THE EFFECTS OF HUMAN ACTIVITY AND ENVIRONMENTAL VARIABILITY ON LONG-TERM CHANGES IN ADÉLIE PENGUIN POPULATIONS AT PALMER STATION, ANTARCTICA

by

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ABSTRACT

Human activity associated with tourism and research along the western Antarctic Peninsula has increased significantly over the past 25 years and predictions are this trend will continue. The potential effect these activities may have on wildlife populations has thus become an important wildlife conservation issue because wildlife and human activity tend to converge on the same ice-free areas. To examine if human activities due to tourism and research were negatively impacting Adélie penguins (*Pygoscelis adeliae*), I undertook a study that compared long-term population trends and other demographic parameters at visited and non-visited (control) sites on Torgersen Island, a popular destination near Palmer Station, Anvers Island.

A necessary prerequisite for detecting human impacts on wildlife populations is an understanding of the underlying factors associated with natural demographics. Recent evidence suggests that variability in Adélie penguin demography may be due in part to interactions between the topography of the breeding habitat and patterns of snow deposition. To test this idea, I developed a hillshade model of the island and used regression and discriminant function analyses (DFA) to examine population/landscape interactions. I then applied the results of these analyses to human impact questions.

Results suggest that population trends on Torgersen Island are strongly affected by colony aspect and colony area. Colonies with south-facing aspects are decreasing faster than colonies with north-facing aspects. Smaller colonies are also decreasing faster than larger colonies. Both trends are likely due to interactions between the effects of enhanced snow deposition and decreasing egg/chick survival due to predation and flooding.

To look for possible human effects, I paired colonies by area and aspect on visited and control sides of Torgersen Island. Tourism appears to be having no detectable impact on Adélie penguin breeding population size or breeding success on Torgersen Island; comparisons between population trends in visited and control sides of the island were either not significant or inconsistent with site-specific tourist visitation patterns. Some types of research, however, especially when associated with small colonies, may be detrimental to the long-term survival of these colonies.

INTRODUCTION

Human presence in Antarctica has historically been associated with negative, often devastating, effects on wildlife populations. Following the initial wave of exploration more than two centuries ago, first sealers and then whalers harvested many species of marine mammals to near-extinction (Bond and Siegfried 1979, Knox 1994). The sealing and whaling stations built to support the commercial harvest, especially in wildlife-rich areas such as South Georgia, Macquarie Island and the Antarctic Peninsula (e.g., Port Lockroy, Wiencke Island; Whaler's Bay, Deception Island), also had negative effects on surrounding seabird communities. Penguins by the tens of thousands were slaughtered for the production of unique oils or used to fuel the boilers that rendered oil from seals. Egging and hunting to supply food to the crews manning the stations also took a toll, and the resulting cumulative impacts led in many cases to the decimation of seabird populations at local to regional scales (Cawkell and Hamilton 1961, Croxall et al. 1984, Rounsevell and Brothers 1984, Culik et al. 1990, Woehler and Johnstone 1991).

Although the focus of human activities has shifted during the last 50 years from the exploitation of wildlife populations to scientific research and tourism, concerns about the real and potential impacts of anthropogenic activities still remain. These concerns are not unfounded. Where nesting areas were destroyed to facilitate station construction, as occurred in some extreme situations, penguin populations exhibited predictable decreases and only minimal recovery (Culik et al. 1990, Wilson et al. 1990). Gradual shifts by breeding populations of penguins away from research stations have also been documented (Reid 1968, Thompson 1977, Woehler et al. 1994), and an experimental study by Giese (1996) that used station personnel as proxy tourists demonstrated that Adélie penguins (*Pygoscelis adeliae*) exposed to "tourism" had a lower reproductive success and more stress-associated behaviors.

However, to the extent that these observations warrant some concern about how research and tourism may impact wildlife populations, there is also a growing controversy regarding cause and effect. This has developed in response to investigations that reveal patterns unlike those described above. At some localities, for example, penguin populations either remained stable or actually increased following station construction and increased human activity (Young 1990, Parmelee 1992, Acero and Aguirre 1994). A controlled study by Cobley and Shears (1999) on tourist impacts at Port Lockroy, western Antarctic Peninsula, indicates that Gentoo penguins (*Pygoscelis papua*) not only increased dramatically in the area, but also showed no differences in reproductive success at visited and non-visited sites despite the presence of thousands of annual visitors. In a similar study, Fraser and Patterson (1997) demonstrated that there was no correlation between long-term changes in Adélie penguin populations in the vicinity of Palmer Station, western Antarctic Peninsula, and the human use histories of area rookeries. Comparable findings were also reported by Stonehouse (1965) and Taylor et al. (1990), who observed that over the course of long-term monitoring, variability in breeding populations of Adélie penguins in undisturbed control areas followed the patterns seen in areas impacted by human activity.

One benefit of this controversy is that subsequent debates have, in turn, led to the formation of a consensus view within the broader community of scientists, government representatives, environmental groups and tour operators on how to clarify the issue of cause and effect. Three significant components have been recognized.

The first is to understand the nature of the problem and the potential sources of conflict. In Antarctica the activities of both humans and wildlife are focused on a small fraction of the landscape, namely the fringe of ice-free land that surrounds the continent. For wildlife this fringe offers breeding and resting areas, as well as unrestricted access to the marine resources on which most species depend. To humans these same ice-free regions are the prime staging areas for research and associated logistics operations, and the focal point of virtually all tourist activities, which are drawn to these areas due to the presence of wildlife. Sources of conflict are thus defined in terms of potential competition for space as research, and especially tourism, continue to develop (Harris 1991, Enzenbacher 1992).

The second is to incorporate research on human impacts within the broader scope of ecosystem studies. Variability in Southern Ocean ecosystems is strongly coupled to the direct and indirect effects of sea ice conditions, which can affect the demography of seabirds and marine mammals over a range of space and time scales (Testa et al. 1991, Fraser et al. 1992, Emslie et al. 1998, Smith et al. 1999). Except for the rare situations where construction activities may actually alter breeding habitat (e.g., Culik et al. 1990, Wilson et al. 1990), human activity is likely to manifest as an additive or cumulative impact, meaning detection will be difficult unless the causes of natural variability are understood (Fraser and Trivelpiece 1994, Woehler et al. 1994, Fraser and Patterson 1997).

The third is to encourage the development of long-term predator demographic studies to understand and prevent human impacts related to research and tourism. The debate on cause and effect regarding human impacts can partly be traced to conclusions that are based on different scales of measurement (Fraser and Patterson 1997) in which short-term studies that examine responses at the scale of the individual (e.g., Nimon et al. 1995, Giese 1996) are compared to long-term studies that look at change at the colony and population scales (e.g., Wilson et al. 1990, Blackburn et al. 1991, Cobley and Shears 1999, Cobley et al. in press). Previous exposure to disturbance, habituation, age structure, group or colony size and edge effect are but some of the variables that can complicate the comparison and interpretation of such scale-specific studies (van Heezik and Seddon 1990, Wilson et al. 1991). The proposed predator studies, originally implemented in the Southern Oceans to examine the effects of another human activity, commercial fishing (Bengtson 1978, Knox 1994), recognize that long-term demographic data may offer a standard by which to determine if observed variability is due to natural or human-induced factors (Whitehead et al. 1990, Fraser and Trivelpiece 1994, Woehler et al. 1994).

Project Scope and Rationale

The first expedition tour vessels sailed to Antarctica in the early 1960s, but the popularity of expedition touring in this region did not begin to increase until 1970 (Holdgate 1990, Enzenbacher 1992). Since 1970, the annual number of tourists visiting Antarctica has increased nearly ten-fold, exceeding 10,000 during the 1998/99 summer season (NSF 1999). Numbers are not evenly distributed around the continent, however, and it is estimated that 90% of the tourists visit the western Antarctic Peninsula (NSF 1999). The region has become a choice destination for several reasons, but the primary reason is that from the southern tip of South America, access to Antarctica only takes 2-3 days by ship. The presence of international airports and major port facilities also provide key logistical support to ships and their passengers. These are also the reasons that during the past 25 years most countries have built more research facilities on the west side of the Antarctic Peninsula than in any other region of Antarctica (Harris 1991).

Another western Antarctic Peninsula attraction is its wildlife. The peninsula region has a disproportionately greater amount of ice-free land in close proximity to the ocean, which attracts birds and marine mammals in staggering numbers. The opportunity to see penguins is one of the main features bringing tourists into the region, with especially popular locations receiving in excess of 3000 visitors per season (Naveen 1996, NSF 1999). All three *Pygoscelid* penguin species occur here, including greater than 300,000 pairs of Adélie penguins, over 1.1 million pairs of Chinstrap penguins (*P. antarctica*) and nearly 50,000 pairs of Gentoo penguins (Woehler 1993). Penguins occur along the entire length of the western Antarctic Peninsula, and being flightless, tend to nest close to shore, often in large, dense colonies. Apart from being especially conspicuous, nest sites in close proximity to the deep anchorages required by expedition tour ships also makes penguins highly accessible to tourists and potentially vulnerable to disturbance (Culik et al. 1990, Wilson et al. 1991). Penguins are therefore ideal candidates to examine some of the disturbance questions and dynamics presented in the earlier text, and the main reason why I selected Adélie penguins for the research I conducted in the vicinity of Palmer Station, a U.S. research facility on Anvers Island, western Antarctic Peninsula (Fig. 1).

Patterns of Human Activity and the Distribution of Adélie Penguins

Fraser and Patterson (1997) recently summarized the broad patterns of wildlife-human interactions in the vicinity of Palmer Station, thus only the patterns most relevant to my research are presented here. Adélie penguins breed on five island rookeries (Fig. 2) that together held 15,200 breeding pairs when they were first censused in 1975. At the time of this census, these rookeries were open to all forms of human activity, including recreation by station personnel, research and tourism. In 1978, however, Litchfield Island was declared a Specially Protected Area (SPA) under the Antarctic Treaty. The island was thus closed to all recreation and tourism, and remains closed today. In 1990, similar restrictions were imposed on Cormorant, Christine and Humble islands. Research, though still sanctioned on these islands, occurs by permit only, and is restricted to activities that ensure minimum disturbance to wildlife populations.

