Antarctic Science 10 (4): 449–454 (1998)

Spatial relationships of Adélie penguin colonies: implications for assessing population changes from remote imagery

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Abstract: The relationship between colony area and population density of Adélie penguins *Pygoscelis adeliae* was examined to determine whether colony area, measured from aerial or satellite imagery, could be used to estimate population density, and hence detect changes in populations over time. Using maps drawn from vertical aerial photographs of Adélie penguin colonies in the Mawson region, pair density ranged between 0.1 and 3.1 pairs m^{-2}, with a mean of 0.63 ± 0.3 pairs m^{-2}. Colony area explained 96.4% of the variance in colony populations (range 90.4–99.6%) for 979 colonies at Mawson. Mean densities were not significantly different among the 19 islands in the region, but significant differences in mean pair density were observed among colonies in Mawson, Whitney Point (Casey, East Antarctica) and Cape Crozier (Ross Sea) populations. The relationship between colony area and population may be locality- and/or species-specific, and a robust data set is required to validate the relationship.

Received 22 October 1997, accepted 14 April 1998

Key words: Adélie penguin, Mawson, population change, population monitoring, remote sensing

Introduction

Adélie penguins *Pygoscelis adeliae* are the most widely distributed penguin species around the Antarctic continent, with an estimated population of approximately 2.5 million pairs (Woehler 1993, Woehler & Croxall 1996). The current focus on the role of Adélie penguins in the Southern Ocean ecosystem, and the concomitant interest in monitoring their populations around the Antarctic (Agnew 1997), has stimulated an increasing interest in the use of remote-sensing methodologies for monitoring populations at broader scales. Local population changes in colonies associated with stations or research facilities may be due to human disturbance (eg. Fraser & Trivelpiece 1994, Woehler *et al.* 1994). There is clearly greater value in documenting changes in penguin populations and trends on regional scales (eg. Antarctic Peninsula: Croxall & Kirkwood 1979, Ross Sea: Taylor *et al.* 1990, Prydz Bay: Whitehead & Johnstone 1990) by using alternative methodologies such as aerial photography (Taylor *et al.* 1990, Guinet *et al.* 1995) and satellite imagery (Bhikharidas *et al.* 1992, Bhikharidas & Peterson 1993, Guinet *et al.* 1995). The detection of population changes using these alternative technologies are dependent on assumptions of area-population ('density') relationships that have yet to be examined (but see Taylor *et al.* 1990). For example, Guinet *et al.* (1995) reported a 66% increase in the population of king penguins *Aptenodytes patagonicus* at the Iles Crozet based on differences in colony extent in aerial and satellite photographs 26 years apart, assuming a constant density of penguins within the colony concurrent with the increase in area.

This study examines the variability in the relationship between area and breeding population size of Adélie penguin colonies in the Mawson region, East Antarctica. The aim of the present study is to identify sources of variability (methodological and intrinsic), and to quantify these variabilities in estimating the density of pairs within colonies, thus addressing the broader issue of monitoring population changes by the use of remote sensing technologies. By quantifying this variability, preliminary estimates are then derived of the number of replicates required to identify population change by measuring changes in colony areas.

Methods

Study region

The total breeding population of Adélie penguins in the Mawson region (67°35'S, 62°45'E), East Antarctica was estimated at 82 500 ± 10% pairs in 979 colonies in 1988–89 (Woehler *et al.* 1989). The number of colonies on an island ranged between three and 321, and the total population on islands ranged between 79 and 21 994 pairs (Woehler *et al.* 1989), Fig. 1. For mapping and digitizing purposes, colony data (area and perimeter) were obtained from maps drawn from vertical aerial photographs taken in the Mawson region in December 1988 at an altitude of 500 m (Woehler *et al.* 1989). In drawing these maps, colony perimeters were taken to be the outermost penguins present within each colony, joined with a straight line, and discontinuities in ornithogenic soil were used to demarcate colonies.

