasionally, the most likely cause of egg loss could not be determined, either because nest records were incomplete or because the most likely cause could have equally been predation or desertion. In these instances, cause of egg loss was recorded as 'unknown'.

Egg loss after prolonged incubation occurred at three nests in this study. In these cases it was assumed that eggs failed to hatch because they were infertile or because they became addled. Since no distinction could be made between these situations, and since infertility was unlikely to be attributable to human activity, none of these cases has been included in any analysis.

RESULTS

Hatching success and chick survival

In both colony size classes, hatching success and chick survival were highest for control colonies and lowest

Table 1. Number of nests in which at least one chick hatched and number of nests in which at least one chick was raised to two weeks of age for colonies subjected to three experimental treatments

Experimental treatments were replicated over two colony size classes. Numbers in brackets represent the percentage reduction in breeding success due to treatment when compared to the performance of control colonies in the same size class. When expressed as a proportion of 1, these percentage reductions correspond to the actual critical effect size due to treatment.

Colony size	Experimental treatment	No. of nests	No. of nests hatching at least one chick (% reduction c.f. control colony)	No. of nests raising at least one chick to 2 weeks (% reduction c.f. control colony)
Smaller	Recreation	37	18 (47)	5 (80)
	Nest check	44	26 (35)	8 (72)
	Control	46	41	31
Larger	Recreation	75	68 (8)	62 (11)
	Nest check	74	71 (3)	67 (2)
	Control	63	62	58

for colonies subjected to recreational visits (Table 1). These differences were significant for smaller colonies, but not for larger ones (Table 2). Nest checking also significantly reduced hatching success and chick survival in the smaller colony, but there was no significant difference between the effect of nest checking and that of recreational visits in either size class (Table 2).

Differences in hatching success and chick survival between the smaller colonies were associated with medium to large critical effect sizes, reflecting a moderate to strong effect due to treatment (Table 1). These results were also associated with high statistical power (Table 2). Critical effect sizes in larger colonies were very small (Table 1) and corresponded to low statistical powers (Table 2). When critical effect size was increased to 0.2 (reflecting a 20% reduction in breeding success) statistical powers of between 65 and 70% were achieved for larger colonies. When a hypothetical effect size of 0.5

was used (representing a 50% reduction in breeding success due to treatment), powers of up to 99% were recorded for both larger and smaller colonies (Table 2).

Effect of disturbance, colony size and nest position

Two-way contingency table analysis revealed that experimental treatment and colony size both significantly influenced hatching success and chick survival (Table 3), whereas nest position (i.e. whether peripheral or central) did not.

Despite this strong effect due to experimental treatment and colony size, there was no interaction between these variables (Fig. 1; for hatching success $\chi^2 = 0.27$, d.f. = 2, $p = 0.87$; for chick survival $\chi^2 = 0.33$, d.f. = 2, $p = 0.84$). Nevertheless, the effect of disturbance treatments on both hatching success and chick survival was exacerbated by colony size, with lower breeding success at smaller colonies.

Table 2. Chi-square and power analysis results for differences in hatching success and chick survival between experimental treatments

Power results have been subject to sensitivity analysis by arbitrarily altering the magnitude of critical effect sizes. Power in relation to three critical effect sizes is shown. Effect sizes are: (i) the actual effect size detected from my data; (ii) a small effect of 0.2; and (iii) a medium-sized effect of 0.5. Hypothetical power calculations are based on the sample sizes used in this study. As a result they are only calculated once to apply to both hatching success and chick survival. The degrees of freedom in each case are one.

Colony size	Paired variables	χ^2	p	(i) Power (%) associated with the actual effect size shown in Table 1	(ii) Power (%) with a hypothetical effect size of 0.2 (i.e. a 20% reduction in breeding success due to treatment)	(iii) Power with a hypothetical effect size of 0.5 (i.e. a 50% reduction in breeding success due to treatment)
Hatching success						
Smaller	Control*Recreation	18.6	<0.01	98	45	99
	Control*Nest check	12.6	<0.01	92	45	99
	Recreation*Nest check	0.8	NS	10	40	99
Larger	Control*Recreation	2.1	NS	34	65	99
	Control*Nest check	0.7	NS	4	65	99
	Recreation*Nest check	0.5	NS	16	70	99
Chick survival						
Smaller	Control*Recreation	24.2	<0.05	99		
	Control*Nest check	22.2	<0.05	99		
	Recreation*Nest check	0.3	NS	40		
Larger	Control*Recreation	2.7	NS	27		
	Control*Nest check	0.1	NS	2		
	Recreation*Nest check	2.0	NS	20		