Torgersen Island, in contrast, has remained basically unencumbered by restrictions since the mid-1970s with one exception, which is illustrated in Figure 3. Due to the terrain, scenery and accessibility, tourists were historically drawn to the north and northeast sides of the island, which coincidentally was also the side where much of the early penguin research in the area took place because of its accessible landing sites and relative proximity to Palmer Station. In 1990, after consultation with researchers involved in long-term research at Palmer Station, this division was made official by the

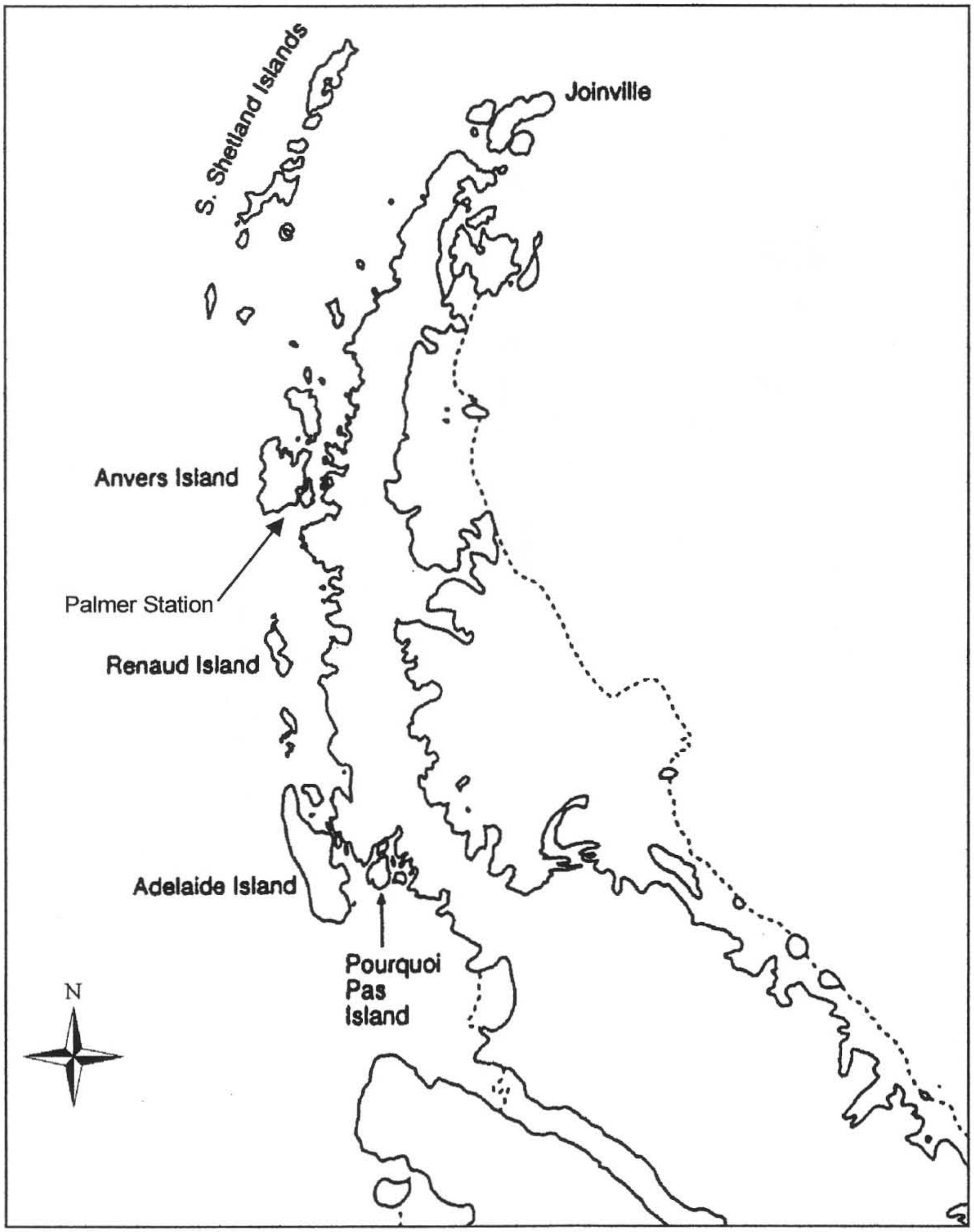

Figure 1. Palmer Station and the Western Antarctic Peninsula.

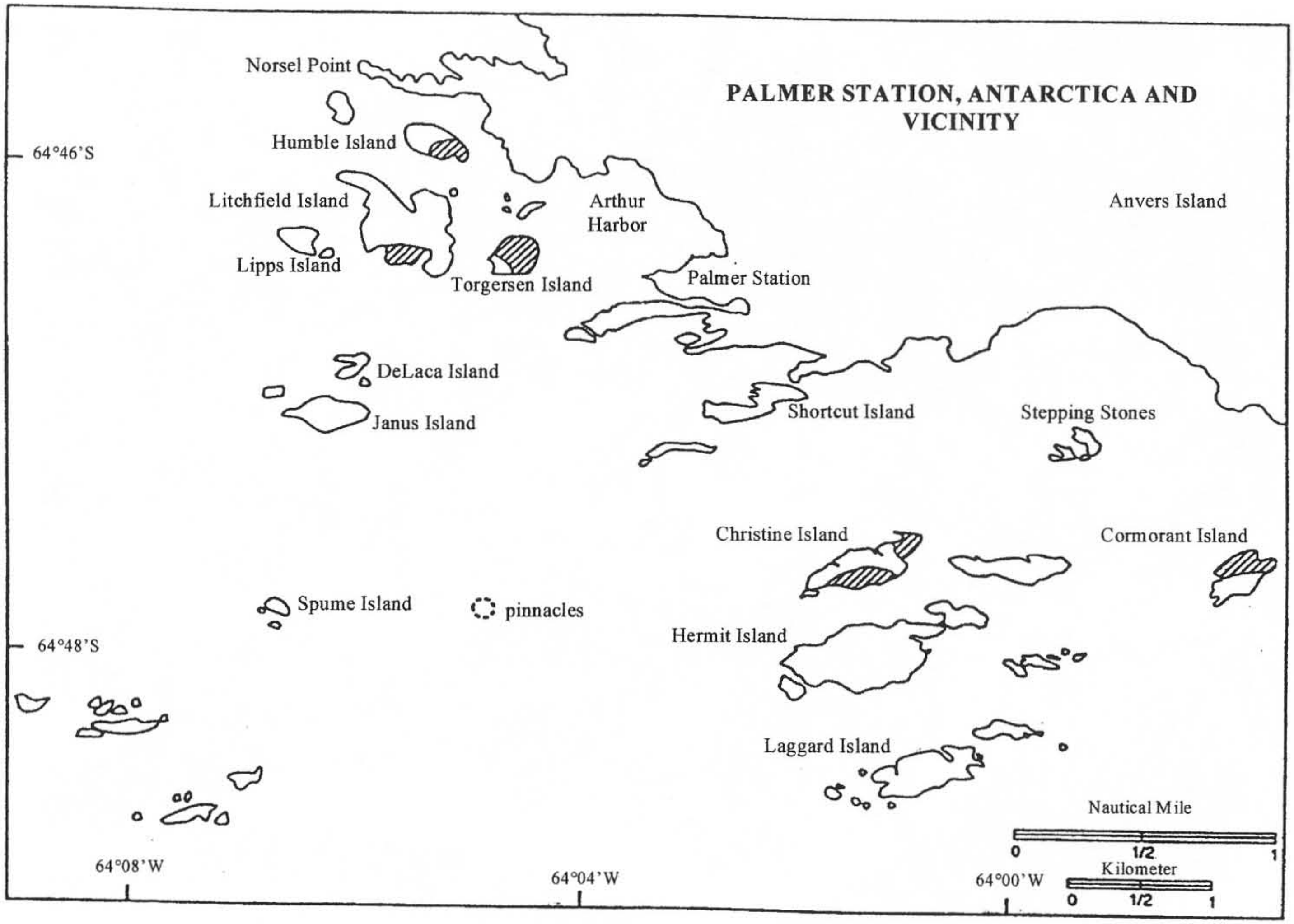

Figure 2. <u>The Location of Palmer Station, Anvers Island</u>. Adélie penguin colonies on surrounding islands are indicated by shading.

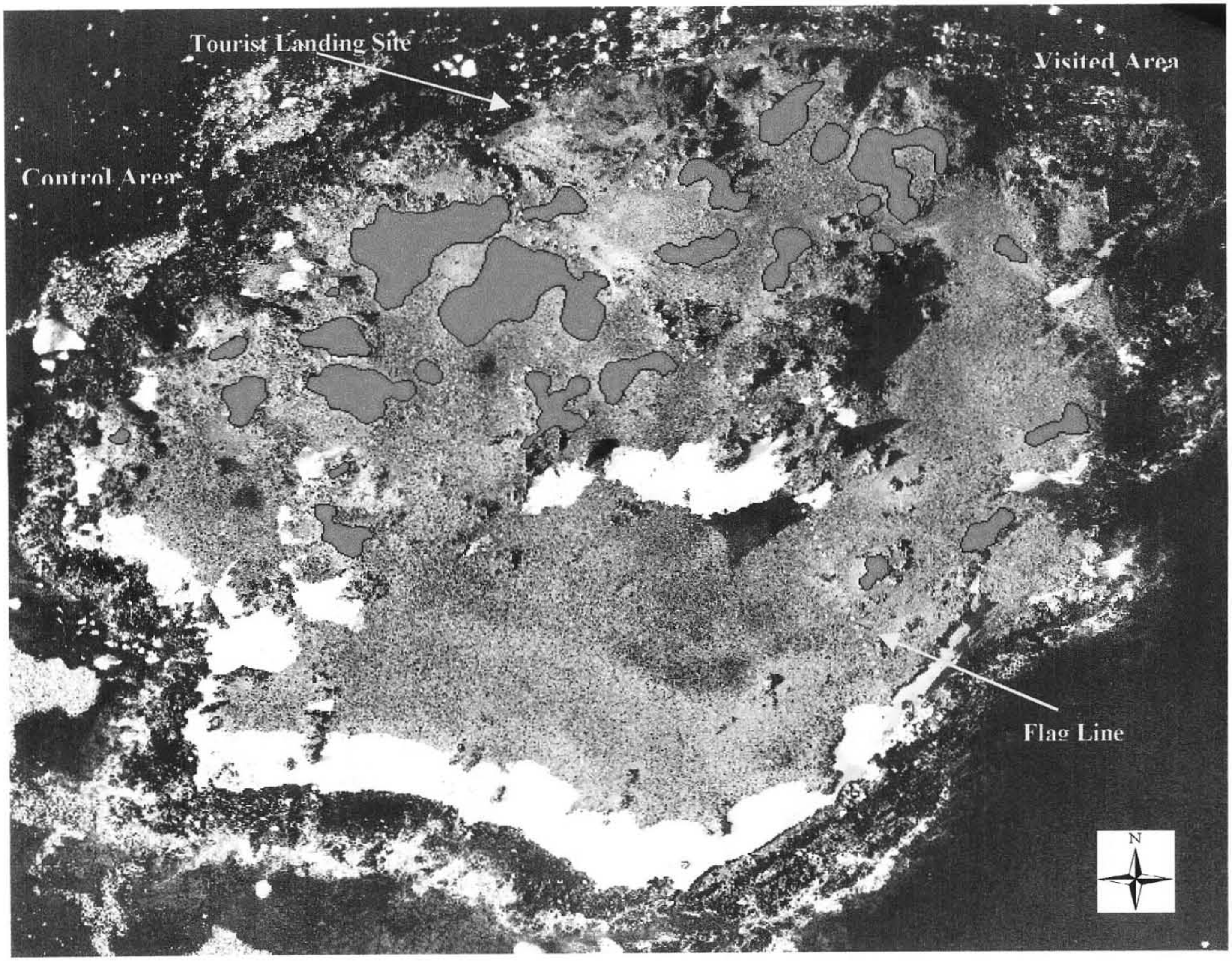

Figure 3. <u>The Location of Adélie Penguin Colonies on Torgersen Island</u>. The yellow flag line delineates visited and control areas.