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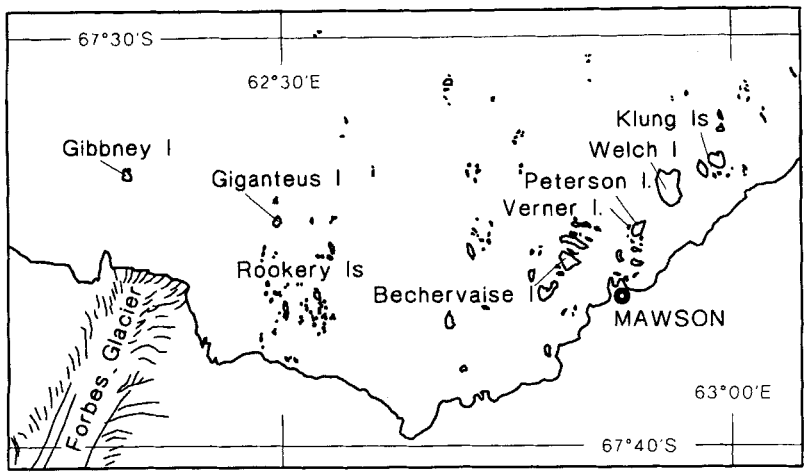


Fig. 1. Map of the Mawson region showing islands mentioned in text.

Analyses

Boundaries of all Adélie penguin colonies were digitized with AutoCAD® 13 (Autodesk Inc. 1995) at a scale of 1:10 000. Area (m^2) and perimeter (m) data were obtained for 979 colonies on 19 islands. Preliminary tests for normality and homogeneity of variances established that the density data (pairs m^{-2}) were positively skewed and highly leptokurtic. Kruskal-Wallis non-parametric ANOVA was used to test whether Adélie penguin colony densities differed statistically between islands, and Student-Newman-Keuls multiple range tests were used to group islands based on colony densities. Power analyses were then used to estimate sample sizes required to detect 1%, 5%, 10% and 20% changes in colony area with a 95% probability, based on variances obtained from five replicates of eight colonies' areas. The populations of these eight colonies ranged between 6 and 616 pairs, a range embracing more than 96% of the colonies measured for this study. Statistical tests were conducted using the BIOΣTAT I and III packages (Pimental 1991, 1994), and all means are reported ± 1 s d.

Table I. Summary statistics for Adélie penguin colonies on 19 islands at Mawson.

Island	Number of colonies	Total population pairs	Mean density pairs m^{-2}	s d	s e	CV
Béchervaise	26	679	0.893	0.531	0.104	0.595
Gibbney*	51	19324	0.617	0.196	0.027	0.318
Giganteus	78	6795	0.860	0.453	0.051	0.527
Klung	89	3018	0.654	0.285	0.030	0.436
Peterson	4	614	0.917	0.251	0.126	0.274
Rookery	196	21994	0.627	0.324	0.023	0.517
Rookery 2	59	4117	0.608	0.259	0.034	0.426
Rookery 3	50	1200	0.511	0.228	0.032	0.446
Rookery 4	6	252	0.694	0.168	0.069	0.242
Rookery 5	10	738	0.651	0.173	0.055	0.266
Rookery 6	7	3047	0.736	0.174	0.065	0.237
Rookery 7	25	2364	0.826	0.370	0.074	0.448
Rookery 9	6	2767	0.697	0.125	0.051	0.179
Rookery 10	8	189	0.577	0.327	0.116	0.567
Rookery 11	3	409	0.576	0.265	0.154	0.460
unnamed Forbes	5	1421	0.578	0.206	0.092	0.356
unnamed Klung	4	79	0.393	0.321	0.160	0.816
Verner	31	1232	0.824	0.415	0.075	0.504
Welch*	321	11328	0.536	0.272	0.015	0.507

s d is standard deviation, s e standard error and CV the coefficient of variation (mean/standard deviation).
*indicates that not all colonies on the island were measured in this study

Results

Nest – area relationship

The density of pairs within colonies ranged between 0.1 and 3.1 pairs m^{-2}, with a mean of 0.63 ± 0.33 pairs m^{-2}, and a median density of 0.59 pairs m^{-2} (Fig. 2). Island mean densities ranged from 0.39 pairs m^{-2} on an unnamed island west of Klung I with four colonies to 0.92 pairs m^{-2} on Peterson I, with four colonies (Table I). Excluding the islands

