

USING HIGH-RESOLUTION SATELLITE IMAGERY TO ASSESS POPULATIONS OF
ANIMALS IN THE ANTARCTIC

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Dedication

To Chris Buyarski, for all you do.

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CHAPTER ONE: CONSERVATION APPLICATIONS OF HIGH-RESOLUTION REMOTE SENSING IN THE SOUTHERN OCEAN

Introduction

The need to detect and predict change in our environment is greater than ever, as human-induced climate and habitat changes have rapidly increased during the last 50 years, impacting virtually all of Earth's biomes (Millennium Ecosystem Assessment 2005). Species diversity has drastically reduced largely due to habitat loss (e.g., tropical deforestation, conversion to agriculture), ecosystem function is in jeopardy across the world, and our oceans have been severely overfished (Myers et al. 2000; Brooks et al. 2002; Millennium Ecosystem Assessment 2005; Hoffman et al. 2010; Jackson 2013). Extinction rates are equivalent to the last major extinction episode at the end of the Cretaceous period (Barnosky et al. 2011). However, data necessary to gain a regional to global understanding of changes to ecosystems and populations cannot be gathered from field data alone, as models from relatively small-scale studies are incapable of predicting global consequences of human activities (Kerr and Ostrovsky 2003). Incorporating scale-appropriate remote sensing data to ecological and conservation research is imperative to focus conservation, management, and policy decisions regarding our natural environment.

Some of the most rapidly changing ecosystems on the planet can be found in Antarctica (Vaughn et al. 2003; Montes-Hugo et al. 2009; Schofield et al. 2010; Doney et al. 2012; Murphy and Hoffman 2012; Smith et al. 2014). For example, as air temperatures have increased markedly since 1950 on the Antarctic peninsula (Meredith

and King 2005; Schofield et al. 2010), >70% of glaciers have retreated (Cook et al. 2005), along with substantial loss in extent and duration of sea ice (Stammerjohn et al. 2012) and correlated decreases in ice-obligate species such as the Weddell seal (*Leptonychotes weddellii*), Adélie (*Pygoscelis adeliae*), chinstrap (*Pygoscelis antarctica*), and emperor penguins (*Aptenodytes forsteri*; Siniff et al. 2008; Montes-Hugo 2009; Schofield et al. 2010; Trathan et al. 2011; Lynch et al. 2012a; Naveen et al. 2012). Indeed, population declines or extinction of some penguin species are predicted, assuming current rates of sea ice loss (Smith et al. 2003; Jenouvrier et al. 2006; Jenouvrier et al. 2009; Ainley et al. 2010; Lynch et al. 2012a). Furthermore, resources in the Southern Ocean are important economically, due to fishing of krill (*Euphasia* spp.), mackerel icefish (*Champsocephalus gunnari*), and toothfish (*Dissostichus* spp.; Agnew 1997; Croxall and Nicol 2004; Griffiths 2010; Brooks 2013). The changing environment coupled with extraction of key prey and competitors from the Southern Ocean food web creates a substantial need for informed conservation and resource management. However, gathering necessary data to make such management decisions remains difficult, as little is known about the life cycle of toothfish (Blight et al. 2010; Ainley et al. 2012a; Ainley et al. 2012b) and direct data on krill abundance and distribution is expensive to gather and prone to error (Croxall and Nicol 2004; Demer 2004). Thus, using krill and toothfish predators (e.g., Adélie penguin, Weddell seal) as a proxy for understanding abundance and distribution of their prey remains the most viable option for building accurate resource use models and setting appropriate catch limits (Agnew 1997); and to best gain information at regional- to global scales, remote sensing of predator populations in the

Southern Ocean is likely to be the most efficient and cost-effective complement to Antarctic field work.

For more than 40 years, remote sensing platforms have gathered a multitude of ecological and climatological data on a routine basis. Landsat has been the satellite platform of choice in many ecological research studies (Cohen and Goward 2004), and has been widely used for a range of ecological applications (Leimgruber et al. 2005), including research on vegetation monitoring and phenology (Rouse et al. 1974; Melaas et al. 2013), forest structure and productivity (Nemani and Running 1989; Cohen et al. 1995; Steininger 2000), species modeling (Dymond et al. 2002), and habitat assessments (Mack et al. 1997; McComb et al. 2002). The spatial resolution of Landsat has increased over the years, but even the highest-resolution (15 m) still precludes the more detailed analysis necessary for fully understanding species distributions, particularly for animals. Use of satellite imagery in animal studies has traditionally focused on habitat assessment/mapping and environmental proxies for abundance or diversity. Indeed, identification of animals from space is difficult, as most species are smaller than the largest pixel of available satellites, and revisit times are too infrequent for meaningful comparisons (Gillespie et al. 2008). However, advances in technology over the past 15 years have changed this scenario such that direct assessments of animal populations may now be possible with high-resolution satellite imagery.

Very high resolution (VHR) satellite imagery here refers to images with spatial resolutions of 0.5-2.4 m (DigitalGlobe, Inc., and GeoEye platforms), and is a relatively recent augmentation to remote sensing for ecology and conservation. While the use of

VHR images in ecology has increased through time as costs have decreased, most VHR imagery has been used to address research in temperate, tropical or coastal regions (Mumby et al. 2002; Carleer and Wolff 2004; Clark et al. 2004; Nagendra and Rocchini 2008; Nagendra et al. 2010). Until recently, assessing populations of animals in polar regions had never been addressed using VHR images, although the implications and capabilities of methods associated with analysis of VHR images create an important case for its use in population assessment.

Because of the influx of recent research using VHR imagery to assess populations of predators in polar regions, my goal is to review the literature and discuss the implications for conservation of ecosystems and biodiversity, and sustainable resource use in the Southern Ocean. This review is intended to promote further discussion regarding use of VHR images in ecological and conservation research in similarly remote areas, where these data can provide much needed information for conservation efforts.

Direct remote sensing of ice-obligate vertebrates

Assessing vertebrates with VHR imagery in polar regions has some interesting advantages. Despite the inaccessibility of much of these areas for field work, the lack of vegetation and relatively cloud-free conditions make using VHR imagery easier, more efficient, and less expensive than field campaigns. The polar orbits of these satellites also make revisit times more frequent than in others areas of the world, enhancing temporal comparisons. Recently-launched high-resolution satellites (i.e., GeoEye and DigitalGlobe platforms) have revolutionized ecological research in polar regions, through both direct and indirect assessments of animal populations.

Direct assessment here refers to visually identifying individual animals on satellite images, similar to aerial survey methods. However, despite very high spatial resolutions, only the larger animals can be directly identified in 0.6 m imagery (i.e., typically only the panchromatic—“gray-scale”—images are suitable for this due to their higher resolution). The first study to use VHR on a large-bodied, Arctic species was Boltunov et al. (2012), who determined the satellite parameters applicable to walrus (*Odobenus* spp.) research in the Russian Arctic. Researchers used EROS B images with different off-nadir angles and cloud cover to determine the best conditions for identifying (and ultimately assessing) walrus from high-resolution imagery. While the authors did not specify a maximum off-nadir angle or cloud cover for assessing walrus, the best images were directly overhead (0° off-nadir) and cloud-free. It is important to consider that higher off-nadir shots resulted in the inability to detect individuals, as future research planning for walrus or other species can benefit from this information. With the advent of Worldview-2, and the upcoming launch of Worldview-3, higher spatial and spectral resolutions may prove to be useful tools for also assessing animals in the water (Fretwell et al. 2014).

Recently, VHR imagery was also used to determine a method for assessing polar bear (*Ursus maritimus*), another large-bodied, ice-obligate species of concern in the Arctic. Stapleton et al. (2014) used a unique combination of high-resolution imagery within a mark-recapture framework (i.e., Huggins model; Huggins 1989) to compare counts from images to results from mark-recapture distance sampling to assess the population of polar bears on Rowley Island, Canada. Using images two years apart (one “active” image from September 2012 and one used as a reference from September 2010)

that covered the entirety of the island, two observers compared images for differences. The idea here was that snow and ice conditions for Rowley Island should be similar between years at that time, making polar bears the only items on the landscape that reasonably would move between images; spotting a large white dot on a snow-free landscape in 2012 but not in 2010 indicated a likely polar bear. Observers independently assessed images and then compared results in a double-observer method, commonly used in wildlife research (Nichols et al. 2000). Results indicated that assessing high-resolution imagery was comparable to aerial survey methods, and also more precise. Given polar bears have a circumpolar distribution and are of conservation concern (DeRocher et al. 2013), VHR image assessment could very well fill in gaps in our knowledge of distribution and abundance of these top marine predators in the Arctic.

Indirect assessment of populations

While direct assessments of populations are isolated to large-bodied mammals at this point (even whales; see Fretwell et al. 2014) due to resolution restrictions, indirect assessments are another method of determining population status, particularly in the Antarctic. As with many ecological studies that incorporate satellite imagery, the first penguin-remote sensing study was conducted with Landsat images (Schwaller et al. 1984; Schwaller et al. 1989), and suggested a strong correlation between pixels identified as Adélie penguin guano on images, with the number of breeding pairs on Ross Island, Antarctica. Nearly 20 years later, Fretwell and Trathan (2009) used Landsat to determine colony locations of emperor penguins along the sea ice of the entire coastline of Antarctica. Schwaller et al. (2013) recently assessed the Adélie penguin population at a

continental scale with Landsat, but excluded the Antarctic peninsula. In each of these cases Landsat resolution (15 m-30 m) was not optimal for an assessment of abundance due to coarser resolutions. Higher-resolution images, closer to those found in aerial photographs (e.g., Woehler and Riddle 1998; Chamailles-James et al. 2000), would be necessary for estimating population size.

Shortly after the first VHR satellites launched (Quickbird-2 and Worldview-1), Barber-Meyer et al. (2007) used VHR images to develop a method for estimating abundance of emperor penguins using supervised classification techniques. Using only panchromatic images, researchers compared population estimates predicted from image and statistical analysis to aerial and ground surveys at seven colonies in the Ross Sea, Antarctica and found a large variance in their predictions. Absolute deviation from ground counts varied substantially (0.2-128%; Barber-Meyer et al. 2007). However, this work was important in identifying strengths and weaknesses of the method and provided recommendations for future work, noting that pan-sharpened multispectral images (images with enhanced spatial resolution by “sharpening” the multispectral images to match the higher resolution of their panchromatic pair) would provide greater power in differentiating items on the landscape.

Building on this work and the recent identification of colony locations around the coastline, Fretwell et al. (2012) used a similar supervised classification technique to assess the first global estimate of emperor penguins. However, this study did incorporate pan-sharpened images, which allowed for enhanced identification of the spectral classes (i.e., guano, ice and penguin pixels). With ground-validated data to inform a robust

regression that transformed number of penguin pixels to number of penguins, authors found nearly 600,000 emperor penguins in Antarctica in 2009 at 46 colonies. This analysis identified an additional seven colonies previously unknown to science, and was the first to address a global population of an important indicator species with regard to climate change and Southern Ocean resources.

Over the past several years, much research has built upon previous methods (Schwaller et al. 1989; Woehler and Riddle 1998; Barber-Meyer et al. 2007; Fretwell et al. 2012; Mustafa et al. 2012), and has focused almost solely on Antarctic penguins because they are an indicator species for the health of the Southern and the relative availability of its resources (i.e., krill and fish; Ainley 2002a; LeBohec 2012). Naveen et al. (2012) used VHR imagery combined with ground counts and reports in the literature to find a drastic decrease in the chinstrap penguin population over 25 years at Baily Head on Deception Island, which is off the western coast of the Antarctic Peninsula. Researchers manually delineated the guano stain in each image and found the colony had collapsed substantially in just seven years; further analysis with historic records identified that Baily Head was at less than half its population in 1989 (Shuford and Spear 1989). Similarly, LaRue et al. (2013) combined high-resolution imagery with historic air photos to calculate available habitat for Adélie penguins on Beaufort Island in the Ross Sea, also by manually delineating the boundaries of the guano stain on each image. This study found that glacial retreat on the island over >50 years resulted in habitat release and associated population increase at Beaufort Island, and also had an effect on emigration rates within the southern Ross Sea metapopulation. Both of these studies demonstrate the

powerful combination of data fusion between historic photos and information, recent images, and field and weather data. These studies represent important applications of remote sensing to better understand population change of Southern Ocean predators.