National Science Foundation (NSF), thus restricting virtually all human activity to the north and northeast sides of the island. This included the roughly 1,200 tourists that annually visited this penguin rookery, all recreational use by station personnel and any research that in particular relied on protocols that might result in significant disturbance to breeding penguins. No restrictions were imposed on locations where more benign research activities could take place on Torgersen Island (i.e., similar to those permitted on the other island rookeries). These management decisions resulted in a unique experimental setting for examining the consequences of human activity on Adélie penguins, as levels of exposure ranged from colonies afforded nearly complete long-term protection to colonies that were annually exposed to varying levels of research and visits by tourists. Torgersen Island was thus the focal area of my research.

Environmental Factors Regulating Penguin Demography, Background Hypotheses

The point was made earlier in the text that detecting human impacts would be difficult unless the causes of natural demographic variability in wildlife populations were identified and understood. Changes in Adélie penguin populations in the western Antarctic Peninsula have been linked to at least two sources of environmental variability. Because Adélie penguin overwinter survival depends on the availability of sea ice, which in this marine environment forms primarily with the onset of cold, mid-winter temperatures, Fraser et al. (1992) hypothesized that regional scale decreases in Adélie penguin abundance were linked to a corresponding decrease in the frequency of cold years with heavy sea ice due to climate warming (Figure 4. Several studies support these postulated relationships between changes in temperature, ice cover and Adélie penguin population fluctuations (Fraser et al. 1992, Fraser and Trivelpiece 1996, Emslie et al. 1998). Smith et al. (1996), for example, have shown that the region's mid-winter temperatures have increased 4-5° C in the last 50 years. Correspondences between the region's paleoclimate and paleoecology also show Adélie Penguin populations expanding and contracting during cooling and warming periods, respectively (Emslie 1995, Smith et al. 1995, Emslie et al. 1998).

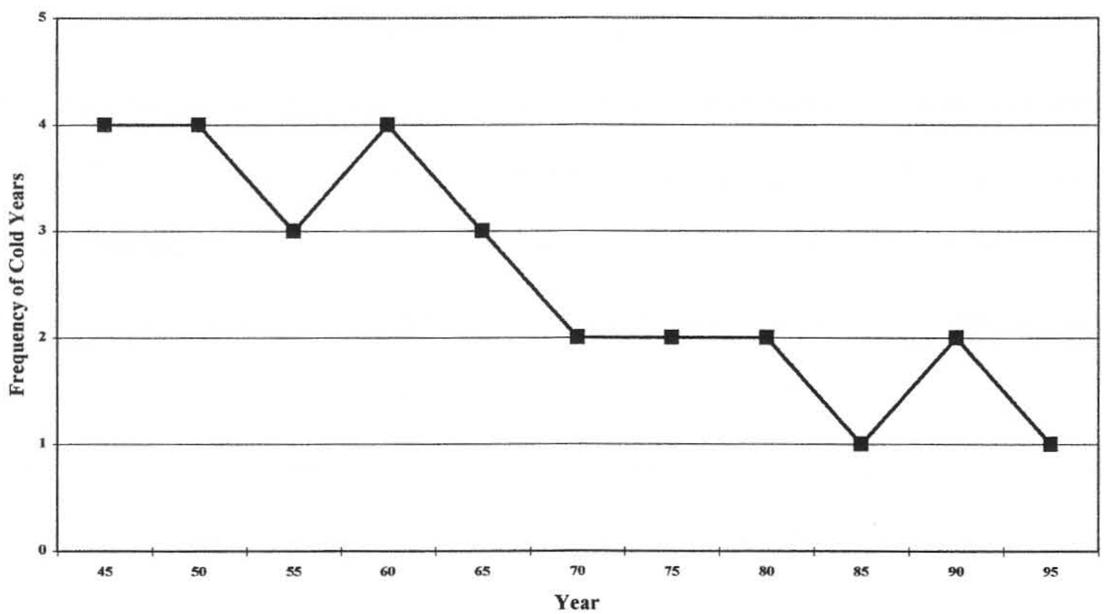

Figure 4. Changes in the Frequency of Cold Years Between 1945-1995. The frequency of cold years, or years in which the average surface air temperature was –4.3°C or below, have decreased from 4 out of every 5 during the 1940s to only 1 or 2 out of every 5 years during the last 25 years. These cold years are associated with winters of extensive sea ice formation. Adapted and updated from Fraser et al. 1992.

The second source of Adélie Penguin demographic variability due to environmental factors was recently described by Fraser and Patterson (1997) and Fraser et al. (in prep.), who use the term "landscape effect" to differentiate this local-scale source of population variance from the larger-scale "marine effect" implicit in the Fraser et al. (1992) hypothesis described above. This landscape effect is linked conceptually to Pulliam's (1988) work on habitat-specific demography in that it shares the idea that variability in breeding habitat quality can induce changes in demography that are specific to the habitat in question. For example, in the Palmer Station area (Fig. 2), the Litchfield Island Adélie penguin population has over the last 23 years decreased by 65% versus 43% for the nearby Torgersen Island population (Fraser et al. in prep). Fraser and Patterson (1997) and Fraser et al. (in prep.) have postulated that these island-specific differences in penguin population trends occur because colonies with south aspects are more vulnerable to the effects of increasing snow accumulations during the spring breeding season. Climate warming in the polar regions is expected to produce more precipitation (Roots 1989, King and Turner 1997), and recent findings indicate that snow deposition has been increasing in the western Antarctic Peninsula for the past 100 years (Thompson et al. 1994). The Litchfield Island rookery is entirely south-facing, and in the Palmer Station vicinity snow, deposition on these landscapes is further magnified by prevailing N-NE winds (Fraser and Patterson 1997). This suggests that the position of a penguin colony on the landscape may naturally predispose it to population changes that may be independent of trends shown by other colonies at local scales. These findings were key to interpreting the results of my research on human impacts.

Research Objective

The main objective of my research was to determine if patterns of human activity on Torgersen Island, either in the form of tourism or research, showed a correspondence with changes in Adélie penguin populations and aspects of their breeding biology and reproductive success. To meet this objective, I considered two of the hypotheses suggested by the preceding text, namely:

1. That long-term Adélie penguin population changes were habitat specific, with south-facing colonies experiencing a greater decrease than north-facing colonies, and
2. That human activity represented an additional population stressor, with effects manifested equally on south- and north-facing colonies.

METHODS

Study Area

Torgersen Island (64° 46' S, 64° 04' W), the focal site of my research, lies inside Arthur Harbor approximately 1 km southwest of Palmer Station (Fig. 3). This island measures approximately 400 meters in diameter and is bisected by an east-west ridge that roughly divides the landscape into north and south halves (Fig. 3). With the exception of this ridge, which is 18 m above sea level at its highest point, the island's topography is for the most part level and featureless. Torgersen Island is sparsely vegetated due to an absence of soil and scree covers much of the surface. No birds or mammals breed on the island except Adélie penguins. The Adélie penguin rookery, however, is one of the largest in the region, and its close association with a major U.S. research facility has made Torgersen Island an important destination for tourists and researchers since the early 1970s when the area's first studies on avian ecology were initiated (review in Parmelee 1992). This research effort, it is important to note, continues today in the form of two major ecosystem-scale studies: the U.S. Antarctic Marine Living Resources Program (AMLR, established in 1986) and the Palmer Station Long Term Ecological Research (LTER, established in 1990) program (reviews in Fraser and Trivelpiece 1996, Fraser and Patterson 1997). These programs provided essential, long-term background data on Torgersen Island Adélie penguin populations that I used in this research for further interpretation of human impacts during 1993-1996 to test hypotheses and interpret results.

The climate in this sector of the western Antarctic Peninsula falls under a Maritime Antarctic regime and is strongly moderated by oceanic factors (Smith et al. 1995). As a result, and in contrast to continental Antarctica, significantly milder and wetter conditions tend to prevail. Annual surface air temperatures at Palmer Station average -2.3° C, and precipitation in the form of both rain (c. 40 cm/yr.) and snow (c. 70 cm/yr.) is common throughout the year (Smith et al. 1995 and 1996). This precipitation is commonly carried by moisture-laden cyclones that move through the area at weekly intervals. The predominant winds associated with these low pressure systems are north-northeast, meaning that in winter and early spring snow naturally accumulates on the lee side (south-southeast) of prominent topographic features (Fraser and Patterson 1997).

Sea ice, which typically forms during late winter, is also regularly present in the area, but annual extent, cover and duration are highly variable and cyclical. Years of heavy ice with extensive spatial and temporal coverage occur once every 5 years on average (Fig. 4) and intervening years may exhibit only modest sea ice development (Fraser et al. 1992, Stammerjohn 1993, Stammerjohn and Smith 1996). The presence or absence of sea ice combined with the tracks followed by cyclones entering the region determine the extent to which polar or maritime conditions prevail in the area (Baker and Stammerjohn 1995, Smith et al. 1999). Changes from polar to maritime conditions can also occur rapidly sometimes in as little as 24 hours. If heavy snow cover is present, it can melt quite suddenly, resulting in nest flooding and egg or chick mortality.

Further detailed descriptions of the area's glacial history, climate, geography, terrestrial ecosystems, sea ice patterns and seabird populations can be found in published accounts by Rudolph (1967), Rundle (1973), Watson (1975), Parmelee (1992), Smith et al. (1995), Fraser and Trivelpiece (1996), Smith et al. (1996), Stammerjohn and Smith (1996) and Emslie (1998).