Table 3. Two-way contingency table analysis of hatching success and chick survival against three independent variables: experimental treatment, colony size and nest position

Breeding success parameter	Source	d.f.	Chi square	P
Hatching success	Experimental treatment	2	14.19	0.001
	Colony size	1	47.00	0.001
	Nest position	1	0.38	0.53
Chick survival	Experimental treatment	2	9.01	0.01
	Colony size	1	90.23	0.001
	Nest position	1	1.85	0.17

Causes of egg loss

Likely causes of egg loss for all colonies are shown in Fig. 2. In the smaller colonies subjected to recreation visits and nest checking, predation by south polar skuas occurred significantly more often than in the smaller control colony ($\chi^2 = 14.1$, d.f. = 2, $p < 0.01$, Fig. 2). There were not enough instances of egg loss in the larger colonies to perform statistical analysis.

Predation pressure by skuas at Rookery Lake was relatively intense throughout the breeding season. Approximately 15 breeding pairs occupied territories near penguin colonies. In addition to this, a large melt pool, 1 km from the study site, was regularly used as a roost and bathing area for up to 50, predominantly non-breeding, birds at a time. It is therefore likely that

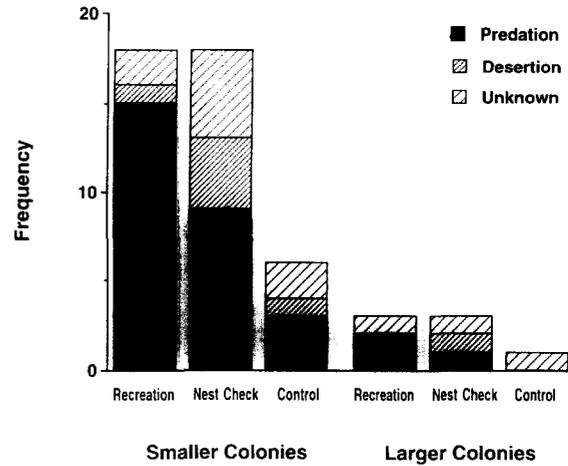


Fig. 2. Causes of egg loss during the incubation phase expressed as the number of individual cases of predation, desertion and unknown cause.

the intensity of skua predation at Rookery Lake was much greater than that exerted by just 15 breeding pairs. A conservative estimate of 30 pairs of skuas foraging predominantly on the Rookery Lake colonies results in a ratio of 215 penguin pairs per skua pair.

DISCUSSION

Effects of nest checking and recreational visits on breeding success

This study shows that the breeding success of adelic penguins in smaller colonies can be significantly affected by human disturbance in the form of regular nest checking and recreational visits. Results for both hatching success and chick survival were associated with high statistical powers (in smaller colonies), suggesting that trends were true in nature rather than artefacts of the experimental design.

Breeding success at larger colonies followed the same pattern of response to disturbance as smaller colonies; however, in larger colonies differences due to treatment were not statistically significant. These results reflected a small critical effect size and were associated with low statistical powers, indicating that the current design had a limited ability of detecting small (subtle) effects due to treatment. When effect size was arbitrarily set at 0.2 (reflecting a 20% reduction in breeding success due to disturbance), statistical power for tests between larger colonies increased to a maximum of 70%. Consequently, if investigators were hoping to detect a 20% reduction in breeding success due to disturbance, they could apply the current experimental design for larger colonies and be 70% certain of detecting a significant result should one exist. When effect size was increased even further to 0.5 (a medium sized effect), statistical power rose to 99% in both large and small colonies. These results illustrate the relationships between sample size, effect size and statistical power, where only larger, more dramatic, effects can be detected with a high level of confidence from even relatively small sample sizes (Kraemer & Thiemann, 1989).