Due to the influx of these new techniques and tools found associated with VHR images, researchers have found utility for other aspects of understanding penguin colonies in the Antarctic. For example, Lynch et al. (2012b) used VHR images to differentiate penguin species on the Antarctic peninsula from differences in guano stain between species, Fretwell et al. (2014) found that emperor penguins breed on ice shelves in years of unfavorable sea ice, and LaRue et al. (unpublished data) analyzed VHR images, and suggested that emperor penguins may move between colonies more frequently during environmental perturbation. Very high resolution imagery is becoming an invaluable tool, not only for basic research involving population abundance and distribution, but it has also provided insight into the behavioral ecology of some of Antarctica's most iconic and ecologically important species.

Biodiversity conservation in polar regions

Because the Antarctic is a remote and potentially dangerous place in which to live and conduct field work, it is inherently less understood than readily accessible areas of our planet. However, rapid change in the Southern Ocean is making it more important to gain a greater understanding of ecosystem function for conservation of biodiversity, and climate and resource-use models. It is crucial to use the most advanced tools to study the effects and drivers of environmental change in the Antarctic.

The Southern Ocean represents just 10% of the world's ocean area, yet it contains

~280 of known, endemic species of fishes (Eastman 2005), is important feeding grounds for whales (Laws 1977; Laws 1985; Ichii and Kato 1991), contains the most pristine body of water on Earth (the Ross Sea; Halpern et al. 2008), and is home to endemic species, such as Adélie and emperor penguins. However, our southern-most ocean is also economically important. Fisheries take >160,000 tons of krill and 1,000 tons of icefishes annually with a market value of ~\$160 million (Brooks 2013). Fishing in the Southern Ocean is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), an organization committed to an ecosystem-based approach to resource management with a mission to oversee rational use of Southern Ocean resources. Any exploitation of resources must be such that changes cannot be undone within 20-30 years (Agnew 1997; Brooks 2013). One important way CCAMLR manages the Southern Ocean ecosystem is to understand and monitor the distribution and abundance of krill predators, which includes penguins and seals (Agnew 1997). In the case of the Adélie penguin, this means that any data on diet, foraging patterns, breeding success, and survival have been recorded at easily accessible locations, typically in proximity to research stations. Given very few of the ~250 Adélie penguin colonies in Antarctica are regularly monitored, and that a recent study found the global population to be nearly 50% greater than previously estimated (Lynch and LaRue 2014), current resource use models may be severely underestimated and catch limits for krill may be set too high. Rational use of the Southern Ocean, in this case, may be in jeopardy. Thus, the only feasible method of assessing regional to global population change of the important krill predator, the Adélie penguin, is through analysis and annual monitoring of VHR

images. In no other way are we capable of gathering such high-resolution data that would most precisely identify changes in distribution and abundance, and lead to accurate models of sustainable resource use.

Another important, economically viable resource that may be exploited in the Southern Ocean is the Antarctic toothfish (*Dissostichus mawsoni*), particularly in the Ross Sea. The Ross Sea, located approximately 2500 km south of New Zealand, is the most pristine body of water on the planet (Halpern et al. 2008) and is home to 25% of the world population of emperor penguins (Fretwell et al. 2012; Smith et al. 2014), ~30% of Adélie penguins (Ainley 2002a; Lynch and LaRue 2014; Smith et al. 2014), thousands of Weddell seals and killer whales (*Orcinus orca*); and also the Antarctic toothfish (sold in restaurants as Chilean seabass). Antarctic toothfish represent an important piscine predator in the Ross Sea, as it is prey for Weddell seals and killer whales (Ainley and Siniff 2009; Ainley 2012), and competes with Adélie and emperor penguins for smaller species, such as Antarctic silverfish (*Pleuragramma antarctica*). The current issue for the Ross Sea is its protection from toothfish fishing, which may already be having impacts on ecosystem function (Ainley 2002b; Ainley and Siniff 2009; Ainley et al. 2012a; Ainley et al. 2012b). After >15 years of fishing in the region, studies have shown a decrease in occurrence of Type C killer whales (Ainley 2010), Weddell seals have decreased substantially in the northern portions of the region (Ainley et al. 2014), and scientific catch of toothfish has decreased significantly (Ainley et al. 2012b); however, Adélie penguin populations have increased markedly (LaRue et al. 2013; Lyver et al. 2014; Lynch and LaRue 2014). Such changes may be indicative of a trophic cascade that would

result from the increased take of toothfish from the system. Furthermore, because very little is known about basic aspects of the toothfish life cycle (i.e., age at first reproduction, fecundity, survival; Eastman and DeVries 2000; Ainley et al. 2012b) that would inform fishery catch models, CCAMLR decision-makers are currently reliant on accurate population data about toothfish predators and competitors. As evidenced by the Antarctic Pack Ice Seals (APIS) Program research cruises that took place in the early 2000's, the Antarctic coastline is logistically challenging and an expensive mode of gathering the necessary, annual abundance estimates (Bengston et al. 2011) that are needed for management decisions to be made. Analysis of VHR imagery is currently the only feasible method for estimating annual abundance of these important predators in the Ross Sea and the rest of the inaccessible Southern Ocean.

Conservation of biodiversity in other remote areas

While Antarctica and the Southern Ocean are remote and inaccessible, so too are many other areas of important conservation concern that could benefit from analysis of VHR imagery. For example, the abundance and demography of most polar bear ecoregions in the Arctic remain largely unknown, although it is largely predicted that decreasing sea ice conditions in the Arctic will negatively impact survival (Regehr et al. 2007; Rode et al. 2012; Derocher et al. 2013). Given that polar bears are an important indicator of environmental and climate change, and are harvested in some regions yet protected in others (Derocher et al. 2002; Peacock et al. 2010), knowledge of regional status of populations would augment conservation and management efforts. Other indicators of environmental change in the Arctic are Pacific walrus (*Odobenus*

rosmarius), bowhead whales (*Balaena mysticetus*), and beluga (*Delphinapterus leucas*; Laidre et al. 2008); having remote access to data through which population counts can be made would certainly fill gaps regarding direct contribution of sea ice changes, fisheries, and/or harvest on regional populations.

Use of remote sensing in animal conservation and ecological research has focused primarily on habitat as a proxy for abundance or species richness, particularly outside of polar regions (Peterson et al. 2006; Raxworthy et al. 2006). Given my review, I suggest the possibility of VHR imagery to be used in conservation research on other, large-bodied animals in similarly remote areas. For example, the African savannah is an endangered biome that encompasses >10 million km² (Riggio et al. 2012) and is home to many ungulate species (African buffalo [*Syncerus caffer*], zebra [*Equus quagga*], wildebeest [*Conochaetes* spp.]) that congregate in large herds, in reliable areas at specific times of year (Vesey-Fitzgerald 1960). Routine monitoring of these areas or migration routes could provide insight to changes in population size and distribution and has the potential to inform future research efforts. A possible next candidate through which to test the use of VHR imagery could be African elephants (*Loxodonta africana*). It is possible that elephants would be identifiable from images with little ground validation, and there is much interest in status and distribution of threatened populations (Stephenson and Ntiamoa-Baidu 2010). Given the incredible conservation efforts expended on several elephant populations and their savanna habitat, it may be crucial to add another tool from which pertinent conservation decisions can be made.

Ecologists and conservation biologists have slowly adopted geospatial technologies

and remote sensing into their research (Turner et al. 2003; Boyle et al. 2014). However, remote sensing, and VHR imagery in particular, is needed to understand some of the most basic population parameters in order to further gain knowledge about environmental drivers of species distributions and changes. Given the vast challenges facing biodiversity globally, it is imperative that ecologists and conservation biologists gain exposure to available remote sensing and geospatial tools, and collaborate with such experts to address challenges in some of the world's most remote areas.

CHAPTER TWO: SATELLITE IMAGERY CAN BE USED TO DETECT
VARIATION IN ABUNDANCE OF WEDDELL SEALS (*LEPTONYCHOTES
WEDDELLII*) IN EREBUS BAY, ANTARCTICA

Introduction

Weddell seals (*Leptonychotes weddellii*) are found along the coast of Antarctica, where fast ice is present for a significant portion of the year. Females are philopatric (Stirling 1969a; Stirling 1974; Croxall and Hiby 1983; Cameron and Siniff 2004; Cameron et al. 2007; Hadley et al. 2007) and form traditional haul outs for pupping where persistent tide cracks reliably offer access from the ocean to the ice surface (Tedman and Bryden 1979; Siniff et al. 2008). While one of the best-studied marine mammal populations in the world exists in Erebus Bay (Hastings and Testa 1998; Cameron and Siniff 2004), less is known about populations of Weddell seals elsewhere around the Antarctic continent. The paucity of data regarding population status of seals is largely due to the logistical difficulties of accessing potential seal habitat in areas of Antarctica that are not in close proximity to research stations. Knowledge of seal distributions and numbers in other areas would be valuable for a variety of reasons. First, when attempting to understand the dynamics of local populations, it would be useful to know the status of nearby populations that may be involved in temporary immigration/emigration exchanges (Cameron and Siniff 2004; Rotella et al. 2009). Further, information on population status from numerous locations around the continent will be important for monitoring the species' overall status and its responses to environmental change (Siniff et al. 2008). Thus, developing methods for attaining

knowledge of Weddell seal status throughout Antarctica is important to understanding the ecology of sea ice seals and to assessing the potential impacts of climate change or other anthropogenic influences on upper top-trophic predators.

Knowledge of Weddell seal abundance at diverse locations will also be useful for more general monitoring of the Antarctic marine system. For example, Weddell seals are an important predator of Antarctic toothfish (*Dissostichus mawsoni*; Ponganis and Stockard 2007), which have become the target of a fishery in the Ross Sea (Ainley and Siniff 2009; Blight et al. 2010). Given the difficulties of using standard methods to monitor toothfish in Antarctic pack ice conditions, and in keeping with CCAMLR's precautionary and ecosystem management principles (Constable et al. 2000; Croxall and Nicol 2004), it would be desirable to monitor seal numbers along with fish harvest to evaluate fishery impacts on this important top-level predator and its food web.

Traditional monitoring methods for pinnipeds include using aircraft or aerial photography to census populations in the Arctic (McLaren 1966; Burns and Harbo 1972; Lavigne et al. 1982; Gilbert 1989; Johnston et al. 2000; Bester et al. 2002; NMML 2007), and intensive on-the-ground counts on shore-fast ice (Siniff et al. 1977) or ship-based line-transect surveys through pack ice (Gelatt and Siniff 1999; Ackley et al. 2003; Southwell et al. 2004; Flores et al. 2008; Bengston et al. 2011) in the Antarctic. Weddell seals haul out on the surface of shore-fast ice to give birth, suckle young, rest and molt, so employing imaging techniques to obtain population trends along the Victoria Land coast of the Ross Sea is feasible. Aerial surveys have previously been used to count seals in the Ross Sea (Smith 1965; Stirling 1969b). However, technology has advanced such

that the use of satellite imagery may now be used to conduct significant research in the Antarctic (Barber-Meyer et al. 2007; Fretwell and Trathan 2009; Fretwell et al. 2012), while minimizing the substantial efforts and impact to the Antarctic environment of ground and aerial survey methods (Eberhardt 1979; Green et al. 1995; Southwell 2005a).