Terminology and Patterns of Human Activity

In this study, the term "colony" is used to describe a discrete, contiguous group of breeding penguins and the term "rookery" refers to a group of geographically isolated colonies (Penney 1968, Ainley et al. 1983). Furthermore, capitalizing on the division established by the National Science Foundation in 1990 that restricted tourism to the northeast and east sides of Torgersen Island (Fig. 3), I use the terms "visited side" and "control side" to identify those portions of the island where tourism was and was not permitted, respectively. Thus, at the beginning of the time period bracketed by my analysis (1989-1998), the Torgersen Island rookery consisted of 23 colonies that ranged in size from 30 to 1,400 breeding pairs. Of these colonies, 12 (3310 breeding pairs) were located on the visited side of the island and 11 (4625 breeding pairs) on the control side. Sub-colonies, of which there were four associated with three of the 23 main colonies, were not treated independently in any analyses because these were typically contiguous with the parent colonies early in the breeding season. In other words, they emerged as distinct sub-colonies late in the season, usually following the loss of breeding birds due to repeated flooding events that channeled water into particular areas of the parent colonies.

The control and visited sides of the island were subjected to different types of human activity during the 10 years bracketed by my analysis. The activities of AMLR and

LTER researchers, which included censusing, flipper-banding and daily nest checks of sample groups to determine breeding success, were divided equally between the two sides of the island as part of the general long-term objectives of these programs. Superimposed over these research activities, but restricted only to the visited side of the island, were the activities of tourists and recreating station personnel. A third and final type of activity, also restricted to the visited side of the island but encompassing only two seasons (1995-1996), were the research efforts of avian physiologists. This group's activities were similar to those of AMLR and LTER researchers, but included additional protocols that called for behavioral observations, serial blood sampling and repeated intrusions into the colonies to catch marked adults and chicks. Given this partitioning in the types of human activity and potential for disturbance, I tested the null hypothesis that there were no differences in Adélie penguin breeding success and breeding population trends between the visited and control sides of Torgersen Island.

Data Categories and Collection Methods

Long-Term Breeding Population Censuses

Data have been collected on Torgersen Island since 1974 and subsets of the data have been recently used in studies by Fraser and Patterson (1997), Smith et al. (1999) and Fraser et al. (in prep.). I used a subset of this database, the years 1989-1998, for analysis in my study. These censuses recorded active nests (at least one egg present) at all 23 Adélie Penguin colonies found on Torgersen Island. Data collection followed international protocols (CCAMLR 1992) in that censuses were conducted during the peak egg-laying period (7-25 November) and involved a minimum of three counts per colony by independent observers. These standardized protocols aim to reduce error between counts to ± 5% or, in the case of large colonies (>1000 breeding pairs), to ± 10%.

Breeding Chronology and Reproductive Success

As a complement to the longer-term breeding population data, I monitored the breeding success (chicks crêched/pair) of Adélie Penguins during the years 1993 (150 pairs), 1994 (200 pairs) and 1995 (200 pairs) on both sides of Torgersen Island. On the visited side of the island, I used historical (WR Fraser, unpubl. notes) and contemporary data on tourist dispersion patterns (see below) in a stratified, randomized block design to determine where reproductive sample groups (RSGs) were placed within the colonies. The objective was to have RSGs in locations that captured the range of variability in tourist visits associated with specific colonies. RSG locations on the control side of the island were selected in accordance with procedures in use as part of the AMLR and LTER programs (see CCAMLR 1992). RSGs consisted of circular, 5-nest groups situated randomly within the first 2 m of colony peripheries to minimize disturbance in accessing interior breeding sites during nest checks. Due to the 'edge' effect, periphery nests typically have a higher failure rate than central nests (Tenaza 1971, Ainley et al. 1983, Barbosa et al. 1997). However, the disturbance associated with monitoring interior nests can be excessive and subsequently impose extensive influences on a greater proportion of neighboring nests. Although limited to the first 2 m of colony periphery, RSGs nonetheless included breeding pairs up to 3 nests interior from the edge. Both members of the pair were banded at each nest site with numbered, color-coded flipper bands to further aid nest identification. RSGs were monitored daily to obtain information on laying, hatching and survival using the techniques described by Ainley et al. (1983). RSG monitoring was typically discontinued when chicks entered the crêche stage as individuals could no longer be associated with specific nests.

Snow Measurements

Snow depth (cm) was measured in November to coincide with peak egg laying at a subset of colonies on the visited and control sides of Torgersen Island during the 1995 season. Snow depths were recorded at 1 m increments to a distance of 5 m, perpendicular to the colony periphery beginning 1 m from the outermost penguin nest. Measurements were taken on each of the 4 cardinal axes around the colonies.

Tourist Monitoring

Tourists visited Torgersen Island between December and March of each season. I monitored their movements during 1993-1995 by censusing every 20 minutes and recording (total number and location) their position relative to specific Adélie Penguin colonies (Fig. 3). Censuses were completed from the highest vantage point on Torgersen Island so that all colonies were equally visible and my presence would not affect tourist movements. This point was approximately 20 m from the closest colony and 200 m from the most distant. Only tourists standing within 15 m of colony boundaries were counted in the censuses. I used known distances between landscape features and colony boundaries to determine if tourists were within the 15 m census area to validate their inclusion in the counts.

Aerial Photography and Digital Terrain Models

During the 1998/99 season, Dr. William R. Fraser coordinated a cooperative project between the United States Geological Survey (USGS), the British Antarctic Survey (BAS) and the National Science Foundation (NSF) to map the southwest coast of Anvers Island using low altitude (450 m) aerial photography. Once the preliminary stereoscopic photos were available, a Rockwell Precise Global Positioning System (GPS) receiver with sub-meter accuracy was used to geo-rectify the images and map the perimeters of the entire region's active and extinct Adélie Penguin colonies (Sanchez 1999). These data were also used in the production of Digital Terrain Models (DTM) of the islands occupied by penguins.

To examine the hypothesis that penguin population trends were habitat-specific, I used the Torgersen Island DTM layer in ArcView 3.2 (Environmental Systems Research Institute 2000) to create a hillshade model of the island. These models are used to simulate a variety of landscape processes that depend on interactions between topography and a forcing variable, such as solar radiation or wind scour. A gray scale is typically used in hillshade models to simulate and differentiate the effects of these interactions. This gray scale develops from 2 input parameters: the azimuth, or direction relative to true north from which the forcing variable originates, and its elevation angle relative to the horizon. Because I was interested in differentiating between north and south aspects on the island as a proxy for determining patterns of snow deposition, I based the model's azimuth on a 12-year record of wind direction at Palmer Station during storm events (defined as any period of having sustained wind speeds greater than 25 knots for a period of 5 hours or more). I then used existing residual snow banks on the Torgersen Island aerial photographs to determine the wind elevation angle that best replicated the position of these snow banks. The model's azimuth was thus set at 10° and its elevation angle at 20°. Information on colony area, perimeter, shape (standardized ratio of perimeter to perimeter of a standardized circle using area), elevation and colony-specific aspect was also extracted from the Torgersen Island DTM and hillshade layers

To test whether the addition of human activities resulted in population trends that were different from those observed on the control side of the island, the Torgersen Island hillshade model guided the selection of Adélie penguin colonies used in the comparisons between the visited and control sides of the island. This ensured that colonies were matched by habitat, but differed in terms of their exposure to human activity. To remove the possibility of an effect due to colony size (see Ainley et al. 1983) in these comparisons, I also matched the colonies being compared by breeding population size in 1989/90, the beginning of the period encompassed by this study.

Data Analysis

Analyses involving long-term breeding population changes encompassed 10 seasons (1989 - 1998), whereas analyses involving short-term reproductive success encompassed 3 seasons (1993 - 1995). However, due to the effects of often unfavorable weather and ice conditions early in the season, study sites were either not always accessible at the same time each season or gaps developed in the data. Thus, in the long-term data set, some of the colonies censused in 1993 were counted late; late censuses were manifested as outliers that were removed from the analysis. In the short-term data, the analyses performed use the combination of seasons and/or colonies that provide the most consistent data available in the 3-year record. As a result, not all of the parameters being investigated encompass 3 years of comparative data. This is especially true of the snow measurements, which were not obtained until 1995 and hence should only be considered here as supporting or corollary data that may provide further insights regarding possible mechanistic links between breeding success and environmental variability.

Statistical analyses were completed using Statistica 99 (Statistica 1999) and Prism 3.02 (GraphPad 2000). Student's t-tests were used to compare breeding success between visited and control RSGs. Linear regression was used to analyze differences in breeding population parameters (e.g., breeding population size, breeding success, nest loss and chick loss). Linear discriminant function analysis (DFA) procedures were employed to examine the effects of habitat variables on the breeding population change. Given the dichotomous nature of the data (visited vs. control, north aspect vs. south aspect), a linear DFA approach was used to evaluate the predictability of group membership. Following Chan (1972), missing data points in the linear DFA were replaced by empirical means. Based on partial lambda values, subsets of variables were identified and prioritized for linear regression analysis. Classification tables, eigenvalues and Wilks' lambda values were examined to evaluate the discriminatory power of the chosen model. Linear DFAs were also conducted to evaluate the ability of breeding biology parameters to discriminate between the tourist-visited and control sides of Torgersen Island.

RESULTS

The Torgersen Island Hillshade Model

The Torgersen Island hillshade model is shown in Figure 5. Based on model parameters (see Methods), the white to black scale simulates areas on the island receiving the least and most amounts of snow, respectively. Indeed, by comparing the model with Figure 3, one can see that the presence of residual summer snow banks closely agree with the model's grayscale. These snow banks develop in the winter and spring, and depending on how much precipitation falls, generally do not melt out until late February. As this model suggests, the east-west ridge that bisects Torgersen Island sharply divides the landscape according to aspect, with predominantly dark areas facing south (approximately 55% of the total island area) and predominantly light areas facing north (the remaining 45% of the total island area).