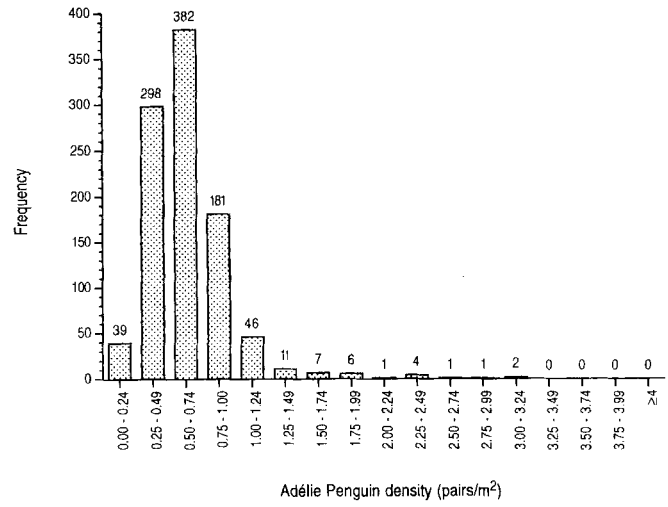


Fig. 2. Frequency distribution for breeding pair densities (pairs m^{-2}) for 979 Adélie penguin colonies in the Mawson region in the 1988–89 season, in 0.25 m^2 increments. Frequencies shown for each bin.

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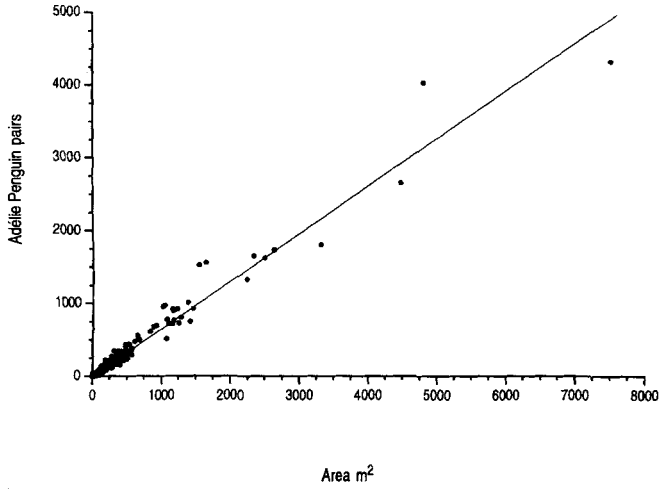


Fig. 3. Relationship between colony area (m^2) and colony population (breeding pairs) for 979 Adélie penguin colonies in the Mawson region in the 1988–89 season.

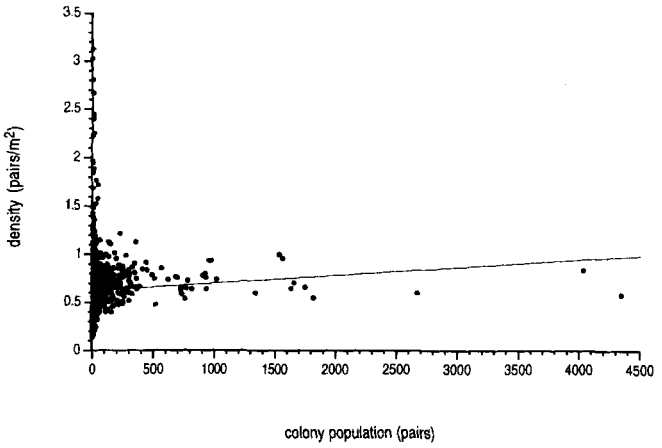


Fig. 4. Relationship between colony population (pairs) and density per colony (pairs m^{-2}) for 979 colonies in the Mawson region in 1988–89. The relationship is not significant.

with only three or four colonies, colony area explained between 90.4% (Verner) and 99.6% (Gibbney, Rookery 7 and Rookery 9) of the observed variance in colony population (Fig. 3). In the Mawson region, colony area explained 96.4% of the measured variance in colony populations ($n = 979$).

The variance of pair densities was not correlated with the total population on each island ($r = 0.052$, $n = 19$), but was significantly, positively correlated with mean pair density per island ($r = 0.489$, $0.05 > P > 0.02$). The mean density of pairs and the number of colonies on an island were not correlated ($r = 0.176$, $n = 19$), and the mean density of pairs was not correlated with the total breeding population on each island ($r = 0.121$, $n = 19$). Pair density was not correlated with colony population (Fig. 4, Fig. 5).