Studying Weddell seals in the Ross Sea using satellite imagery has already been suggested in the literature (Barber-Meyer et al. 2007), and distribution and abundance around the continent has only recently been addressed by the international research program, Antarctic Pack-Ice Seals (Bester et al. 2002; Bester and Stewart 2006; Bengston et al. 2011); United States' efforts within the Ross Sea occurred during 1999-2000 (Ackley et al. 2003; Bester and Stewart 2006; Bengston et al. 2011). Thus, I wished to determine whether satellite imagery could be used to reliably identify adult Weddell seals hauled out on the ice, and whether counts determined from imagery could provide accurate information about known abundances. Here I present findings that suggest high-resolution (0.6m) satellite imagery can be used to identify occurrence and to detect changes in abundance of a Weddell seal population. The cost of high-resolution imagery has made this kind of research difficult in the past, but satellite imagery is becoming more available and costs are declining. my methodology will likely facilitate similar research in the future, and may allow an efficient, cost-effective way to study polar pinnipeds in areas where little is known about distribution and abundance.

Methods

My study area comprised approximately 420 km² of Erebus Bay (Figure 2.1), in southeast McMurdo Sound, Antarctica (lat. 77°12' S, long. 166°35' E). Much of Erebus

Bay is covered by fast ice for most of the year, owing to its southerly location, the presence of several small islands, and the entrapment of ice by the Erebus Ice Tongue. Wind and tidal action on fast ice, the presence of small islands, and pressure generated by movements of the Erebus Ice Tongue create reliable perennial haul-out sites where Weddell seals establish reproductive colonies (Stirling 1969a). I focused search efforts on reliable haul-out locations within Erebus Bay (Wilson 1907; Smith 1965; Figure 2.2) where continuous mark-recapture studies were initiated in the 1960s (Smith 1965; Stirling 1969a; Siniff et al. 1977) and where recent ground counts coincided with available satellite imagery.

I gathered high-resolution satellite images of Erebus Bay during November 2004-2006 and 2009, and December 2007. I used WorldView-1 (panchromatic, 0.6m resolution) and QuickBird-2 (2.4m multispectral and 0.6m panchromatic) images, which were identified through the vendor's search tools (www.digitalglobe.com). Local times of image capture ranged from 1000-1300 hours, and these images were the only suitable, cloud-free images of the area as of December 2009. Each image was then analyzed for its utility. To do so, a remote sensing analyst determined, without knowledge of ground count results, which images and haul-out locations within each image to use based on image quality. Criteria for including a haul-out location in analysis were: 1. sufficient quality of the image (i.e., low banding, cloud-free, and few shadows); 2. the entirety of a haul-out location was captured within the image; and 3. the dates of ground counts and satellite images were within 7 days of each other. If any haul-out location on any image did not meet all 3 criteria, it was omitted from analysis.

One observer counted seals from the imagery at each suitable haul-out location on each image. The number of haul-out locations compared per date differed based on image quality and the spatial coverage of each image. For example, Big Razorback Island was captured on the image dated 12 November 2006, so I counted the number of seals present and compared those results to ground counts made at that location and on that date. Ground counts at locations that were not represented on a given image were not used for comparison for the image date. I only made comparisons of seal counts at haul-out locations where the image and ground counts were spatially and temporally comparable (within 7 days).

All QuickBird-2 images were then pansharpened (i.e., increase in image quality by merging lower-resolution multispectral with higher-resolution panchromatic imagery to create one high-resolution, multispectral image) to 0.6m resolution, and imagery searches were completed in ArcGIS 9.3 (ESRI 2009). I confirmed presence of seals in images and then recorded seal counts by overlaying a blank shapefile on the image and placing a single point on each location of a suspected seal. I searched each image at a scale of 1:2,000 (Figure 2.3) without prior knowledge of ground count data. The total number of seals at each location per image date was recorded in the GIS shapefiles.

Ground counts were conducted in Erebus Bay, Antarctica from 1000 hours to 1800 hours at 3-6 day intervals from early November until mid-December each year. These counts recorded all individual adult seals, individual pups, and adult-pup pairs. Because Weddell seals that are hauled out are highly detectable (Rotella et al. 2009), I am confident that these ground counts missed very few seals that were present on the ice

surface at the time of the count. Thus, my measure of abundance from ground counts was the actual count on the surface on a given day at a given haul-out site. Repeated counts on marked animals can be used with mark-recapture methods (Williams et al. 2002) to estimate actual abundance (Rotella et al. 2009) but that was not my focus in this effort. Here, I was interested in knowing if counts of seals on the ice made on the ground would strongly correspond with counts of seals via satellite image.

For each location and date for which I had associated ground and satellite counts, I calculated the number of seals counted by each method, and the proportion of ground-counted adult seals that were detected by satellite across all haul-out locations that could be used across a given year. I excluded pups from all comparisons because I assumed that pups, which even at weaning generally are less than half the size of adults, would be less likely to be detected in 0.6m resolution imagery. Pearson's correlation coefficient was calculated for annual counts from the two approaches, and for counts from the two approaches at individual haul-out locations. I also determined change in abundance through years at 3 haul-out locations where ≥ 3 satellite-to-ground count comparisons were possible, and calculated Pearson's correlation coefficient for each location through time.

Results

My results indicate that useful information about seal abundance can be obtained from high-resolution satellite imagery. During 2004-2009, five images of haul out locations within Erebus Bay were used to compare image counts to ground counts, and each haul-out location defined (Figure 2.2) was compared at least once. One location

was compared four times and two locations had only one satellite-to-ground count comparison (Table 2.1). A total of 21 satellite-to-ground count comparisons were made across the five images (Table 2.1). Annual satellite counts summed across multiple haul-out locations had a strong, positive correlation with accompanying ground counts ($r = 0.98$, $df = 3$, $P < 0.003$) and would have been useful for detecting the major changes in annual ground counts (Figure 2.4). When calculated at the individual haul-out level, image counts also had a strong, positive correlation with ground counts ($r = 0.80$, $df = 19$, $P < 0.001$). I further determined strong correlations and detected changes in abundance of seals present on the ice at haul-out locations with ≥ 3 ground-to-satellite comparisons (Figure 2.5).

Across the five years, 1,000 seals were detected on the five annual images, which represented 71.7% of the 1,394 seals known to be present from ground counts (Table 2.1). However, satellite counts did not detect a constant proportion of the seals detected in ground counts. In 2004, when the fewest seals were recorded on ground counts, counts from imagery detected only 30% of the seals known to be present. In contrast, during the two most recent years, in which ≥ 385 seals were detected on ground counts, image-based counts detected $\geq 82\%$ of seals known to be present (Table 2.1).

Discussion

My work provides an important step forward in polar ecology by demonstrating that remote sensing data can be used effectively to identify presence and determine abundance of the Weddell seal population within Erebus Bay, Antarctica. This study combined a few important factors that contributed to the strong results. First, the Weddell

seal population of the Erebus Bay area was an ideal test population because of its accessibility and proximity to McMurdo Station and because of how much is known about the current and historical population abundance of adult seals there (Smith 1965; Stirling 1969a; Siniff et al. 1977; Testa and Siniff 1987; Hastings and Testa 1998; Cameron and Siniff 2004; Hadley et al. 2007). Long-term population datasets are rare for large, long-lived animals (Fossey and Harcourt 1977; Croxall and Kirkwood 1979; Garrott and Taylor 1990; Micol and Jouventin 2000) and the population of seals in Erebus Bay provided a unique opportunity for the count comparisons needed to establish strong correlations between ground and satellite counts.

Secondly, because it is nearly impossible to count all animals present in a population (Williams et al. 2002), it is important to conduct surveys during a peak in the population to minimize missing individuals (Eberhardt et al. 1979; Green et al. 1995; Boyd et al. 2010). Ideally, such counts of seals should occur after birthing when adult females are more likely to be on the surface and available for detection (Eberhardt et al. 1979). Thus, the time of year I compared images to ground counts was important because the population peaks in October-December (Stirling 1969a; Tedman and Bryden 1979; Siniff 1981), when pregnant Weddell seals haul out in groups in Erebus Bay and remain on the ice for several weeks after pups are born (Lindsey 1937; Stirling 1969a). This is also the season when annual ground counts are conducted (Rotella et al. 2009; D.B Siniff, J.J. Rotella, R.A. Garrott, personal communication). Comparisons were made during an ideal time, when the population was at its peak and when a relatively large proportion of individuals were visible on the ice. It is, however, worth noting that the

counts here do not represent the actual abundance of seals present in the study area because on any given survey a large proportion of adult seals, especially males (Stirling 1969a; Gelatt et al. 2000; Gelatt 2001), may be in the water and undetectable with ground or satellite counts. Regardless, mark-recapture estimates of population abundance from repeated surveys within a year do indicate that counts from any single survey are positively correlated with abundance estimates that do take failed detections into account (J.J. Rotella, R. A. Garrott, and D. B. Siniff unpublished data).

Marine mammal populations are generally difficult to census, and direct observations in particular are often hindered by inaccessibility and difficult logistics (Eberhardt et al. 1979; Gelatt and Siniff 1994; Green et al. 1995; Boyd et al. 2010; Bengston et al. 2011). This approach minimizes several disadvantages of traditional census methods. First and quite importantly, high-resolution satellite imagery eliminates any effects of observer presence on the individuals in the population that would normally occur by walking near, sailing by, or flying over the area (Buckland et al. 2001; Southwell 2005a). Although such effects are not problematic for Weddell seals, human presence can cause major disturbance in breeding colonies of some pinniped species. Use of satellite imagery provides a passive way of viewing a truly undisturbed population. Second, the imagery I used has a wide swath, which provided me with an image of $\geq 400\text{-km}^2$ for each comparison date. The possible area covered by several satellite images per day ($>5,000\text{ km}^2$) would potentially allow the observation of a much larger region than would be logistically possible to cover on foot, plane, or ship in one day. Third, using satellite-based survey methods would allow us to readily obtain

replicate counts, and would provide the potential to develop rigorous sampling schemes across large areas. For example, coastal areas already known to be breeding sites for Weddell seals could be repeatedly surveyed during the peak of pupping in November to evaluate changes through space and time. Analyses of data across multiple years could then be used to learn about how similar or dis-similar population changes might be across large areas. The technique described here could also be used to identify other large aggregations of seals, if images for coastal areas were repeatedly surveyed when many seals are hauled out (e.g., November pupping season or January when adult seals stay near breeding colonies during the annual molt [Burns and Kooyman 2001]). Surveys in pack-ice areas that have been shown to support large numbers of other seals (Bengston et al. 2011) can be also be used to monitor other species and non-breeding aggregations of Weddell seals. As the methods here did not evaluate the performance of the survey technique in pack ice, it would be ideal to initially pair satellite surveys with information from traditional methods to facilitate comparisons. If correlations between counts from traditional and satellite methods are strong, it could be possible in the future to obtain more information remotely.

Another disadvantage of conducting such rigorous sampling by ship or aircraft-based platforms is that such methods are typically limited by high cost and logistical difficulties, and some areas of Antarctica are impossible to reach. My methods that used satellite imagery, which was provided through federal licensing agreements, GIS software, and 1-2 observers would cost a fraction of what would be spent gathering the same data on the ground, especially when scaled to cover large or inaccessible areas.

Finally, optical satellite imagery can be combined with remotely-sensed sea ice data to correlate patterns of abundance and distribution of seals, providing a broader-scale understanding of the effects of sea ice on seal ecology.