Adélie Penguin Demography and Landscape Effects

Island-Scale Patterns

Figure 6 and Table 1 summarize how Adélie penguin colonies are distributed on Torgersen Island and the changes that have occurred in the population over a 10-year period. Although the south-facing portion represents a slightly larger area (55% vs. 45%), only 10.6% of the island's total penguin nesting area occurs there. This area included 7 colonies that in 1989 contained 1301 breeding pairs, or 16.4% of the 7,935 pairs present on the island. In contrast, the north-facing portion of the island included 16

Figure 5. Hillshade Model of Torgersen Island. The colored areas represent Adélie penguin colonies. The transition from light to black shading represents gradients in landscape aspect; lighter areas are north-facing and are typically scoured free by predominant winds.

colonies that together encompassed 89.4% of the total area covered by nesting penguins, or the remaining 83.6% of the breeding population. This positive association between the respective total areas covered by penguin colonies and the lighter shades produced by the model (Fig. 5) strongly suggests that aspect is a strong determinant of breeding habitat suitability. Adélie penguins on Torgersen Island were clearly drawn to north-facing habitats, which by implication (e.g., Fig. 5) were areas where topography was not likely to accumulate snow.

Table 1. North/South Side Comparison of Adélie Penguin Colonies on Torgersen Island Between 1989/90 and 1998/99.

	North Side	South Side
Total Percent Area of Torgersen Island	45%	55%
Percent Area in Adélie Penguin Colonies	89.4%	10.6%
Number of Colonies	16	7
Breeding Population in 1989/90 (# pairs and % total)	6634 (83.6%)	1301 (16.4%)
Breeding Population in 1998/99 (# pairs and % total)	4493 (89.2%)	544 (10.8%)
Percent Change, 1989/90 – 1998/99	-32.2%	-58.2%
Number of Colony Extinctions (1989-1998)	0	1

To further examine if there was a correspondence between aspect and long-term trends in the Adélie Penguin population, I compared the 10-year population trend of the 7 south-facing colonies with the trend shown by the 16 north-facing colonies. The results

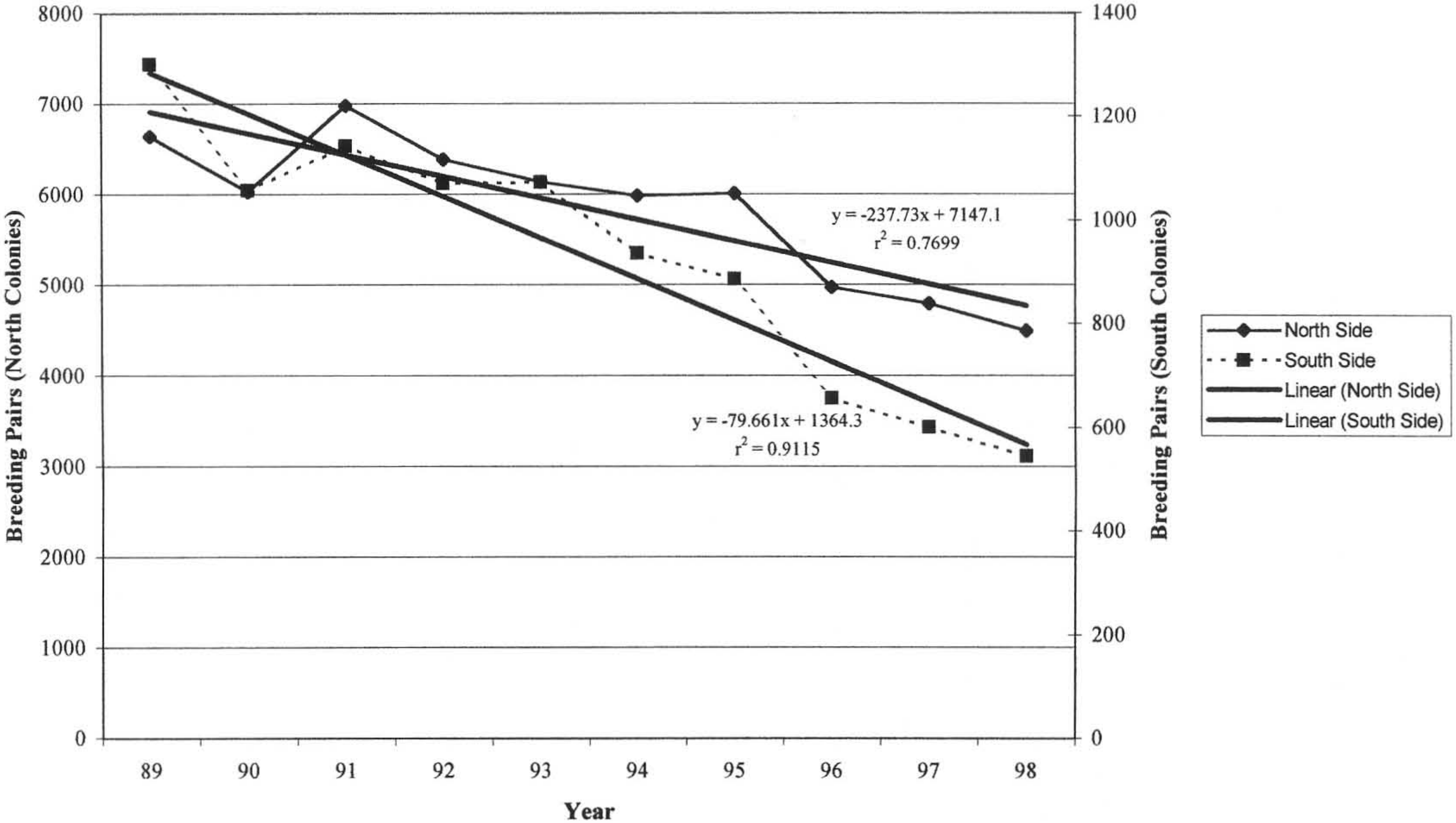

Figure 6. Adélie Penguin Breeding Population Trends on the North and South Sides of Torgersen Island. Note that two y-axes are used to represent breeding populations on the north and south sides of Torgersen Island. Over the ensuing 10-year period, north colonies decreased by 32% versus 58% for the south colonies. The slopes of the lines are significantly different ($p=0.00383$, $F_{1,16}=11.415$).

are shown in Figure 6. Over the same time period, the colonies with a south-facing aspect decreased by 58.2% vs. a 32.2% decrease for the 16 colonies with a north-facing aspect. The difference in the slopes of the regression lines was highly significant ($p = 0.00383$, $F_{1,16} = 11.415$).

Colony-Scale Patterns

As the next step in looking at possible correspondences between Adélie penguin breeding population change and landscape effects, I narrowed the scale of interest to that of the colony. Fraser and Patterson (1997) speculated that egg or chick mortality, perhaps induced by colony-specific features such as size or elevation, must also be considered to better understand the underlying mechanisms driving natural variability in these populations. This possibility was addressed by first using a 4-variable linear discriminant function analysis (DFA) to test whether colony-specific habitat components could be used as predictors of group membership. This membership was determined by conservatively classifying individual colonies into low decrease (<25% change) or high decrease (>25% change) groups based on their respective trends during 1989-1998. This delimiter was chosen because it most closely approximated a discontinuity apparent in the colonies between moderate and extreme breeding population decreases over the 10-year time span of this analysis. The variables considered in the DFA analysis were colony aspect, elevation, shape (perimeter/area ratio) and area, which were calculated using the Torgersen Island DTM and corresponding ArcView functions. Linear regression analysis was used to see how breeding biology parameters based on the 1993-1995 RSG data supported the model results generated by the DFAs.

In the 4-variable DFA (Wilks' lambda = 0.331), elevation did not contribute to the discriminatory power of the model (partial lambda = 0.961). Elevation was thus removed from the DFA and the remaining 3-variable model reevaluated. In the 3-variable model (Wilks' lambda = 0.344), colony aspect and area (partial lambda values of 0.526 and 0.564, respectively) were the best predictor variables of group membership; colony shape (partial lambda = 0.812) did not contribute substantially to the discriminatory power of the model. Table 2, which summarizes the resulting classifications based on these 3 variables, indicates that only one colony (4.35%) of the 23 was misclassified by the model, thus reinforcing the importance of habitat-specific features in predicting colony-scale population trends.

Linear regression analysis strongly supported the DFA model results. Colony aspect (Table 3) and colony area (Table 4) were both significant predictors of several breeding success parameters. Also important given the snow/aspect hypotheses (cf. Fraser and Patterson 1997, Fraser et al. in prep.) previously discussed, is that there was a significant inverse relationship between the number of chicks crêched per colony and snow pack persisting into late November, the peak-egg laying period for Adélie penguins. Colony elevation was not significantly correlated with any of the population variables measured. Interestingly, average productivity and colony shape were not significantly correlated ($p<0.15$, $r^2=0.10$), although other studies have suggested that area-rich, rounder colonies with a lower proportion of 'edge' are important determinants of breeding success (Tenaza 1971, Ainley et al. 1983).

Table 2. Breeding Population Change Discriminant Function Analysis Classification Table. The linear DFA classification table for the prediction of colony-specific breeding population decreases based on low (<25%) or high (>25%) percent decrease between 1989/90 and 1998/99. Shown are the number and percent of the colonies that were classified into low and high decrease categories.

Group	Percent Correct	Colonies classified into Low	High	Total
Low (<25%)	85.71	6	1	7
High (>25%)	100.00	0	16	16
Total	95.65	6	17	23

Table 3. Relationships Between Colony Aspect and Breeding Success Parameters. Coefficients of determination from linear regression analyses showing the predictive ability of colony aspect on several Adélie penguin breeding success parameters. A single outlier (Colony 8) was identified by residual analysis and removed from the breeding population decrease analysis.

	r^2	p-value	Analysis Years
Long-Term Breeding Population Change	0.36	P<0.003	1989/90 – 1998/99
Breeding Population Decrease (percent decrease), excluding Colony 8	0.50	P<0.0007	1993/94 – 1995/96
Chick Loss (Percent Change)	0.38	P<0.004	1994/95 – 1998/99
Colony Size (Breeding Pairs)	0.47	P<0.0006	1994/95 – 1998/99
Average Productivity (total chicks/total breeding pairs)	0.28	P<0.01	1994/95 – 1997/98

Table 4. Relationships Between Colony Area and Breeding Success Parameters. Coefficients of determination from linear regression analyses showing the predictive ability for the effect of colony area on reproductive parameters of Adélie penguins. Residual analysis identified a single outlier (Colony 7) in the colony-specific egg loss regression; results are presented both with and without the outlier.

	r^2	p-value	Analysis Years
Colony-specific Egg Loss at RSGs, including Colony 7	0.50	P<0.005	1993/94 – 1995/96
Colony-specific Egg Loss at RSGs, excluding Colony 7	0.75	P<0.00002	1993/94 – 1995/96
Breeding Success (total chicks/total breeding pairs)	0.31	P<0.009	1997/98

Table 5. The Relationship Between Snow Depth and Breeding Success. Coefficients of determination from linear regression analyses showing effects of snow depth on reproductive parameters of Adélie penguins. A single outlier was identified by residual analysis; results are reported both with and without the outlier (Colony 17).

	r^2	p-value	Analysis Years
Breeding Success (total chicks/total breeding pairs) by Maximum Snow depth in Late November, including Colony 17	0.46	P<0.03	1995/96
Breeding Success (total chicks/total breeding pairs) by Maximum Snow depth in Late November, excluding Colony 17	0.78	P<0.001	1995/96

Adélie Penguin Demography and Human Effects

Tourist Flow and Distribution

Twenty vessels visited the Palmer Station area during the 3 years that I conducted tourist censuses on Torgersen Island. Typical visits to the island lasted 3-4 hours and involved groups of 10-50 people. Figure 7 illustrates the annual distributions of tourists relative to the 12 penguin colonies found on this side of the island. This pattern, which historical data suggest is long-standing in the area (WR Fraser, unpubl. data), is clearly not homogeneous. Colonies nearest the landing site (9-11 and 15) received the highest numbers of visitors, while those farther away (1-5) received the fewest. Colonies 1-4 were also more difficult to reach, as they occur to the south and east of the ridge that bisects Torgersen Island (Fig. 5).