Comparison with earlier studies

There are two data sets on pair densities in Adélie penguins, but both have small sample sizes. Penney (1968) estimated area and nesting density for 11 colonies at Whitney Point (66°15'S 110°32'E), Wilkes Land for the 1959–60 season, expressing his data as area (m^2) per pair. Converting his data to pairs m^{-2} results in a mean density of 1.4 ± 0.28 pairs m^{-2}, a density that is more than double that for the Mawson region obtained here. The second study gave a mean pair density of 0.9 ± 0.31 pairs m^{-2} for eight colonies (Oelke 1975). Both of these mean densities are significantly different from those at Mawson (SNK: $Q = 3.319$ and $Q = 2.775$, respectively, both $P < 0.05$) and from each other (SNK: $Q = 2.775$, $P < 0.05$).

Power analyses

The number of replicates required to detect changes in colony area covaried with colony area and the magnitude of the difference in area to be detected, with an exponential increase in the number of replicates required as both colony size and area difference to be detected decrease (Fig. 6). Thus, using maps generated at 1:10 000 scale, to detect a 1% change in area with 95% probability, 52 area replicates are needed for a colony occupying an area of 100 m^2. The required number of replicates decreases rapidly with an increase in the change in area to be detected: 5% ($n = 5$), 10% ($n = 4$) or 20% ($n = 3$). To detect similar changes in a colony of 800 m^2, the detection

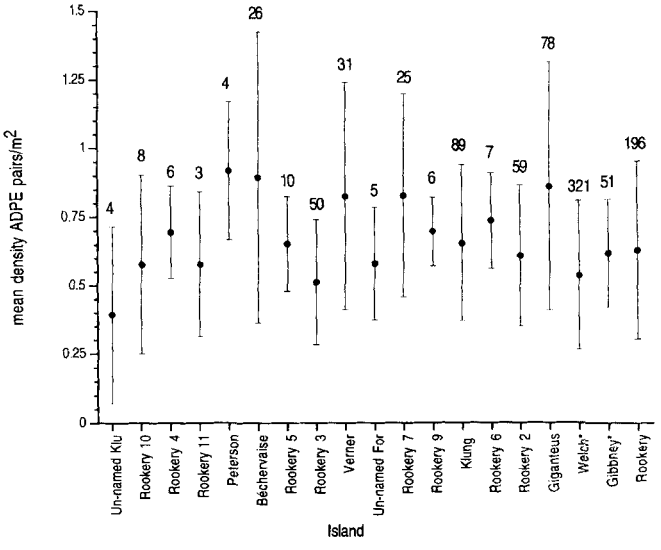


Fig. 5. Mean density of Adélie penguin pairs ± 1 s d (pairs m^{-2}) for the 19 islands in the Mawson region in 1988–89. Means ± 1 s d, ordered by breeding population size (pairs). The number of colonies on each island are shown, and the * indicates that not all colonies on Welch and Gibbney islands were measured.

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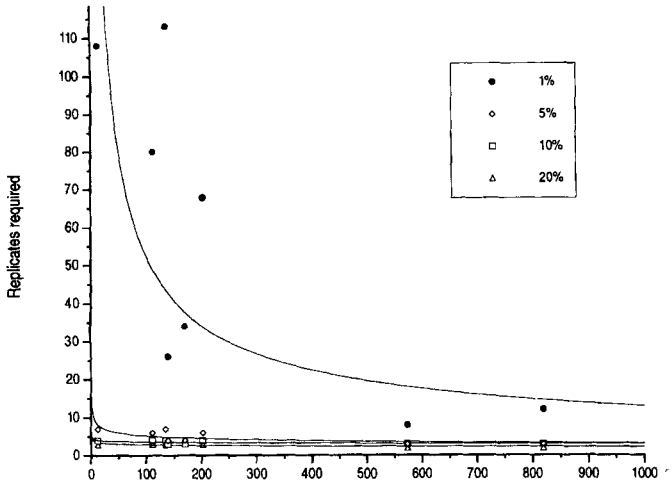


Fig. 6. Replicates required to determine 1% (●), 5% (◊), 10% (□) and 20% (Δ) changes in colony area with 95% certainty, based on 5 replicates of 8 colonies (see Methods). The relationships for 1%, 5% and 20% are all significant (1%: $r = 0.768$, 5%: $r = 0.766$, 20%: $r = 0.603$, all $0.05 > P > 0.02$), while the 10% relationship is not ($r = 0.603$, $P > 0.05$).

of a 1% change in area requires 15 replicates, and as before, this decreases with an increase in the area difference to detect: 5% change (3 replicates), 10% (3) or 20% (2). The number of required replicates is independent of the trend in colony area: differences in colony extent can be positive (colony growth) or negative (colony decrease).