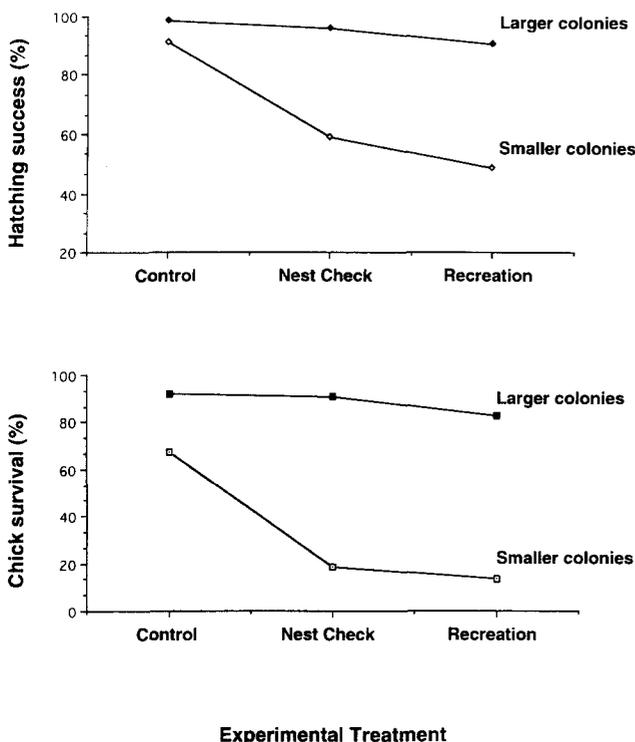


Fig. 1. Variation in breeding success across three treatments representing varying levels of disturbance: control, nest checking and recreation. Treatments were replicated over two colony classes (larger and smaller). Breeding success is expressed as hatching success and chick survival.

Causes of egg loss

In this study, predation by skuas was the most likely cause of egg loss in smaller colonies exposed to disturbance. The proportion of skuas to penguins at Rookery Lake was much higher than at other sites, such as Cape Hallet (72°18'S; 170°13'E), where there were 350 penguin pairs per skua pair (Maher, 1966) and 439 penguin pairs per skua pair (Trillmich, 1978). Penguins at Rookery Lake were therefore subject to relatively intense levels of skua predation.

Human disturbance can affect predation by increasing the opportunities for predators to procure prey. Some predators of gulls, for example, show evidence of learning to associate human disturbance with increased access to prey, either during disturbance (Kury & Gochfeld, 1975) or immediately after it (Gotmark & Ahlund, 1984). Penguin colonies that are disturbed might also be less able to resist predator attacks (Young, 1990) and this might be because disturbance acts to attract skuas (Stonehouse, 1965).

Investigator disturbance has been reported for a number of seabirds (Cairns, 1980; Safina & Burger, 1983), but is infrequently documented for adelic penguins. At Cape Crozier (77°29'S; 169°34'E), however, penguins with a history of disturbance from scientific activities had lower breeding success than those with no such history (Oelke, 1975). Similarly, birds exposed to daily nest checks throughout the breeding season at Cape Bird (77°13'S; 166°28'E) had lower breeding success than control colonies visited only twice over the same period (Davis, 1982). This result was not statistically significant and was attributed to higher skua predation around disturbed colonies. At present, the role of human disturbance in attracting skuas to adelic penguin colonies is not clear and requires further investigation.

Human disturbance can also affect egg loss by exposing nest contents to the elements, thereby accelerating egg cooling. When adelic penguins are approached, they usually rise off their nests, and temporarily expose eggs and chicks. Ambient temperatures in Antarctica even in mid-summer, can cause rapid egg cooling up to a rate of 0.07°C/s (Derksen, 1977).

In this study, colonies exposed to recreational visits consistently had the lowest breeding success of all colonies in both size classes. This result was surprising, since nest checking would be expected to represent a higher intensity disturbance event for an individual bird.

At Rookery Lake, birds exposed to recreational visits were disturbed for between 20 and 40 min every day of the breeding season, representing a visitor frequency of between four and eight times that of the nest-check and control colonies. Relationships between the frequency of disturbance and reductions in seabird breeding success have been reported for black skimmers *Rhynchops niger* (Safina & Burger, 1983) and auklets (Piatt *et al.*, 1990). These results were attributed to the increased exposure of nest contents to predators, conspecifics and thermal stress. In this study, egg cooling during regular visits had an unknown effect on egg survival, but it is possible that the frequency of visitation,

rather than the type of intrusion, was the critical factor influencing breeding success.

The relationship between colony size, nest position and the causes of egg loss

Few studies have documented the influence of colony size on breeding success in adelic penguins, but results from this study suggest that it affects the manner in which individuals within colonies respond to human disturbance. Oelke (1975) found highest breeding success in colonies of between 20 and 175 breeding pairs and lowest breeding success in colonies with fewer than 20 nests. Lower breeding success in smaller colonies is often explained by the higher proportions of peripheral nests to central nests resulting from area to perimeter relationships. Long-term studies of adelic penguins indicate that peripheral nest sites are often occupied by younger birds who lack the experience to compete for favoured, central nesting positions. Observed differences in breeding success between edge and central nesting penguins might be due to age-related factors of breeding and also feeding experience (Spurr, 1973). In addition, peripheral birds might be subject to higher predation and interference from conspecifics (Tenaza, 1971).