Visited vs. Control Side Population Trends

Results thus far suggest that colony aspect and colony area are the most significant predictors of change in Adélie penguin populations on Torgersen Island. To look for possible effects due to human activity, subsets of colonies were matched by size and aspect on the visited and control sides of Torgersen Island. Population trends for the north visited/control and the south visited/control are compared in Figures 8 and 9. For north-facing colonies (Fig. 8), the slopes of the linear regressions were not significantly different between visited and control colonies ($p = 0.202$, $F_{1, 16} = 2.094$) even though 3 of

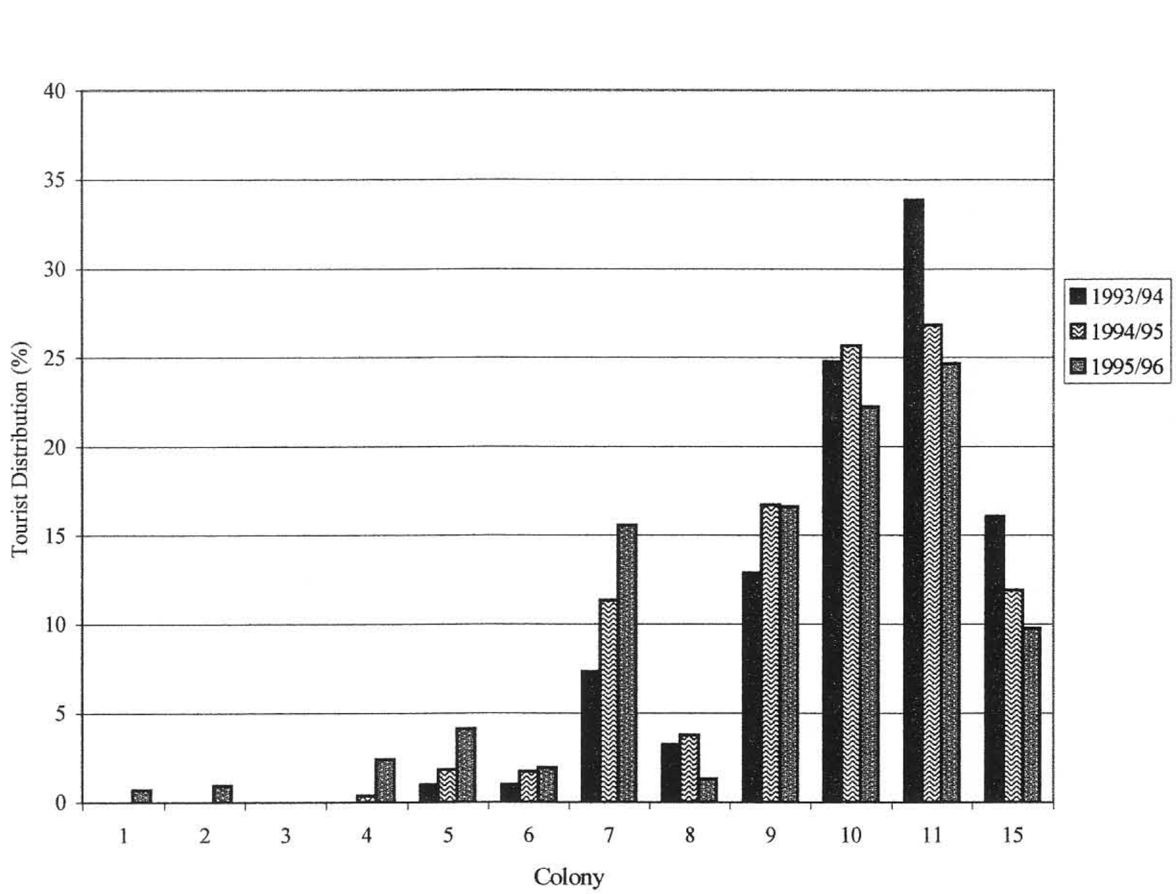

Figure 7. <u>Tourist Distribution Around Adélie Penguin Colonies on the Visited Side of Torgersen Island, 1993-1996</u>. Tourist 'flow' patterns during the 3-year study were consistent with historical patterns on Torgersen Island.

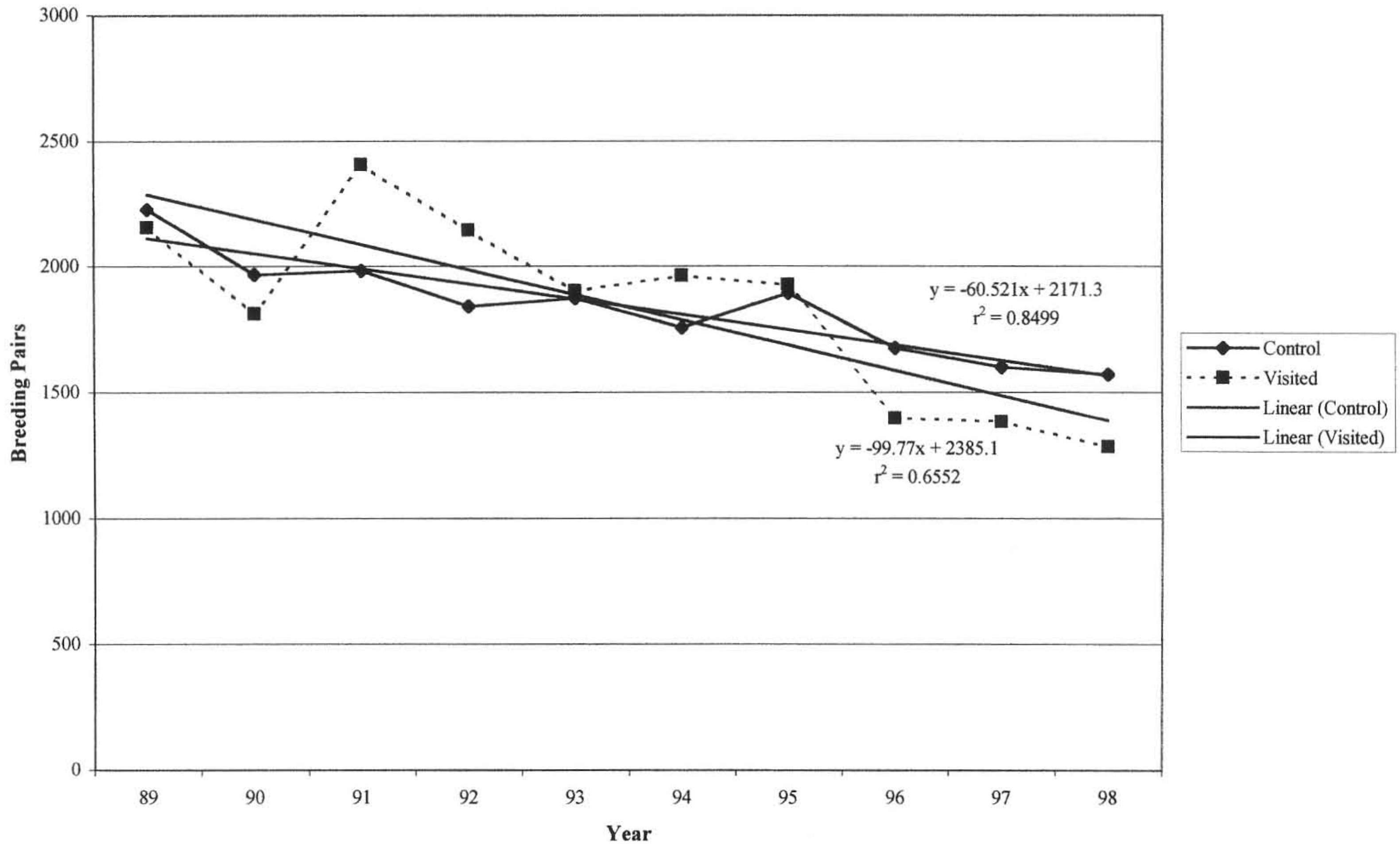

Figure 8. Adélie Penguin Breeding Population Trends on the Control and Visited Sides of North-Facing Colonies on Torgersen Island. The trends are based on 5 pairs of colonies that were matched by size at the start of the study (1989). The slopes of the lines are not significantly different (p=0.202, $F_{1,17}$=2.094).