Discussion

Limitations of the current data set

The present study is limited to a large data set from one species in one region in one year. At present there is no time series of photographs available to test whether changes in colony populations would have been detected from measurement of colony area alone. These limitations prevent an assessment of the applicability of the results obtained in the Mawson region to breeding populations of Adélie penguins elsewhere in the Antarctic. Breeding populations of Adélie penguins exhibit fluctuations over a wide range of temporal scales, ranging from intra-seasonal to decadal. At present there are no data to test whether there are changes in colony density associated with these population fluctuations. We are presently unable to describe the relationship between a colony's population and its density with time, or how the relationship behaves with changes in colony population. Despite these constraints, the results obtained for the colonies in the Mawson region are consistent with results obtained at Whitney Point, in that nesting density increased with increasing colony population (Fig. 4 and Evans 1991). This relationship is not significant, but a significant population-area relationship may be obtained for Adélie penguins with a more accurate area data set in the future.

There are methodological limitations. The percentage error associated with the digitizing of the colony boundaries will remain the same irrespective of the mapping scale used, but the density estimates generated will be more accurate for larger colonies than for small colonies at the same scale. For example, at a scale of 1:1000, a 10% error in the colony area estimate will result in a greater error than at a scale of 1:10 000. Further, the methodological error in digitizing the colony boundaries that is incorporated into calculating density estimates will decrease with increasing colony area.

The shape of the curves obtained by power analysis are derived from the variances obtained in this study, and thus the curves obtained here (Fig. 6) are applicable only to the current data, and are dependent on the scale used for mapping. Other data sets obtained from aerial photographs at other scales will be characterized by different variances and the curves obtained in other studies will determine the number of replicates required to detect changes in other colonies at other sites.

Comparison with previous studies

The difference between the mean pair densities obtained here and in Penney's study are remarkable, given Penney's mean density is nearly 2.2 times that calculated for the colonies in the Mawson region, and more than 1.5 times that at Cape Crozier. Penney calculated the areas occupied by colonies by tape measure transects through the colonies before they were occupied; no further details are provided. Penney (1968) and Oelke (1975) gave no details on what method(s) were used to estimate colony areas.

Since Penney surveyed the colonies at Whitney Point, the population has increased from 1122 pairs in 14 colonies in 1959–60 to 4714 pairs in 36 colonies in 1992–93 (Woehler *et al.* 1994), and has continued to increase (E.J. Woehler unpublished data). Ten of the 14 colonies have increased in area concurrent with increase in population (Woehler *et al.* 1994), and it was noted that the rate of increase in the colonies at Whitney Point was related to the age of the colony, with older colonies increasing less rapidly than more recently established colonies (Woehler *et al.* 1994).

One possible scenario is that the Whitney Point colonies were at a 'saturation' density in 1959–60 when originally surveyed, and the population increase has occurred through the establishment of 22 new colonies in preference to an increase in area or density of those colonies extant in 1959–60. Topography constrains approximately two thirds of the colonies at Whitney Point (Evans 1991), and one hypothesis is that the observed population increase since 1959–60 could only occur with the establishment of new colonies, rather than expanding or increasing the density of colonies present in 1959–60. In contrast, the colonies at Cape Crozier were decreasing at the

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time of Oelke's study, and may represent a density characteristic of colonies whose population is decreasing. At present, such propositions are highly speculative, and will remain so until sufficient temporal data are available to examine density-area relationships within and among localities, and how the relationship changes with time, if it does at all.

Alternatively, the difference in mean densities between Whitney Point and colonies in the Mawson region may be due to methodological differences used to calculate colony areas. This study made use of aerial photographs on which colony boundaries are easily determined, while Penney measured colony extents along an unrecorded number of transects through colonies. Oelke (1975) only measured colonies with populations between 17 and 42 pairs, and may have biased his calculations by the use of a small sample size and small colony sizes. At least some of the difference among means from the three localities (Mawson region, Whitney Point and Cape Crozier) must result from the different methods used, but the magnitude of these difference cannot be determined.

The final alternative hypothesis is that the observed differences are real, and reflect regional differences in behaviour, topography or some other determinant(s), or a combination of them, that affect nesting density of Adélie penguins at different breeding localities. Until more data are available from a wider range of localities, we are unable to offer generalizations on the relationship between colony population and colony size, and the effect of various parameters on the relationship.