Counts from satellite imagery were consistently lower than the ground counts of adult Weddell seals. However, I accurately captured changes in abundance across years at 3 haul-out locations (Figure 2.5). But the disparity between the ground counts and the satellite counts may be due to the time of day images were acquired. Because the QuickBird-2 and WorldView-1 satellites have polar orbits, the time of day when images were on-nadir (i.e., directly vertical over the study area) was always between 1000 and 1300 hours. It is well-known that Weddell seals have a diurnal haul-out pattern (Smith 1965; Stirling 1969a; Stirling 1969b; Siniff et al. 1971; Lake et al. 1997), with the largest proportion on the ice between 1200-1900 hours (Siniff et al. 1971; Lake et al. 1997). Satellite images were collected just before the most inactive portion of the day, and the seals counted were only a proportion of what would likely be hauled out later during the day. It seems likely that part of the discrepancy between counts was due to collection time of satellite images during the day.

Further, I noticed that detection rates of seals from the imagery were not consistent, ranging from a low of 30% in 2004 to a high of 88% in 2009. Annual variation in total ground counts and in ice surface conditions was high, which provided a useful dataset for evaluating the utility of counts from satellite images. During the study period, ice conditions and seal numbers were strongly influenced by a massive iceberg that blocked the usual advection of sea ice from the area during 2004-2006 (Arrigo et al.

2002; Siniff et al. 2008). During the first several years of the study, the ice was unusually thick with larger and more extensive pressure ridges than are typically experienced in the area. These large pressure ridges and jumbled ice within Erebus Bay made the detection of seals on the ice more difficult, leading to lower detection rates from the satellite imagery. After the iceberg broke up in 2006, pressure ridges gradually diminished in size and extent and the smoothness of the ice surface increased. Data succeeded in capturing seal response to these conditions (Figure 2.5).

However, the consistent under-identification of seals from satellite imagery suggests that for future work, applying some kind of correction factor may be warranted (Eberhardt et al. 1979; Erickson et al. 1989; Bengston and Stewart 1992; Lake et al. 1997; Southwell 2005b; Boyd et al. 2010; Bengston et al. 2011), should the objective be to determine exact population densities of Weddell seals. I did not include a correction factor for this study because this was beyond the scope of my initial investigation. My goal here was to demonstrate the utility of high-resolution satellite imagery for identifying and enumerating seals on the sea ice surface, which could potentially be used for providing an index of abundance, and further as a trend indicator for seal populations in the Antarctic.

High-resolution satellite imagery is a powerful tool for remotely evaluating both the biotic and abiotic components of ecosystems (Boyd et al. 2010). Antarctic ecology is particularly intriguing, because photo identification of ice-dependent, marine species can be fairly straight-forward (Barber-Meyer et al. 2007; Fretwell and Trathan 2009; Fretwell et al. unpublished data), as animals are easily detected and identifiable. Further, as

satellite technology enhances and resolution increases, improvements in the utility of this method will also likely increase. However, I found that weather conditions were one of the most constraining factors to the success of my study. Should these methods be applied in other polar locations or to other species (such as walruses, polar bears, or even large cetaceans), one must realize an almost sole dependence upon cloud-free imagery devoid of shadows, in order to gain any knowledge about animal presence. Short, temporally-dependent studies (on the order of days or weeks) may not be able to utilize such high-resolution imagery, as sustained cloud cover or excessive banding could render an entire study useless (Figure 2.6). The optical nature of QuickBird-2 and WorldView-1 satellites further dictates a dependence on daylight conditions. During the winter in polar regions the use of QuickBird-2 or WorldView-1 imagery to answer ecological questions is not possible. So, while the use of optical imagery in polar regions has several advantages, it also provides some constraints that must be considered prior to conducting similar studies.

Remote sensing of Weddell seals in Erebus Bay indicated a strong, positive correlation ($r=0.98$) between counts of adult Weddell seals from satellite imagery and actual ground counts collected during the same time. Given my indications here that satellite counts can provide information about relative abundance and, more importantly, changes in relative abundance, I am confident that my technique can be applied to search for seals in larger areas where abundance is unknown and where general population trends have never been observed. For example, across broad areas one could examine which populations grow, shrink or remain unchanged as sea-ice conditions change, as

fish harvesting practices vary, or as other environmental conditions change through time. One could also investigate possible spatial structuring of population units by monitoring populations separated by varying degrees of distance and occupying locations with different environmental attributes.

It would be useful to conduct further work in Erebus Bay using repeated counts of colonies, assessment of diurnal haul out patterns, and comparisons of rigorous mark-recapture estimates of absolute abundance (Rotella et al. 2009) with estimates obtained from satellite imagery to determine how well counts from imagery represent absolute abundance. Regardless of the results of such work, my current results indicate that much can be learned about relative abundance. Given that, it is clear that the method presented here can readily identify which sites along the Antarctic coast are or are not occupied by seals under various environmental conditions. Although presence/absence data does not contain as much information on population state as what is provided by data on absolute abundance, recent work has demonstrated the great utility of having occupancy data, especially at broad spatial scales and over a broad range of conditions (MacKenzie et al. 2005; Fretwell and Trathan 2009). Moreover, Weddell seals are disappearing fast enough in some areas of the Antarctic Peninsula (Siniff et al. 2008), that quantitative, relative abundance may provide a useful indication of ecosystem change.

CHAPTER THREE: A METHOD FOR ESTIMATING COLONY SIZES OF ADÉLIE PENGUINS USING REMOTE SENSING IMAGERY

Introduction

Adélie penguins (*Pygoscelis adeliae*) are distributed around the Antarctic continent, with an estimated population of approximately 2.6 million breeding pairs (Woehler 1993). Considered an indicator species of ecosystem change in the Southern Ocean (Ainley 2002a; Ainley 2002b; Kerry et al. 1997), Adélie penguins are heavily dependent on sea ice (Fraser et al. 1992, Wilson et al. 2001) and are sensitive to changes in the abundance and distribution of krill (e.g. *Euphausia superba*, *E. crystallorophias*) and fish (e.g., *Pleuragramma antarctica*; Scofield et al. 2010, Saillely et al. 2013), which comprise the majority of their diet (Ainley 2002a). In fact, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), the international organization responsible for managing fisheries in the Southern Ocean, considers Adélie penguins to be one of the core elements of their CCAMLR Ecosystem Monitoring Program (CEMP). Concern over Southern Ocean resources has been fueled partly by evidence that Adélie penguin populations are declining rapidly on islands of the northern Antarctic Peninsula, but increasing in the southern Antarctic Peninsula region (Trivelpiece et al. 2011, Lynch et al. 2012a, Saillely et al. 2013) and the Ross Sea region (Ainley et al. 2005; Ainley et al. 2010; Lyver et al. 2011). The rapid and spatially varying changes in Adélie penguin populations and the implications of these changes to broader ecosystem integrity make it essential to understand the underlying environmental mechanisms, thus preserving this species' value to CEMP. However, the isolation and

sporadic distribution of colonies (Woehler 1993; Ainley 2002a) and financial and logistical challenges associated with Antarctic field work challenge continental-scale, or even regional surveys of Adélie penguins. Only 10-15% of known populations are monitored with any regularity, and it is likely that some Adélie populations remain undiscovered (Woehler and Croxall 1997; Ainley 2002a; Southwell and Emmerson 2013). The inaccessibility of portions of the breeding habitat for this important indicator species has driven a surge of interest in satellite imagery as a means for remotely studying Adélie populations. Because of its life history (breeds in the open, in dense concentrations, with seasonal population dynamics well understood) the Adélie penguin is a model for assessing how remote sensing imagery can be used to track the distribution and abundance of seabirds with similar characteristics.

Remote sensing of penguin populations was first demonstrated with Landsat in the 1980s when it was discovered that guano at Adélie penguin colonies could be differentiated from the surrounding landscape, and that there was a relationship between the number of pixels identified as guano and the number of breeding pairs of Adélie penguins on Ross Island, Antarctica (Schwaller et al. 1984; Schwaller et al. 1989). Since that time, many studies have used various remote sensing platforms (e.g., Landsat, SPOT, aerial photographs, QuickBird-2) to detect the distribution and change in penguin populations (Bhikharidas et al. 1992; Chamaillé-Jammes et al. 2000; Fretwell and Trathan 2009; Naveen et al. 2012; Fretwell et al. 2012; LaRue et al. 2013; Schwaller et al. 2013). For instance, Chamaillé-Jammes et al. (2000) used georeferenced aerial photography in a GIS to address population change in king penguins (*Aptenodytes*

patagonicus) over several decades, and aerial photographs have been used to determine a strong relationship between sub-colony area (m²) and number of Adélie penguin pairs in east Antarctica (Woehler and Riddle 1998). Landsat was used to identify colonies of emperor penguins (*Aptenodytes forsteri*; Fretwell and Trathan 2009), a study that was followed by the first global census of a species from space using very high-resolution (VHR) images (Fretwell et al. 2012; 0.6m resolution, e.g., QuickBird-2 from DigitalGlobe, Inc). Researchers documented a >50% decline in chinstrap penguin (*P. antarctica*) numbers during a 30-year period at Baily Head on Deception Island, Antarctic Peninsula, when ground counts were combined with VHR imagery (QuickBird-2 and WorldView-1; ~0.6m resolution; Naveen et al. 2012). Finally, VHR images were recently combined with historic aerial photos to quantify decadal population change of Adélie penguins on Beaufort Island, Ross Sea (LaRue et al. 2013). Clearly, remotely-sensed data have the capacity to inform researchers, resource managers and conservationists about distribution and population size of penguins, but the extent to which these can supplement or even replace field counts needs to be assessed.

Remotely-sensed data of medium-resolution (e.g, Landsat; 15m resolution) can provide distribution and presence/absence information (Schwaller et al. 2013), whereas higher-resolution images (up to 0.2m resolution in the case of aerial photos; 0.6m in VHR satellite imagery) can be used to estimate population size of remote colonies of seabirds. Landsat images are likely too coarse to track Antarctica's smallest populations and aerial surveys in remote areas can be prohibitively expensive in Antarctica (or elsewhere). Further, over-flights of some most penguin colonies are can be precluded by poor

weather, remoteness, or prohibition related to conservation. Thus, VHR satellite images present a viable alternative for estimating Adélie penguin abundance and tracking changes in occupancy (e.g., colonizations and extinctions) at a regional or continental scale. However, to date no studies have identified specific methods for applying VHR imagery at such a range of large scales. Thus, a model for predicting abundance from guano area colony “footprint” is required before I can confidently estimate global abundance and trends of Adélie penguins. Herein, I describe the first comprehensive assessment of this technique using the guano footprint, and the uncertainties associated with estimating abundances from high-resolution satellite imagery.

Based on the previous literature and experiences in Antarctica, I hypothesized that the area of current-year guano, which is a different color having a different spectral quality than older guano, would be correlated with the number of Adélie penguin breeding pairs, and could therefore be used to estimate abundance (Schwaller et al. 1989; LaRue et al. 2013). I determined a relationship between the area of current-year guano and the number of breeding pairs counted during the same season by combining VHR satellite imagery (i.e., DigitalGlobe, Inc., GeoEye) with spectral analytic techniques adapted from Fretwell et al. (2012). Using colonies within the Ross Sea and near Palmer Station, Antarctic Peninsula, as test cases because ground-validation was available, my goal was to develop a statistical model linking guano area to number of breeding pairs that could be used for estimation in future population surveys of Adélie penguins.