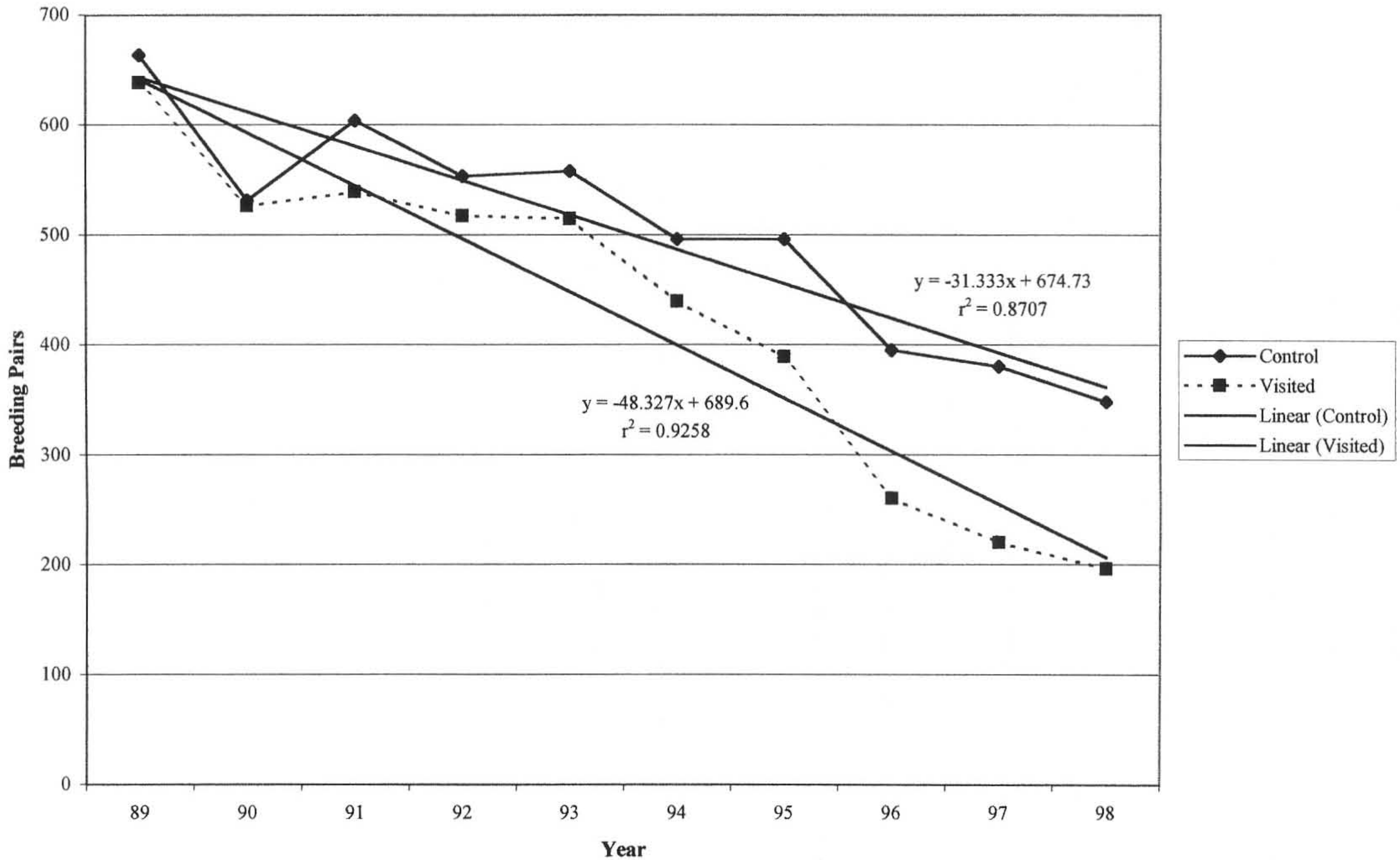

Figure 9. Adélie penguin Breeding Population Trends on the Control and Visited Sides of South-Facing Colonies on Torgersen Island. The trends are based on 4 pairs of colonies that were matched by size at the start of the study (1989). The slopes of the lines are significantly different ($p=0.0180$, $F_{1,16}=6.940$).

the 5 colonies representing the visited side of the island in the comparison (Fig. 7; colonies 9, 11 and 15) were among the most heavily attended sites (see Fig. 7). RSG breeding success comparisons between north-facing visited and control sites were also not significant during the three years of tourist monitoring (Table 6). In contrast, significantly different slopes were evident between the breeding populations of the south-facing colonies (Fig. 9, $p = 0.0180$, $F_{1, 16} = 6.940$). Although this may imply an effect due to tourism, it is worth noting that all 4 of the colonies (1-4) representing the visited side of the island in the south-facing colony comparison were in the areas least attended by tourists (Fig. 7). Interestingly, as in the northern colonies, t-tests revealed no significant differences between RSG-based breeding success comparisons for the south-facing colonies (Table 7).

Table 6. Aspect-Specific Breeding Success Comparisons Between RSGs in North-Facing Visited and Control Colonies. Breeding success is measured as the total number of chicks crêched per pair in RSGs during the 1993/94 through 1995/96 seasons. See Appendix A for further reproductive success data.

Year	Productivity (±SD)		p (T<=t), two-tailed	n (visited, control)
	Control	Visited		
1993/94	1.25±0.29	1.51±0.21	0.232	13, 9
1994/95	1.37±0.06	1.53±0.06	0.102	12, 17
1995/96	1.58±0.06	1.60±0.08	0.864	12, 19

Table 7. Aspect-Specific Breeding Success Comparisons between RSGs in South-Facing Visited and Control Colonies. Breeding success is measured as the total number of chicks crêched per pair in RSGs during the 1993/94 through 1995/96 seasons. See Appendix A for further reproductive success data.

Year	Productivity (±SD) Control	Visited	p (T<=t), two-tailed	n (visited, control)
1993/94	1.60±0.12	1.56±0.23	0.896	3, 5
1994/95	1.47±0.01	1.60±0.14	0.492	3, 5
1995/96	1.07±0.17	1.08±0.13	0.965	3, 5

To further assess the implied conclusion that human impacts have no measurable effects on Adélie penguin populations, linear DFA was used to see if a model could discern between tourist and control colonies. Four potential predictor variables were considered: the change in number of breeding pairs, the percent decrease in breeding pairs per colony, the percent decrease in the number of chicks produced per colony and the number of chicks crêched/pair/colony. The resulting 4-variable model (Wilks' Lambda = 0.750; $p < 0.242$, $F_{4,18} = 1.506$) was a poor discriminator of group membership and misclassified 6 of the 23 colonies. Because all of the resulting partial lambda values were >0.89 and the model produced a low eigenvalue (0.335), the DFA was repeated using the two variables that contributed the most discriminatory power- percent decrease in the number of breeding pairs (partial lambda = 0.890) and the number of chicks crêched/pair/colony (partial lambda = 0.910). The discriminatory power of the 2-variable model did not improve (Wilks' lambda = 0.793; $p < 0.098$, $F_{2, 20} = 2.611$), and the eigenvalue remained low (0.261). Table 8 shows the resulting classification. Two of the

12 (17%) visited-side colonies and 4 of the 11 (36%) control colonies were misclassified, suggesting that tourist activities did not impact these demographic parameters enough to discern group membership.

Table 8. Human Activity Discriminant Function Analysis Classification Table. Results of the linear DFA are given for the prediction of tourist and control colonies. Shown are the numbers and percent of colonies that were classified as visited or control status.

Group	Percent Correct	Colonies classified into Visited	Control	Total
Tourist (visited)	83.33	10	2	12
Control (unvisited)	63.64	4	7	11
Total	73.91	14	9	23

DISCUSSION

The Adélie penguin is the only *Pygoscelid* species with a circumpolar distribution and a breeding range that spans nearly 20 degrees in latitude (Watson 1975, Parmelee 1992, Woehler 1993, Williams 1995, Fraser and Trivelpiece 1996). Adélie penguins thus inhabit an area that varies extensively in terms of the quality and availability of breeding habitat, marine resources and exposure to other wildlife and human activity. Until recently, accounting for differences in Adélie penguin population trends relied on explanations focused primarily on variability in the marine environment (e.g., Fraser et al. 1992, Smith et al. 1999). Evidence that these explanations could not account for the differences in trends observed in some local populations, however, led Fraser and Patterson (1997) to propose that demographic influences involved a minimum of two scales of processes. Variability in the marine environment was the most likely explanation for regional-scale trends because the processes would encompass metapopulation scales (i.e., through changes in climate, sea ice or food web processes; Whitehead et al. 1990, Blackburn et al. 1991, Fraser et. al. 1992, Stammerjohn 1993, Smith et al. 1999). Variability in nest site characteristics associated with the terrestrial breeding habitat, on the other hand, was the most likely explanation for differences in local-scale trends because the influences only encompassed specific populations (i.e., imposed through mechanisms such as the earlier described landscape effect; Fraser and Patterson 1997, Fraser et al. in prep).

Although this marine/terrestrial model has now emerged as a more robust explanation of demographic variability in Adélie penguins (cf. Fraser and Trivelpiece 1996, Trivelpiece and Fraser 1996, Smith et al. 1999), aspects of this model remained untested, and its potential application for detecting and interpreting the effects of human activity have not been addressed. It is from this perspective that I discuss the results of this study.

Landscape Effects and Adélie Penguin Demography

The null hypothesis associated with this study is that there are no differences in the breeding population trends of Adélie penguins between the visited and control sides of Torgersen Island. This hypothesis is rejected based on the analyses suggested by the hillshade model (Fig. 5). Despite the relatively gentle topography of Torgersen Island, the Adélie penguin population on the south-facing slope of the island's east-west ridge (Fig. 5) exhibited significantly different trends than the population on the north-facing slope (Fig. 6). Over the same time period, south-facing colonies decreased at a rate nearly double that of the north-facing colonies (58% vs. 32%, respectively). These findings concur with those of Fraser and Patterson (1997), who observed that south-facing colonies on nearby Litchfield Island (Fig. 2) were decreasing at a faster rate than others found in the local rookeries due to the effects of greater snow deposition on the lee side of major topographic features. Interestingly, the population on Litchfield Island has decreased by 47% since 1989, a change quite similar to that of the south-facing colonies on Torgersen Island. Ainley and LeResche (1973) and Yeates (1975) have also observed that the presence and persistence of snow-free land may be a major determinant of colony location and persistence.

Aspect was identified as a significant predictor of several demographic parameters by both DFA model results (Table 2) and regression analysis (Table 3). Breeding population decrease was the lowest in colonies with west and northwest aspects and most extreme in colonies with an east or southeast aspect. By coupling these results to the observation that a significant inverse relationship existed between breeding success and persisting snow pack in late November (Table 5), a mechanism can be proposed to account for the aspect-specific population trends seen on Torgersen Island. Natal philopatry and site fidelity are highly developed behaviors in Adélie penguins. A study by Ainley et al. (1983), for example, indicated that 96% of adults returned to the same breeding site, suggesting that relocation is not a "behavioral option" often expressed by the species. Adélie penguins are also long-lived (Williams 1995), and there is evidence based on marked adults in the Palmer area that breeders may persist at the same colonies for at least 15 years (Fraser, unpubl. data). Over these time scales, colonies with south- and southeast-facing aspects may thus be losing breeders due to the combined effects of poor reproductive success induced by increasing snow deposition on these landscapes and poor overwinter survival.

Colony area was also identified as a significant predictor of breeding success parameters by the DFA model (Table 2) and regression analysis (Table 4). Small colonies have decreased at a faster rate than large colonies on Torgersen Island (Fraser et al. in prep), and one can see that south-aspect colonies tend to be smaller (Fig. 3). Young

(1994) reported that Adélie penguin colonies below a threshold size (ca. 50 pairs) are unable to persist due to greater instances of predation on the colony periphery. Robertson (1986) also reported that breeding success of Gentoo penguins, a congener of Adélie penguins, decreased within smaller colonies.