Considerations for assessing population growth

Ainley *et al.* (1995) argued that aggregative factors in Adélie penguins such as colony philopatry and social facilitation leading to breeding synchrony at the metapopulation level over-rode dispersive tendencies to avoid prey depletion through competition. They argued that at the metapopulation scale, which includes all individuals in the population such as pre-breeders, failed breeders and breeding individuals, this unequal relationship between dispersive and aggregative tendencies resulted in highly clustered Adélie penguin colonies. At finer scales (at the individual colony level), Evans (1991) showed that the topography of the breeding locality influenced the ultimate area of, and density of Adélie penguin pairs within, a colony. Such results indicate that a range of forces operating over a wide spectrum of temporal and spatial scales determine where and when colonies are established and their resulting growth.

Populations (within colonies) of Adélie penguins can increase in one of three ways:

1) an increase in the area of the colony while the nesting density remains constant,
2) the area occupied by the colony and the nesting density increase, and
3) the area occupied by the colony remains the same but the nest density increases.

Clearly these three possibilities have serious consequences for identifying population changes by the use of aerial or satellite imagery to obtain colony areas. Further, based on the results from Whitney Point over a 30 year period, the age of a colony may influence population–area relationships (Woehler *et al.* 1994).

At present there are no time series of aerial photographs available over a 10 or 20 year time period against which to test these scenarios. However, an analysis of the nearest-neighbour distances within 35 Adélie penguin colonies at Whitney Point showed that the mean nearest-neighbour distance within a colony decreased with increasing colony population, ie a density-dependent relationship existed within these colonies (Evans 1991). The inverse relationship was significant and non-linear ($r = -0.459$, $0.005 > P > 0.002$), irrespective of the topographical constraints imposed upon the shapes and sizes of colonies. As the colonies increased in population, they became more densely packed. These results are consistent with data from maps of Whitney Point showing most colonies present in 1958/59 had increased their areas only slightly between 1958–59 (Penney 1968), 1989–90 (Woehler *et al.* 1994) and 1992–93 (E.J. Woehler unpublished data), despite the total population of Adélie penguins in the area increasing more than four-fold, and where the majority of the population increase has been in the establishment of 22 new colonies (Woehler *et al.* 1994, E.J. Woehler unpublished data). Based on these results, it would be difficult to establish a population change within a colony based simply on a change in area or perimeter. Further, diurnal (Wilson *et al.* 1989) and intra-seasonal (Penney 1968) fluctuations in colony attendance must be incorporated into colony population calculations.

If the results of Evans (1991) are consistent among other breeding populations of Adélie penguins, we would expect a positive slope to the correlation between colony population and density (ie as population increases, so the density increases). For the Mawson colonies investigated here (Fig. 4) the correlation is positive, despite the non-significance of the relationship. This result suggests that a generalization of Evans' results may be possible for comparable data from other localities.

It is possible that different penguin species' colonies will 'behave' in different manners, depending on topography and behaviour. Thus, it is likely that the relationship between colony area and population size may be locality-specific and/or species-specific. Clearly, density data (pairs m^{-2}) are fundamental to attempts to monitor penguin populations using aerial and satellite imagery with the aim of determining the status and trends of the population(s) under investigation. If a population increases in size without a concurrent increase in density, then aerial or satellite imagery can be used to estimate colony area (m^2) and a multiplier (pairs m^{-2}) can be applied to estimate population size (breeding pairs). Similarly, if a

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colony increases in density without an increase in area occupied, the colony area and its density are required to estimate population size. For both of these scenarios, aerial and satellite imagery can be applied at present scales of resolution. However, if a colony increases in area and in density, a far greater effort will be required before estimates of population size, and from them statements of population trends, can be made.

Monitoring reference colonies is not sufficient in itself to detect population changes in Adélie penguins, as the establishment and loss of colonies will play an important role in regional population dynamics. In order to comprehend fully these dynamics, other colonies within the region will need to be surveyed to detect changes in the number and distribution of colonies, and in their populations. Regional monitoring schemes using remote sensing methods are likely to be used with greater frequency in the future to determine changes in Antarctic and Subantarctic penguin populations.

Acknowledgements

We thank John Cox for preparing the map, and Lee Belbin, Judy Clarke, Bill Fraser, Knowles Kerry, Graham Robertson, Barbara Wienecke and Peter Wilson for their comments on the draft of this manuscript.

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