Methods

My study included 16 Adélie penguin colonies in Antarctica (as per Ainley [2002a]; ten from the Ross Sea, six from the Antarctic Peninsula) that ranged in size from ~100 to >250,000 breeding pairs (Figure 3.1) and were surveyed one or more times between 2004 and 2011. I calculated the area of current-year guano at each colony, first using a supervised classification and subsequently a maximum likelihood classification (MLC) of 4 bands of VHR imagery using ArcGIS 10.1 (Esri 2011). Briefly, a supervised classification allows the user to define pixels of known “class” identity (e.g., new guano, old guano, rock, snow) as a “training” dataset. A maximum likelihood classification identifies each pixel as belonging to one of the classes in a way that makes the training dataset classifications the most likely to occur; this model linking spectral signature and class is then applied to the rest of the image and the likely class of each pixel identified accordingly. The classification procedure allowed us to calculate the guano portion of each image. This supervised classification approach is a hybrid between the fully manual delineation approach described in Lynch et al. (2012b) and the automated methods developed in Fretwell et al. (2012). This method benefits from on-the-ground experience with the species of the classifier.

To model current-year guano area and population size, I first needed ground-validated estimates during seasons and at locations with overlapping with imagery (both temporally and spatially). To estimate the number of breeding pairs at Adélie penguin colonies along Victoria Land in the Ross Sea, collaborators counted individual nesting territories from ground counts and aerial photographs taken approximately 800 m above

ground level (courtesy Landcare Research, New Zealand). I defined “nesting territories” as sites occupied and defended by adults during the egg-laying and early incubation periods (Taylor et al. 1990). My collaborators used photographs that were taken each year as close as possible to 1 December, a date on which colonies are represented almost entirely by one member of each penguin pair, incubating its eggs, with few non-breeders present (Ainley 2002a). On islets adjacent to Anvers Island, Antarctic Peninsula, data for number of breeding pairs were gathered by ground counts during the breeding season in accordance with internationally recognized census protocols (CCAMLR 2004). These data are a public resource provided by the Palmer Long-Term Ecological Research database (<http://pal.lternet.edu/data/>).

I orthorectified (i.e., correct imagery for terrain and internal satellite platform errors) (i.e., corrected imagery for terrain) VHR images for Adélie colonies with the RAMP DEM (Liu et al. 2001) during seasons where ground counts and images overlapped, and further converted images into an equal-area projection to ensure accuracy of area calculations. I then calculated reflectance on each image, and loaded images into ArcGIS 10.1 (Esri 2011). On each image, I identified a colony by visually searching for the guano stain, which typically appears as a bright pink or light gray stain on the rocky or sandy terrain (Figure 3.2; see also Lynch et al. 2012b; LaRue et al. 2013). Using the Spatial Analyst toolbox, I then extracted the part of the image with only the guano stain and pansharpened (creating a higher-resolution multispectral image based on the resolution of the associated panchromatic image) that image subset. I classified a set of pixels based on presence of different items on the landscape (e.g., new guano, old

guano, rock, snow), and calculated the MLC. I checked the classified raster for errors of misspecification and, if necessary, a second training dataset was developed to correct for errors in the first round of classification. Because raster datasets inherently contained area information (each pixel was 0.36 m²), I was able to translate the area classified as “current-year guano” into an area (m²) used by penguins each year.

I also assessed the accuracy of the supervised classification; both the relationship between new guano and population size, and also how my methods estimate area of new guano. Because true reference data (e.g., subcolony areas from GPS data or maps exactly coincident in time with satellite imagery) are almost non-existent, I chose to assess accuracy by manually delineating subcolony areas at colonies where I had personal experience, ground photos, and oblique air photos to inform correct delineations on the satellite images. For my purposes, the manual delineation at three colonies (Capes Crozier East, divided by a snow slope from and West, treated separately, and Cape Royds) was therefore considered the “true” area used by penguins during that year. I then used these three areas as reference data to calculate accuracy for my supervised classification.

To determine accuracy of classification at the pixel-scale, I randomly selected 800 points across images for these three colonies and extracted values from the classified rasters. Because in my classification system, I was only interested in accuracy of the current-year guano area, I further extracted points that represented pixels classified as such ($n = 330$). I then compared those points to the “true” delineations of current-year guano area, and determined the percentage that fell within true boundaries.

To model penguin abundance based on guano area, I first log-transformed both guano area and breeding pairs (from ground/aerial counts) and calculated Pearson's correlation coefficient to determine the correlation between the datasets. I calculated the slope and intercept of the regression, as well as the variance-covariance matrix using PopTools extension within Microsoft Excel, and modeled abundance using an allometric regression:

$$\log(\text{breeding pairs}) = b_1 * (\log[\text{area}]) - b_0,$$

where b_0 is the slope, and b_1 is the intercept of the regression. I calculated confidence intervals and back-transformed log estimates of population size to determine the predicted number of birds at each colony. I also determined the accuracy of modeled estimates by calculating the number of colonies for which the ground estimate was captured within the upper and lower confidence limit ranges.

Results

I found a strong correlation between guano area and colony size ($r^2 = 0.99$, $n = 29$; Figure 3.3), and a mean density of 0.73 (SE = 0.03) breeding pairs/m². Note that this represents an “apparent” density, because the area of guano identified in the imagery may be slightly more or less than the actual area occupied by nests. Abundance estimates from model predictions included 89% of ground counts of Adélie penguins during the same season (Figure 3.4; Table 3.1). I also found that predicted estimates of number of breeding pairs at individual colonies through time were consistent with observed changes in population (Figure 3.5). Despite strong correlations between guano area and Adélie penguin abundance, prediction intervals remained relatively wide (Table 3.1; Figure 3.4).

I found 84% ($n = 278$; range 81-89%) of points classified as current-year guano fell within the true boundaries from manual delineations. The most common class for errors of commission, where points classified as current-year guano were actually a different class, was the “residual guano” class (remnant guano from previous years; Figure 3.2).

Discussion

Adélie penguins are a critical indicator species for the Southern Ocean, and understanding status, distribution and population trends is important to understand underlying factors affecting change in given that the direction of change varies by region (Ainley et al. 2005; Ainley et al. 2010; Lynch et al. 2012a). With >200 colonies of varying sizes spread around the continent (Woehler 1993; Ainley 2002a), the promise of reliably tracking trends in abundance represents a significant advance toward understanding Southern Ocean ecosystems. Within the past decade > 25 new nesting locations have been discovered in east Antarctica and the Amundsen Sea, two relatively little-visited regions (Low et al. 2007; Wilson et al. 2009; Southwell and Emmerson 2013; Schwaller et al. 2013). More broadly, my results offer the possibility of understanding metapopulation dynamics; Adélie penguins are one of the few seabird species for which the interconnected demographics of clusters of one major cluster of breeding populations have been investigated, but these studies have been limited because they excluded nearby colonies in the metapopulation that had limited access for researchers (Ainley et al. 1995; Ainley 2002a; LaRue et al. 2013). Finally, understanding the drivers of the dramatic changes in colony size reported for the Ross Sea region (Lyver et al.

unpublished data 2014) and Antarctic Peninsula (Lynch et al. 2012a; S.F. Sailley unpublished data et al. 2013) require broad perspective. Given the cost and logistical difficulties of surveying penguin colonies far from research stations, the method and model I provide here is a novel way forward in both colony identification and population estimation. I argue that a concurrent, continent-wide survey for Adélie penguin colonies cannot feasibly be done any other way.

This model has limitations worth noting, particularly for future applications. First, the supervised classification portion of my methods cannot be used to automatically detect presence of Adélie penguins on VHR imagery. Quite importantly, the areas I used for this analysis were largely known to me, and I had realistic expectations of relative size, area, and density. Had results been well outside my expectations, I would have been able to identify and search for mistakes; this is a luxury not afforded in areas where much less is known about Adélie presence. The most likely method for automatic detection of Adélie colonies would be identifying the spectral reflectance of guano (Schwaller et al. 2013). However, data indicate that reflectance is variable within and between seasons (P Fretwell pers. comm., LaRue et al., unpublished data). A suite of spectral “endmembers” broad enough to include this variability may also lead to increased false positives, so even automated methods may require considerable validation by biologists experienced in the area of study and also further atmospheric and radiometric corrections. A study of spectral variability was outside the scope of my study but will be required to advance this technique into a fully-automated process. The most robust approach for future monitoring

would be a combination of multiple sensors merged with available field data, and the development of such an approach is already underway.

This supervised classification calculated “current-year guano” pixels accurately (84% accuracy, which is considered acceptable for the method [Foody 2002; Horning et al. 2010]). The most common error was between the “current-year” guano (i.e., guano deposited in the current season; looks typically very pink on images and represents current-year space use) and “residual” or old guano (Figure 3.2; i.e., weathered material in areas between occupied subcolonies that is lighter in appearance). Currently, I have little capability to consistently eliminate these errors due to differences between colonies and between years, and so my methods still had to rely on observer interpretation to amend results for errors of omission and commission. Observer interpretation is an important feature of land cover mapping (Horning et al. 2010), and was quite necessary in my study. It is important to understand that any future applications using this method alone will likely require observers experienced with Adélie penguins, and with interpretation of satellite images.

I did not address the bias inherent to a temporal mismatch between the image and the ground count, as most locations had limited amounts of useable images to do this. Because images from too early or too late within a season could bias my abundance estimates, I avoided images in November when the guano signature is more indicative of the previous breeding season’s guano. Some of my images, however, were taken in January when non-breeders have returned to colonies. It is possible that the infiltration of young birds and their guano deposition could alter the area classified as current-year

guano, although I suspect this discrepancy would be minimal. Young birds typically occupy areas recently abandoned by current-year breeders then busily provisioning crèched chicks (Ainley and Ballard pers. obs). My experience has been that December and January images are best for guano classification.

The model I present here is intended to provide information about apparent density and population size of breeding pairs of Adélie penguins for a given colony. Inference about population health, diet, or movement between colonies cannot be gained from this model alone. Wind, rain, snow, and snow/ice melt all have the capability of displacing substantial amounts of guano that I rely upon for my population estimate. Because environmental conditions are changing rapidly, particularly in the Antarctic Peninsula region (Cook et al. 2005; Ducklow et al. 2007; Montes-Hugo et al. 2009; Lynch et al. 2012a), ground-validated data will remain critical for future model calibration.

High resolution satellite imagery has been widely used for assessing potential habitat for several animal species (Gaston 2000; Nagendra 2001; Turner et al. 2003), and has thus played an indirect role in the assessment of population size and population viability since it first became available (Kerr and Ostrovsky 2003; Buchanan et al. 2008; Gillespie et al. 2008). However, there are extremely few cases in which satellite imagery has been used to directly estimate population abundance, and with a few notable exceptions (Abileah 2002; Thaxter and Burton 2009), the use of high resolution imagery for direct census has been limited to polar ecosystems (Barber-Meyer et al. 2007; Bultunov et al. 2012; Lynch et al. 2012b; Fretwell et al. 2012; LaRue et al. 2013;

Stapleton et al. unpublished data). These tools provide a complementary, cost-effective alternative to ground or aerial surveys, which as noted above in regard to “new” colonies discovered in little-visited regions, have proved impractical. Southwell et al. (2013) briefly synthesize caveats associated with use of high-resolution imagery which include the timing of satellite-derived estimates relative to the breeding phenology of the species and the inability to use optical imagery on cloudy days. Despite the persistent cloudiness associated with much of coastal Antarctica, I was able to obtain a cloud free image for each of the focal colonies in this study. Many of the guano area-ground count comparisons were quite close temporally and given that the amount of guano seen on images likely does not change in size through the season, I am confident that my area estimations and subsequent comparisons are biologically reasonable. However, future work to confirm this would be beneficial.