Somewhat related to colony area is colony shape, or the standardized perimeter to area ratio. Although the correlation between colony shape and the number of chicks surviving to the crêche stage was not statistically significant in this study, other researchers have documented that colonies with a greater proportion of periphery nests have lowered breeding success due to higher egg and chick mortality (Tenaza 1971, Ainley et al. 1983, Robertson 1986, Young 1990 and 1994, Barbosa et al. 1997). A key causal factor appears to be predation and Tenaza (1971) and Young (1994) also indicated that predatory skuas (*Catharacta* spp.) may 'work' these vulnerable colony peripheries beyond the penguins' capacity to rebuff repeated attacks. There is also evidence that unpredictable events, such as years of high snow deposition, may increase the predation risk in colonies that are less area-rich (higher proportion of periphery) under some conditions (Tenaza 1971, Barbosa et al. 1997). It is therefore possible that some combination of these external influences have operated simultaneously on the smaller, south-facing colonies of Torgersen Island. In light of the mechanism proposed above, poor chick survival induced by changing area/ratio dynamics could conceivably add another negative component to south-facing colonies as these decrease in size towards some critical threshold level; this relationship warrants further investigation as part of the continuing LTER research on Torgersen Island.

Human Impacts on Adélie Penguin Demography

A landscape effect on certain aspects of Adélie penguin demography is clearly evident on Torgersen Island, and this study has quantified key components of the hypothesis put forward by Fraser and Patterson (1997). One weak point in this study is that direct, long-term measurements of snowfall are not available for the Palmer region. Hypothesized mechanistic links thus depend in part on the glacial core record, but these do show a significant increase in snow precipitation in the Antarctic Peninsula during the past 100 years (Thompson et al. 1994).

Compensating for this weak point, is the fact that based on long-term data, 2 important terrestrial sources of demographic variability were identified: colony aspect and colony area. Colony aspect and colony area bear directly on detecting human impacts because they allowed comparisons between the visited and control sides of Torgersen Island to be standardized along the habitat features most likely to drive natural variability in these populations at local scales.

Tourist Effects

No effects on the breeding success or population trends of Adélie penguins due to the activities of tourists on Torgersen Island could be detected in this study. Notable is that whether population trends were similar or dissimilar was clearly aspect specific (Figs. 6, 8, 9), rather than dependent on the frequency with which colonies were visited by tourists. Indeed, there was actually somewhat of an inverse relationship here. Tourist distribution patterns (Fig. 7) showed that the colonies on the visited, south-facing side of

Torgersen Island barely registered 5% of all tourist activity, yet showed the most pronounced population decrease (58%) over 10 years (Fig. 9). The north-facing colonies nearest the landing, however, which remained the focal point for tourist activities for the duration of the study (Fig. 3), exhibited population trends that were not significantly different from those in the north-facing control side of the island (Fig. 8). As suggested by Table 8, this lack of a tourist effect is supported by DFA analysis in which group membership between the visited and control sides of Torgersen Island could not be discerned. Furthermore, breeding success comparisons between RSGs within similar aspects (north- or south-facing colonies) revealed no significant differences during the three years of monitoring (Tables 6 and 7).

These results agree most closely with the findings of Cobley and Shears (1999) and Cobley et al. (in press) who also did not find any correspondences between Gentoo penguin breeding success, population trends and tourist activities at nearby Port Lockroy, a popular destination 35 km east of Palmer Station. These results depart completely from the findings of Giese (1996), who detected significant changes in Adélie penguin hatching success or chick survival in the presence of humans. Whether my study is comparable to Giese's (1996), however, is debatable, as the latter encompassed only one season, used base personnel as proxies for tourists and did not examine possible natural sources of variability. Also important, is that unlike Torgersen Island, Giese's (1996) study took place in an area where penguins had no opportunity to habituate to humans. Penguins are known to habituate to human presence and will exhibit varying degrees of tolerance to human activity (Williams 1995).

Possible Research Effects

During the 1995 and 1996 seasons, physiological investigations introduced another scale of activity in the visited area of Torgersen Island. These activities included repeated entries into breeding colonies, serial blood sampling, doubly-labeled water studies and disturbance simulation experiments. Although the various population trends examined did not identify this added activity as a statistically significant event, a biological effect was certainly apparent: post-1994 through 1998, the small south-facing colonies on the visited side of Torgersen Island decreased by 55.3% versus 29.8% for similar south-facing colonies on the control side. This suggested some form of latent effect on these colonies following activities of these researchers. Several studies certainly support this conclusion and identify the effects on future recruitment as the important variable (Reid 1968, Ainley et al. 1983, Woehler et al. 1994, Cobley and Shears 1999).

Davis et al. (1994) noted that in areas of high research activity, the frequent presence of investigators around a colony tends to impact subsequent recruitment into the colonies by new breeders even though no within-season breeding success impacts are observed. These authors also pointed out that smaller colonies may be at greater risk than larger ones (see also Tenaza 1971, Young 1994). Reid (1968) maintained that daily activity associated with their studies prevented young birds from returning to natal colonies, and Ainley et al. (1983) discussed how research methods may have discouraged young birds from remaining near prospective breeding sites. Wilson et al. (1990) suggested that constant human presence did not scare off established breeding penguins, but rather dissuaded young pre-breeders from remaining around prospective colonies. And finally, van Heezik and Seddon (1990) reported that human disturbance both on the landing beaches and in the colony vicinity caused an exodus of young, pre-breeding Jackass penguins (*Spheniscus demersus*).

Final Considerations

Analyses and the Nature of Misclassified Colonies

It would have been desirable to have larger sample sizes in the case of the linear DFA models and some of the regression results. The 4-variable DFA model used in predicting magnitude of colony population change, for example, may have been stronger had there been more colonies (n=23) and fewer predictor variables. Likewise, the linear regression showing a significant negative relationship between breeding success and maximum snow depth during late November, was based on snow measurements obtained at only 9 of the 23 colonies. Nevertheless, examination of some of the misclassified colonies suggests the models were overall quite sensitive and made "biological sense".

In the 3-variable DFA examining breeding population change (Table 2), only one colony is misclassified. Interestingly, this colony is positioned astride the ridge that bisects Torgersen Island, meaning it may show characteristics of a colony in either a north- or south-facing landscape. The Squared Mahalanobis distance from the group centroids is nearly equal for the high and low categories for this misclassified colony. This colony was most likely 'borderline' for discerning group membership simply because the aspect is split on the midline ridge of Torgersen Island.

The 2-variable human impact DFA misclassified 6 colonies (Table 8). Five of these colonies are probably subject to microclimate effects due to their positions near ridges and gullies that may exert localized snow and flooding impacts. Again, the Squared Mahalanobis distances of these colonies were precisely equidistant between group centroids for control and visited groups. Four of these misclassified colonies had also dropped below 50 pairs, possibly a critical threshold (Robertson 1986, Young 1994, Williams 1996). Not surprisingly, the 3-variable DFA (Table 2) correctly identified all 6 of these colonies as belonging to the high decrease group (>25% decrease) based on aspect and area.

Research Scope, Limitations and Management Implications

Antarctic tourism is expected to grow substantially in the foreseeable future, hence the conclusion that no tourism effects on aspects of the demography of Adélie penguin on Torgersen Island could be detected needs to be placed in its proper context. This conclusion does not imply that tourists are having no impacts, but rather that none could be detected above the natural variability in the system. There is also a need to consider the conditions under which these conclusions were reached. Tourism is carefully managed by the National Science Foundation on Torgersen Island in terms of the number of ships permitted (10-12 per season), the number of passengers allowed to land per vessel (<200), the areas that tourists may visit (the visited/control demarcation results in the protection of the largest penguin colonies) and the timing of visits. This management regime may afford some protection to Adélie penguins during especially critical stages in their breeding chronology. Visits typically do not occur until late December (or nearly a month after peak egg laying), a period when penguins may be less susceptible to disturbance. Few other tourist destinations are as carefully regulated, which is one of the reasons researchers and managers are undertaking efforts to develop appropriate guidelines (e.g. Giese 1998). The conclusions reached about tourism in this study should thus be viewed in light of this management scheme alone.

Finally, this study was conducted on an island that has received a consistent level and pattern of visitation for over a decade. The possibility that Adélie penguins habituate to human visitation should not be discounted, as suggested for other penguin species in the presence of human activity (see van Heezik and Seddon 1990, Cobley et al. in press). For this reason, managers may suggest that visits be conducted in areas that have consistently received some level of tourism, rather than concentrating on "expedition touring", in which the focus is to visit new colonies and retreat into areas rarely visited. In addition, given the potentially disproportionate impacts on small breeding groups (see Tenaza 1971, Barbosa et al. 1997), managers may suggest that visits focus activity away from small or isolated colonies.

Future research should consider not only the salient questions at hand, but also how the proposed investigations will affect Antarctic wildlife. In this time of contentious relationships between managers, environmental groups, commercial interests and the well-informed and well-traveled tourist, research must be conducted in a compromise of the most productive, yet applicable and non-invasive methods possible. Furthermore, researchers must take a cautious approach to the selection of a study site and to their understanding of what influences have shaped and continue to drive the population on the local and regional scale. Drawing from Fraser and Patterson (1997), an understanding of the conditions surrounding human presence is vital to discriminating between human and demographic influences.

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APPENDIX A

Colony Descriptors and Breeding Success of Adélie Penguins on Torgersen Island, 1993-1995

Colony	Reproductive Success (±SD)	Number of RSG Sites	Upper and Lower Limit of Population		Visitation Regime	Aspect
1	1.60±0.283	6	150	99	Visited	South
2	1.46±0.76	3	57	33	Visited	South
4	1.20±0.40	6	281	237	Visited	South
6	1.60±0.28	2	102	72	Visited	North
7	1.67±0.16	6	953	899	Visited	North
8	1.48±0.23	5	248*	397	Visited	North
9	1.62±0.21	9	285	241	Visited	North
10	1.53±0.35	9	228	207	Visited	North
11	1.42±0.40	9	254	244	Visited	North
15	1.64±0.22	5	160	146	Visited	North
16	1.33±0.48	18	1271	1175	Control	North
18	1.37±0.39	6	273	258	Control	North
19	1.46±0.28	7	477	467	Control	North
20	1.40±0.13	6	203	178	Control	South
21	1.53±0.27	6	150	126	Control	North
22	1.33±0.70	3	116	89	Control	South

*Census performed late