These phenomena, however, probably do not explain the differences in the performance of larger and smaller colonies in this study. Although larger and smaller colonies differed significantly in the number of nests, there was no difference in the proportion of peripheral to central nests between colonies. Consistent with this was the fact that two-way contingency table analysis revealed no significant effect due to nest position on either hatching success or chick survival, irrespective of colony size. Rather, smaller colonies in the present study probably performed worse because they were below some critical size threshold which negated the benefits usually associated with occupying central nest positions, particularly in relation to excluding skuas (Tenaza, 1971). If disturbed colonies do have difficulty withstanding predator attacks, then a smaller colony size would compound this effect.

The age composition of colonies can also influence breeding success. It is not possible to estimate how age composition may have contributed to results in this study. Smaller colonies are sometimes thought to be new colonies comprising a high proportion of young birds (Tenaza, 1971) and it is possible that age-related inexperience contributed to the poor performance at smaller colonies here. The absence of a significant difference between colonies in the mean weight of birds returning from the first incubation shift, suggests, however, that the birds did not vary considerably in feeding ability, which is also thought to be age-related (Ainley & Schlatter, 1972).

Methods of measuring breeding success in adelic penguins with minimal human disturbance

Regular nest checking probably produces the most accurate record of breeding success in the adelic penguin,

but in small colonies this method can significantly interfere with reproduction. Deciding on methods of measuring breeding success will ultimately be a trade-off between achieving accuracy while gathering information, and minimising disturbance. Some information will inevitably be lost the less frequently a nest is examined, but less frequent visits may produce more meaningful results since these results will not be an artefact of human disturbance.

Estimating overall nest success from counts of occupied nests can be a relatively accurate way of assessing breeding success without significantly disturbing animals. After comparing multiple visit methods (regular nest-checking) with planned visit methods (counts made of the number of active nests coinciding with peaks in laying, hatching and fledging), Mousseau (1984) concluded that the planned visit method offered a more accurate reflection of reproductive performance than other techniques because investigator disturbance was not significant.

Adelie penguins lend themselves to the planned visit method for two reasons. First, they occupy open colonies where individual nests are well spaced according to a regular, social pattern, making it possible to partition and count even quite large colonies. Second, adelie penguin breeding is controlled by stereotyped patterns of colony occupation, such that counts could be accurately timed to coincide with peaks in laying, hatching and fledging.

Future research

Human presence in Antarctica is more likely to expand than it is to contract, placing great importance on the establishment of management guidelines that minimise the impacts of human activities. Penguins respond to disturbance according to gradational, dose-response relationships (see Anderson, 1988), suggesting that it should be possible to identify those human activities that elicit acceptable levels of disturbance and those which exceed acceptable levels. Ultimately, these levels will not be set by science alone but will be influenced by social, ethical, economic and political factors. Nevertheless, carefully designed experiments, comparing responses under 'natural' and 'unnatural' breeding conditions, can provide unambiguous guidelines for managers.

The present study shows that nest checking and recreational visits can significantly reduce breeding success in small adelie penguin colonies. Although the relationship between breeding success, disturbance and colony size was highly significant, these results would benefit from a greater level of replication at the colony level.

The relationship between disturbance, predation and colony size also requires further investigation, most appropriately from intensive behavioural observations. The implications of repeated thermal stress for overall breeding success are unclear and should be examined, since this will influence how frequently visitors will be allowed into colonies. The use of control colonies will be fundamental to any future human impacts research, but methods of obtaining this information without causing disturbance need to be more thoroughly examined.

Deciding on the magnitude of observed response that constitutes a significant effect due to disturbance will also be fundamental to future research on the impacts of human activity on Antarctic wildlife. Commonly, concern and subsequent management is only initiated when dramatic responses to disturbance are reported, such as a 50% reduction in the breeding success of a wild population. Effects of this size are usually statistically significant and relatively easy to detect through experimentation, but they can exceed levels of biological significance, sometimes by orders of magnitude. Decisions therefore have to be made as to the size of the critical effect one wishes to detect prior to beginning research projects. The magnitude of critical effects will be species- and situation-specific such that for some species relatively small effects will be biologically critical and might warrant a management response.

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