Density estimates

To accurately assess the number of birds in a given area, it is crucial to understand nesting density of the species in question. Average apparent nesting density was 0.73 breeding pairs/m², which was consistent with the literature (Table 3.2; Taylor 1961, Penney 1968, Volkman and Trivelpiece 1979, Woehler and Riddle 1998). A factor that may influence density, or changes in density, at Adélie penguin colonies is competition for well-draining nesting areas from other seabirds. Throughout most of their range, Adélie penguins do not compete only among themselves for habitat with any other penguin species; only on the northern Antarctic Peninsula do they interact with the other two pygoscelid species: the gentoo penguin (*Pygoscelis papua*) and the chinstrap

penguin. The model I created considers only physical factors that may affect density, and does not take into account species interactions in predicting population estimates.

However, I recognize that competition for resources (particularly nesting habitat), and continuous changes in abundance of these resources due to changes in precipitation patterns, wind patterns, and glacial retreat (particularly on the Antarctic Peninsula; Fraser and Patterson 1997; Bricher et al. 2008) may impact numbers and density of Adélie penguins (see also LaRue et al. 2013).

Applications

The most direct use of this model would be its application to satellite images of all colonies of Adélie penguins and other Antarctic seabirds. By assessing the VHR imagery for the entire coastline, which is available patchily from (2004-2013), researchers can identify every extant colony and assess its population, thus providing key information necessary to for resource extraction management a sustainable krill fishery. Indeed, a global census of Adélie penguins using VHR satellite imagery has recently been completed (Lynch and LaRue 2014) and future global analyses of this type will allow us to assess population change over spatial scales much larger than has been traditionally possible. Also, a combination of my approach with phenological information could easily be applied to the other Antarctic and sub-Antarctic penguin species (e.g., chinstrap, gentoo, macaroni [*Eudyptes chrysolophus*]), as species identification is possible via satellite imagery (Lynch et al. 2012b).

These methods can be extended to other polar systems, where remote locations of animals preclude accurate estimates of populations. Combining spectral analysis with

biological or environmental information could easily be implemented, for example, on walrus (*Odobenus spp.*). In Arctic Russia, US, and Canada, walrus haul out at predictable rookeries every summer to raise offspring, and are easily identifiable from satellite images (Boltunov et al. 2012), as they congregate in large groups with measurable densities. Indeed, the Pacific walrus (*Odobenus rosmarus divergens*) is currently under consideration for protection under the Endangered Species Act, as decreasing sea ice may have detrimental impacts on population (Laidre et al. 2008). Given their site fidelity, gathering and analyzing images of walrus haulouts over several years is feasible. Another example would be Crozet shags (*Phalacrocorax melanogenis*) on Marion Island, which is in sub-Antarctic waters off the coast of Africa, have decreased by >70% over a ten-year period, a trend that was similar in the sympatric gentoo penguin population (Crawford et al. 2003), both of which are identifiable on VHR imagery (Lynch et al. 2012b).

Because satellite technology is likely to continue to improve, the methods I propose here are an important step in the process of advancing remote sensing, and data fusion in general, for use in estimation of animal populations. Climate and other environmental changes are advancing across the globe, so rapid, repeatable monitoring of species abundance and distribution using remote sensing is quickly becoming an urgent need (Horning et al. 2010). Additionally, ecologists and conservation biologists should be aware that VHR images can be used for finer-scale research purposes across broad geographic distributions. Adapting or combining my methods here with statistical models, other remote sensing platforms, or ground/reference data could easily advance our knowledge of ecosystem and species dynamics in similarly remote areas.

CHAPTER FOUR: CLIMATE CHANGE WINNERS: RECEDING ICE FIELDS
FACILITATE COLONY EXPANSION AND ALTERED DYNAMICS IN AN ADÉLIE
PENGUIN METAPOPOPULATION

Introduction

The adage is that global climate change will identify both winners and losers as the habitats of polar organisms are altered (Glantz 1995). For instance, on one hand, as sea ice extent decreases some species may benefit from increased open-water conditions (i.e., salps [*Salpa thompsoni*], gentoo penguins [*Pygoscelis papua*], cryptophytes; Ducklow et al. 2007, Montes-Hugo et al. 2009); on the other hand, other species may be negatively impacted by a loss of breeding habitat, such as emperor penguins (*Aptenodytes forsteri*; Ainley et al. 2010, Jenouvrier et al. 2009, Jenouvrier et al. 2012). Indeed, in areas of the Antarctic where sea ice is declining (i.e., the Peninsula), the food web has been in flux, as noted by recent studies (Ducklow et al. 2007, Montes-Hugo et al. 2009). However, on the opposite side of the continent, the Ross Sea (located approximately 3,000 km south of New Zealand), is a unique body of water that has been relatively untouched by human activities, and is likely to provide the last sea-ice ecosystem during the present period of climate change (Stammerjohn et al. 2012). Until recently, the food web has been little exploited; there are no invasive species, no widespread chemical pollution, and no mineral extraction activities (Ainley 2002b, Ainley et al. 2010a, Ainley et al. 2012). Therefore, the climate patterns exhibited are likely without complications brought on by many other direct, anthropogenic factors. In the Ross Sea region, changing weather patterns have brought slightly warmer temperatures and stronger winds, with

corresponding increases in sea ice extent and persistence (Ainley et al. 2005, Parkinson 2002, Stammerjohn et al. 2008) and more predictable coastal polynyas (Ainley et al. 2001a, Ainley et al. 2005, Massom and Stammerjohn 2010).

As a result of the earlier-opening and longer-lasting polynyas, the Adélie penguin (*Pygoscelis adeliae*) colonies along the Ross Sea coast grew during the 1980s-90s, affecting almost 40% of the world population (approximately 2.5 million breeding pairs; Ainley et al. 2010a, Taylor et al. 1990, Ainley 2002a). While that rapid population growth has ceased, I report here more recent changes in the Beaufort Island (herein referred to as Beaufort) colony, part of a four-colony cluster that includes 10% of the world population of Adélie penguins (Ainley 2002a). The remaining colonies in this cluster, at Capes Royds, Bird, and Crozier (herein referred to as Royds, Bird and Crozier), are located on nearby Ross Island (Ainley et al. 1995). These colonies and others within the Ross Sea are sensitive to ice sheet and glacier retreat, according to analysis of subfossil remains deposited through the Holocene and back to the previous interglacial period (Emslie et al. 2007, Millar et al. 2012). The colonies on Ross and Beaufort islands are the youngest colonies in the Ross Sea (Emslie et al. 2007), and among these Beaufort has been the only habitat-limited colony in the metapopulation, as it sits upon a gravel moraine hemmed in by cliffs and glaciers (Figure 4.1).

Therefore, I hypothesized that a recently observed increase in breeding pairs and availability of nesting habitat at Beaufort was associated with glacial retreat, and explained a concurrent reduction in emigration from Beaufort to nearby colonies on Ross Island. My study objectives were to: 1) estimate available habitat and population size of

an Adélie penguin colony at Beaufort; 2) calculate change in available habitat and glacial retreat during 1958-2010 (the period for which images are available); and 3) better understand the dynamics within the Ross-Beaufort islands metapopulation.

Methods

The main Adélie penguin colony at Beaufort is located at the island's southwest coast ($\sim 76^{\circ} 58' S$ and $\sim 166^{\circ} 54' E$), approximately 20 km and 50 km north of Bird and Royds, respectively, and 40 km west of Crozier colony, all on Ross Island (Figure 4.2). To estimate population size (i.e., breeding pairs) of the Beaufort Adélie penguin colony during 1983-2010, researchers counted individual nesting territories using aerial photographs taken approximately 800 m above ground level just after onset of incubation (courtesy Landcare Research, New Zealand). I define "nesting territories" as sites occupied and defended adults during the egg-laying and early incubation periods. I used photographs that were taken each year as close as possible to 1 December, a date on which the colony population was represented almost entirely by one member of each penguin pair incubating its eggs, and minimal numbers of non-breeders not on territories (Taylor et al. 1990).

To determine changes in available nesting habitat, I gathered aerial photos taken during the penguin incubation period in 1958, 1983, and 1993 (0.19-0.38 m resolution; USGS, US Navy), and high-resolution satellite images from 2005 and 2010 (0.6 m resolution; copyright DigitalGlobe, Inc.). In ArcGIS 10, I georeferenced images with tie points (e.g., boulders, cliff peaks) on Beaufort to overlay images exactly. Differences between image resolutions meant I were unable to directly delineate actual nest space.

Instead, I calculated available habitat (m^2) for the colony per image year (Figure 4.3) by tracing the maximum extent of the current-year guano stain and subtracting area of unsuitable habitat (i.e., snow and ice cover) within colony boundaries. I interpreted the current-year guano stain by viewing panchromatic (i.e., grayscale) images; active guano areas had a brighter spectral signature than rock or remnant guano stains. I also delineated the edge of the ice field to the north of the colony (Figure 4.3) on each image to understand decadal environmental changes.

Changes in movement of penguins between Beaufort and colonies on Ross Island were addressed by marking 400 near-to-fledging chicks per year at Beaufort during 1999-2010 (excluding 2005 and 2008, when Beaufort could not be reached at the appropriate time of the season). Researchers then intently searched for banded birds at Ross Island colonies in subsequent years (to 2011) and recorded band numbers and reproductive status (Dugger et al. 2010). Each colony was completely searched every 2-7 days throughout the breeding season, and high annual resighting probabilities of banded birds (> 70%) indicate the comprehensive nature of the effort (Dugger et al. 2010). Problems of access to the Beaufort meant researchers could not band-search there sufficiently enough each year to estimate survival or detection rates via mark-recapture directly (Dugger et al. 2010, Dugger et al. 2006). However, age-related survival rates from Bird and Crozier were used to adjust the number of Beaufort-banded individuals within each age-cohort each year that should have been alive and detectable at Royds, Bird, or Crozier during 2001-2011. The result is the proportion of banded Beaufort birds seen at one of the other

three colonies, relative to the total number of Beaufort banded birds potentially alive each year; I define this as a measure of the “emigration rate” from Beaufort to other colonies.

Finally, to address changing weather patterns, I gathered all available temperature records from McMurdo Station (available at <http://www.antarctica.ac.uk/met/READER/>), which is located on Ross Island. I calculated changes in annual summer (averaged monthly November-February) temperatures during 1958-2010.

Results

Available habitat for Adélie penguins at the main portion of the Beaufort colony, on the south coast, increased 71% since 1958, with a 20% increase during 1983-2010 (Figure 4.4). During the same time, population size increased (+84%), as did colony density (0.31-0.49 breeding pairs/m²; Table 4.1). I also found a positive association between colony area and population estimates for years with overlapping data ($n = 3$; Figure 4.4). The extent of the snow- and ice-field to the north of the main colony did not change from 1958-1983, but then retreated 543 m during 1983-2010 (Figure 4.3). Further, in 2004 I observed a newly-founded, disjunct subcolony at the northeast coast of Beaufort. Population estimates from aerial photography there indicated a population increase from 460 pairs to 957 pairs by 2010 (change of 108%), and I also found several Beaufort-banded penguins there.

The emigration rate of Beaufort chicks visiting colonies on Ross Island during 2001-2011 (when band-searching was ongoing) increased sharply from nearly zero in 2002 and peaked at 3% in 2005 (Figure 4.5), despite a relatively stable period of colony size. Subsequently, although more Beaufort birds were available to visit away from

Beaufort, visitation of Ross Island colonies decreased markedly after 2005. Finally, as an indication of changing weather patterns, I found that average summer air temperatures recorded at McMurdo Station increased by 1°C during 1958-2010, with most of the increase occurring during 1980-2000 (Figure 4.6). Average temperatures during October-December, the period of snow melt/ablation within the colony, increased by 3.22 °C.

Discussion

Evidence suggesting that Adélie penguins on Beaufort were “climate change winners” was both the colony expansion, and increases in nesting density and summer temperatures during the 52 year study period. This result of population expansion is markedly different than what might be expected elsewhere within the Adélie penguin’s continental range, where populations are declining due to warming temperatures; for example, on the Antarctic Peninsula (Ainley et al. 2010). Not only did the glacier field to the north of the main colony retreat by hundreds of meters allowing for colony expansion, but the snow patches (i.e., unsuitable habitat) within the colony decreased and eventually vanished. Both of these small-scale (snow patches) and large-scale (glacial retreat) factors driven, at least in part, by increasing temperatures played a role in the increase of the Adélie penguin nesting habitat and colony size. Indeed, the Adélie penguin population in the greater Ross Sea region has expanded over the last 12,000 years, as glaciers have retreated from positions occupied during the Last Glacial Maximum (Emslie et al. 2007, Millar et al. 2012). The population processes observed at Beaufort and within the Ross-Beaufort metapopulation could be prevalent elsewhere; for instance, perhaps in the southern Antarctic Peninsula where glacial retreat and ice shelf

disappearance has recently been particularly rapid (Cook et al. 2005). However, especially warm temperatures in that sector have also led to increased snowfall (Turner et al. 2007) and decreased sea ice, with detrimental impacts on Adélie penguin colonies there (Ducklow et al. 2007, Fraser and Patterson 1997, Trivelpiece et al. 2011).

My results show a response to altered availability of nesting habitat that consequently changed dynamics for the Ross-Beaufort metapopulation, particularly emigration and immigration (Shepherd et al. 2005). The emigration rate of Adélie penguins from Beaufort to nearby colonies was comparable to the highest movement probabilities observed at colonies on Ross Island (Dugger et al. 2010). However, after 2005 the emigration rates from Beaufort decreased rapidly when glacial retreat accelerated, the main colony increased, and the new subcolony was founded on the north shore. These concurrent results suggest that the pressure to emigrate from the main colony at Beaufort decreased as nesting habitat expanded. Notably, some of the space created by the habitat expansion was unsuitable for nesting (steep terrain) and the glacial retreat seems to have been more rapid than the penguins were capable of accommodating. In other words, our analysis detected an initial population expansion, with additional growth perhaps still underway, providing that the factors leading to the overall population increase are still in place. Importantly, the four-colony, southern Ross Sea metapopulation has been growing again after a stable period in the 1990s (Ainley et al. 2010a), but Beaufort only recently has been able to contribute to the population increase as the glacier has retreated. None of the Ross Island colonies are even close to being space limited.

I can only speculate on other environmental and biotic factors that may have played a role in the recent population increase at Beaufort and within the metapopulation. For instance, Adélie penguins of the southern Ross Sea are important predators of crystal krill (*Euphausia crystallorophias*) and silverfish (*Pleuragramma antarctica*) (Ainley 2002b, Ainley et al. 2003), and are also prey of leopard seals (*Hydrurga leptonyx*), with consumption and predation rates varying with colony size (Ainley et al. 2005b, Balance et al. 2009). The availability of crystal krill and silverfish could change as the sea ice season and ice cover changes locally (with earlier polynyas), versus regionally (with greater extent and longer seasons) in the Ross Sea sector (Parkinson 2002, Stammerjohn et al. 2008, LaMesa et al. 2004). However, the direction of that change as possibly driven by trophic factors is currently unknown, because relatively little work has been conducted on those two sea-ice obligate, high-latitude prey species. Additionally, an industrial fishery recently arrived in the Ross Sea and targets a major trophic competitor of Adélie penguins, the Antarctic toothfish (*Dissostichus mawsoni*), which has since declined in prevalence in the region (Ainley et al. 2010a). Both toothfish and penguins prey heavily on silverfish in the southern Ross Sea (Ainley et al. 2003, LaMesa et al. 2004), and it is possible the population increase I report here was partly due to increased silverfish availability. At this stage, I can say little more on the extent to which changed trophodynamics are playing a role in the population growth of neither Beaufort, nor the metapopulation. Nonetheless, massive glacial retreat and snow melt, increases in available habitat, and subsequent decreases in emigration rates from Beaufort Island

indicate that warming temperatures-- related to climate change-- contributed to a change in metapopulation dynamics of Adélie penguins in the southern Ross Sea region.

Finally, despite only three years for comparison, I was encouraged by the potential association between available habitat and population size at Beaufort. On the basis of our results, I suggest that high-resolution satellite imagery is able to index population size of Adélie penguins at Beaufort, and presumably elsewhere. Indeed, satellite imagery has proven a useful tool for detection and abundance estimation of other polar species (Fretwell et al. 2012, Lynch et al. 2012, Naveen et al. 2012). The idea of expanding this technique and remotely assessing Adélie penguin populations is important, given a full census of the global population has never been conducted concurrently, and because this species appears to be especially sensitive to environmental change, which is progressing differently depending on region (Ainley 2002b, Ainley et al. 2010b, Croxall et al. 2002). Rapid physical changes in the Southern Ocean ecosystem are occurring (e.g., ocean temperatures and salinity, sea ice extent; Massom and Stammerjohn 2010, Jacobs 2006) and monitoring Adélie penguin numbers, as an indicator species, would be beneficial to gauge how the sea-ice obligate biota are responding. Despite recent evidence indicating that satellite imagery is remarkably accurate in assessing population changes of another population of pygoscelid penguins (Naveen et al. 2012), more research is needed to investigate the lower threshold of variance/validity for indexing Adélie penguin populations with this technique. Perhaps only large populations or large changes, as at Beaufort, would be detectable.

CHAPTER 5: EMIGRATION IN EMPEROR PENGUINS: IMPLICATIONS FOR INTERPRETATION OF LONG-TERM STUDIES

Introduction

Emperor penguins (*Aptenodytes forsteri*) are an important indicator of the health of the Southern Ocean (Le Bohec et al. 2012) and have become a key study species for understanding the effects of sea ice change on polar marine ecosystems (Jenouvrier et al. 2009, Ainley et al. 2010). As a result of the logistical challenges involved in studying emperor penguins, there have been very few long-term studies of the species. Much of what we know about emperor penguin population dynamics and behavior is based on observational and modeling studies of a single colony at Pointe Géologie, which has been the subject of continuous population counts since 1958 and the only mark-recapture study of the species (1951-1982; Weimerskirch et al. 1985). The Pointe Géologie population was stable from the early 1950's to 1976 and then declined by half over the course of three years and stabilized at the lower level since. Data from banded birds have been used to infer that decreases in adult survival, associated with warmer air and ocean temperatures, were primarily responsible for the decline (Barbraud and Wiemerskirch 2001; Barbraud et al. 2011), and that future declines are likely due to predicted sea ice losses (Jenouvrier et al. 2009, Ainley et al. 2010). However, mark-resight data of banded birds have been modeled assuming strict philopatry among the Pointe Géologie emperor penguins. When Barbraud and Wiemerskirch (2001) conducted their mark-resight analysis, the closest known colony was thought to be >1,500 km from Pointe Géologie, making the probability of emigration very low and analysis of apparent

survival straight-forward. Given this landmark study, there has been much interest in understanding the cause of the drastic decrease in adult survival at Pointe Géologie during the three year period of the 1970's, and what factors are responsible for the present stability and lack of recovery to its pre-1970s abundance.

Since Barbraud and Weimerskirch's (2001) analysis, much knowledge has been gained about the distribution and colony sizes of emperor penguins around the continent. In 2001, only ~30 colonies were known to exist. I now know of 54 locations that have hosted a breeding population of emperor penguins at least once, including six colonies within ~1,500 km of Pointe Géologie (Fretwell et al. 2012). Our improved understanding of emperor penguin biogeography allows us to test the hypothesis that emperor penguins are always philopatric, with the goal of providing an alternative explanation for decreases in breeding abundance, such as was seen over a relatively short time at Pointe Géologie. Philopatry, or the lack thereof, has important implications for the interpretation of existing long-term data, teasing apart drivers of population change (climate, resource extraction, and potentially tourism), and for the design of future population monitoring. To do this, I considered the existing literature, aerial photography and new high-resolution satellite imagery to better understand the movement dynamics among emperor penguin colonies. I find that compelling evidence that emperor penguins are not strictly philopatric, and that the location of emperor penguin colonies is more dynamic than previously thought.

Methods

I used aerial photos obtained during flights in a twin-otter and a Basler, ground counts at select colonies, and literature records for reports on emperor penguin colonies suggesting the establishment of new populations or movement of individuals between colonies. The aerial survey and ground count methods are described in detail in Barber-Meyer et al. (2007) and Kooyman and Ponganis (2013). In addition to ground or aerial counts I used high-resolution satellite imagery (Quickbird-2 images, 0.6m resolution, copyright DigitalGlobe, Inc.) for reconnaissance of the Antarctic coastline and determined the presence of colonies from 2009-2013, when images of emperor penguin colonies first became widely available. Comparison of the recent high-resolution satellite imagery and the historical literature allowed me to document all the known instances of colonization or movement suggestive of non-philopatry among emperor penguins.

Results

I documented at least six cases in which movement of an entire breeding colony or establishment of a new colony strongly suggest a lack of total philopatry in emperor penguins. Apparent flexibility of breeding sites was noted more than 35 years ago, when Jonkel and Llano (1975) observed four pairs of emperor penguins breeding at Inaccessible Island in McMurdo Sound, which is more than 90 km from the nearest breeding colony at Beaufort Island. None of the eggs survived (Jonkel and Llano 1975). Similarly, but on a grander scale, the Mertz Glacier colony lost its breeding habitat in February 2010 when the glacier tongue was broken off by a massive iceberg. During subsequent searches of the Mertz location from Quickbird-2 images (0.6m resolution,

copyright DigitalGlobe, Inc.) during October and November 2010, the colony was not found anywhere within ~200 km of the former colony location. However, in 2011, the putative Mertz colony was relocated approximately 150 km from its previous location—indeed, in the very area searched during 2010. A colony has been present there since 2011.

Second, the Ledda Bay colony was first observed in the Marie Byrd Land region by Fretwell and Trathan (2009) via Landsat images acquired during the early 2000's. However, the first global census of the species that used high-resolution images during October-November 2009 showed that no colony was present (Fretwell et al. 2012), so no estimate was included for that location. In 2010 the colony re-appeared at Ledda Bay (Figure 5.1), but has been absent in every year since. I searched several images per year (to eliminate recent snow fall as a reason for not detecting the guano stain, which is the main evidence for presence of a colony) and am confident that the site has not been occupied since 2010. I also could not find a colony within ~200 km of Ledda Bay that could have represented an alternate breeding location.

Satellite observations have recorded at least two other colonies that have moved considerable distances due to changing ice conditions. The Sanae colony was located in 2009 from Landsat imagery taken in 2002 in an ice creek on the eastern side of the Fimbul Iceshelf. This situation remained until sometime between September 2010 and September 2011, when a large portion of the iceshelf calved, changing the local topography and the sea ice conditions. The colony split into two parts, with the larger part moving into the newly opened ice creek further south. Since this period (in 2012 and

2013) emperor penguins have bred only in this more southerly ice creek. Another example is the Dolleman Island colony, near the eastern base of the Antarctic Peninsula. This breeding site has been located in a number of locations around Dolleman Island. While it was first identified from imagery in 2009, this initial location was near the southeast coast of the island and in 2010 it located to the north of the island, some ~20 km from the original location. In 2011 it was again located in a similar position to its 2009 site.

In the Ross Sea during 2011, variations in size within breeding colonies were large. At Cape Colbeck, the colony has an ideal location approximately 10 km from the sea ice edge, near a polynya, and in a large fast ice field protected by high ice cliffs on three sides. However, in 2011 I noted from satellite images (Figure 5.2) and confirmed from aerial surveys, that a new colony showed up much closer to the edge of the sea ice. Indeed, while the original colony doubled in size between 2008 and 2011 (reaching a size of >9,000 adults), the new colony had >1,100 chicks. To my knowledge, the phenomenon of a “satellite” colony so close to an established colony has never before been observed at this scale. The northern colony did not return in 2012, and while there were no aerial censuses in 2013 to confirm its continued absence, satellite imagery indicates that no outer colony has formed since.

Finally, I discovered a new emperor penguin colony on the Antarctic Peninsula from high-resolution satellite imagery that was not present in the global census conducted during 2009 (Fretwell et al. 2012). I originally found this colony on an image from October 2012 (Figure 5.3) and confirmed its existence in 2013, both of which clearly

show a congregation of emperor penguins on the sea ice. Given the size and persistence of the guano stain from 2012, and observations of moulting adults in Marguerite Bay in 2012 (Hart, Pers. Comm), this was likely comprised of breeding birds. Interestingly, this new colony is located only 190 km from the previous location at the Dion Islands, a colony that recently went extinct due to lack of sea ice (Trathan et al. 2011).

In addition to the evidence stemming from colony relocation and the transient dynamics of satellite colony formation, I also found evidence of large fluxes in colony demographics from the Ross Sea, which has the largest concentration (25%) of emperor penguins in Antarctica (Fretwell et al. 2012) and the longest record of colony size for multiple colonies. Kooyman and Mullins (1990) report high variation in counts of adults at one of the southern-most colonies, Cape Crozier, where variation in counts ranged from a high of >2,000 in 1961 to a low of 127 adults in 1976. Kooyman and Ponganis (2013) noted a rapid decline and recovery in the number of chicks and breeding adults at Coulman Island, which swung from the usual level of >20,000 chicks and adults in 2009, to <10,000 chicks and 12,000 adults in 2010, and back to >12,000 chicks and >25,000 adults in 2011. Delayed sexual maturity among emperor penguins (3-6 years; Williams 1995) makes it difficult to imagine a scenario in which a major decline in adult survivorship is recovered so quickly through recruitment of new breeders. Such a rapid decline and marked rebound is, however, consistent with a scenario of temporary emigration.

Discussion

My observational evidence suggests that movement occurs among colonies of emperor penguins, and that large scale movements among individuals in a colony can lead to a complete relocation of the breeding colony. While data show that emperor penguins are not always philopatric, the rate of movement among breeding locations, and the exact reason individual seek other sites, cannot be quantified from the data available. In light of the evidence that emperor penguins can and do move among breeding locations, and that several newly found significant colonies exist near the Pointe Géologie colony, I suggest that emigration could have explained part of the population decline at Pointe Géologie during the 1970s. Changing environmental conditions may favor plasticity in the emperor penguin's life history strategy with implications for future research, as an understanding of population trajectories will be reliant on the decoupling of climate and other anthropogenic forcing, such as tourism or fishing.

Selection for behavioral plasticity in emperor penguins

Emperor penguins breed on fast sea ice, which changes in concentration, extent, and quality in response to both long-term changes in climate and short-term phenomena such as storm systems and seasonal wind patterns (Liu et al. 2004). During the last glacial maximum, emperor penguins were almost certainly hundreds of kilometers to the north of their current breeding range due to the lack of coastal polynyas, and would need to follow the edge of the sea ice for foraging and chick-rearing (Thatje et al. 2008). Only in the last few thousand years has the retreated sea ice been so close to the Antarctic continent, where I currently find colonies of emperor penguins. Changing sea ice

conditions are not a uniquely new challenge faced by emperor penguins; it is reasonable to suggest that the inherent instability of sea ice would have selected for behavioral plasticity and some degree of non-philopatry to maximize breeding and foraging potential at the ice edge or near polynyas.

Only one study of which I am aware directly tested for emigration and philopatry in emperor penguins. This study found that none of the >6,000 birds banded at Pointe Géologie were recovered elsewhere (Weimerskirch et al. 1985). However, only three other colonies were apparently searched for banded emperors, and these were not even the closest colonies to Pointe Géologie. Moreover, we know that banding has a significant impact on survivorship (Gauthier-Clerc et al. 2004, Saurax et al. 2011), so it is difficult to know whether banded birds are less likely to survive, or even attempt, a long-distance relocation. When emperor penguins were being banded for study, very few colonies were routinely searched for banded birds, and so the information now being made available from satellite imagery is perhaps the most direct evidence yet of the dispersal and colonization potential for this species. At the very least, the inherent instability of sea-ice and the massive fluctuations in its extent over time, suggests that emigration and new colony establishment would be an important element of emperor penguin life history.

Emigration and environmental perturbation

In a series of landmark papers, Barbraud and Wiemerskirch (2001), and Jenouvrier et al. (2005, 2009) used mark-resight data from the Pointe Géologie study with a Cormack-Jolly-Seber model to determine that apparent survival of adults was

inversely related to air temperature, and that a period of unusually warm conditions during 1976-1982 caused a drastic decline in abundance (~6,000 breeding pairs to ~3,000 breeding pairs). Cormack-Jolly-Seber models cannot distinguish between mortality and emigration, so if a marked individual does not return to the colony, it is assumed to have died (Schaub and Royle 2013). Barbraud and Wiemerskirch (2001) assumed no probability of emigration, because at the time the nearest known colony was ~1,500 km away and deemed too far for an individual to disperse, and this sudden decline in numbers was interpreted as a drop in true adult survival. This idea, that the Pointe Géologie colony was geographically isolated and thus closed to emigration and immigration of individuals, has persisted even up until a few years ago (Wienecke 2011). However, I now know that Pointe Géologie has at least six colonies within 1,500 km (Figure 5.4). The Mertz and Dibble Glacier colonies are only 250 km to the east and west, with ~5,000 and ~12,500 breeding pairs, respectively (Fretwell et al. 2012). Emperor penguins can forage ~270 km away from their colonies (Ratcliffe and Trathan 2011) and moulting occurs within the pack ice hundreds of kilometers from breeding colonies (Kooyman et al. 2000, Wienecke et al. 2004). Assuming these neighboring colonies existed at the time, it is entirely feasible that individuals from all three Pointe Géologie area colonies were mixing at shared foraging/moulting grounds or making visits to colonies adjacent to their own.

It is important to note that a similar situation likely occurred at Haswell Island, as Barbraud et al. (2011) observed a similar decline in the 1970s. That study suggested that factors other than changes in sea ice (e.g., banding mortality) should be considered to

explain changes at Pointe Géologie, and further commented that changes in sea ice extent and patterns may increase emigration. The decline at Haswell could also be due to increased emigration as recent satellite imagery has revealed two previously-unknown colonies within 200 km of Haswell, at Shackleton Ice Shelf and Burton Ice Shelf. Interestingly, one of these newly-discovered colonies breeds on the ice shelf—not on the sea ice— in poor sea ice years (Fretwell et al. 2014). It seems that emigration to nearby but previously unknown colonies could explain part of the decreases at Pointe Géologie and Haswell Island during the 1970s.

I have presented several lines of evidence that emperor penguins are not strictly philopatric, including sudden shifts in abundances over time that suggest that the flow of individuals among colonies is not constant but may be promoted by environmental perturbations. I believe that several concurrent factors could have contributed to enhanced rates of emigration in the 1970s. It has been well-established that seabird colonies in the Antarctic are associated with polynyas (Massom et al. 1998, Arrigo and Van Dijken 2003, Ainley 2002, Ainley et al. 2010), and polynya size explains 60% of variation in size of nearby Adélie penguin (*Pygoscelis adeliae*) colonies (Arrigo and Van Dijken 2003). A well-documented regime shift that caused the Southern Oscillation Index (SOI) to turn positive occurred in the 1970s, which resulted in higher sea surface temperatures, greater sea ice extent, and variability in polynya size and productivity (Ainley et al. 2005). Dibble and Mertz Glacier colonies are both associated with much larger polynyas than at Pointe Géologie, and the Shackleton and Burton Glaciers have more persistent polynyas than available at Haswell Island (Arrigo and Van Dijken 2003).

If the regime shift created larger, more productive polynyas, these alternate locations would have been more favorable. Unfortunately, sea ice data gathered by satellites are not available for this period and so I cannot determine that this regime shift affected the relative size or productivity of these polynyas. While the relationship between polynya size and emperor penguin colonies has not yet been addressed, it is possible that environmental conditions driving polynya size may influence the relative rate of movement between colonies and cause a major uptick in emigration of banded birds away from sites less suitable in a particular breeding season.

It is also worth noting that the Astrolabe Glacier retreated during the population decrease, exposing the Pointe Géologie colony, and its associated polynya, to more extreme weather events (Croxall 1987, Williams 1995). Recent observations from the Mertz Glacier have shown that glacial change can result in the relocation of an entire colony. That environmental perturbations can drive significant demographic changes is well documented in other species, such as Weddell seals (*Leptonychotes weddellii*; Testa and Siniff 1987, Ainley et al. 2005, Chambert et al. 2012, Garrott et al. 2012) and Adélie penguins in the Ross Sea (Taylor et al. 1990) and East Antarctica (Jenouvrier et al. 2006). Indeed, the B-15 iceberg caused a similar perturbation in the southern Ross Sea in the early 2000's. By precluding advection of sea ice out of McMurdo Sound (Arrigo et al. 2002), iceberg caused temporary emigration within the Weddell seal population (Chambert et al. 2012) and increased emigration within the Adélie penguin metapopulation (Dugger et al. 2011). Since this time, movement rates have stabilized (Chambert et al., LaRue et al. 2013), as has the Pointe Géologie emperor colony.

I suggest that the regime shift of the 1970s and other changing environmental conditions could have impacted the Pointe Géologie and Haswell Island emperor penguin colonies, both through a decrease in survival rates and through an increase in emigration. Banded birds that didn't return may have emigrated to nearby colonies, similar to well-documented observations of the Adélie metapopulation in the southern Ross Sea (Dugger et al. 2011, LaRue et al. 2013). Until now, there was little reason to believe banded birds could have gone elsewhere. Thus, researchers should remain alert to examples where as conditions change, such as near the base of the Antarctic Peninsula and Terre Adélie to the possibility of the northern emperor penguins repositioning themselves to more southern pre-existing colonies or to the formation of new colonies like near Alexander Island. The formation of a new colony near Alexander Island, which is on the western Antarctic Peninsula where sea ice extent and duration has declined significantly over the past 40 years (Montes-Hugo et al. 2009, Stammerjohn et al. 2012), provides an interesting insight to emperor penguin habitat suitability.

Distinguishing between emigration and mortality in populations is important, as the implications for understanding population dynamics, ecology, behavior, and conservation issues are very disparate. Given the results of Barbraud and Wiemerskirch (2001), several studies have focused on projections of emperor penguin abundance and distribution in response to changing sea surface temperatures and sea ice. These studies have suggested major declines in emperor penguin populations (Jenouvrier et al. 2009), and the loss of nearly all emperor colonies north of 70°S by 2100 (Ainley et al. 2010). Furthermore, the Southern Ocean is important economically, with >160,000 tons of krill

and fish extracted annually (Brooks 2013), which could have detrimental effects on the food web. The ability to separate the effects of environmental and anthropogenic forcing on the Southern Ocean ecosystem is imperative for sustainable ecosystem management through the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). However, if I assume that emperor penguins are philopatric and unlikely to adapt to environmental change, interpretation of population change and drivers of trends could be misinformed. Given recent evidence that emperor penguins breed on glacial and ice shelf ice (Fretwell et al. 2014), I suggest that interpretation of long-term time series and mark-recapture data should allow for movement among colonies to most accurately represent longevity and the influence of climatic perturbations. Emigration from the study colony may be particularly important if climate change encourages resettlement or creates a more dynamic sea ice habitat that favors less philopatric life history strategies. I agree that current trends in climate projections do not bode well for the northern rim or outer coastal continental colonies, but the individual birds may survive and continue to breed in more southerly regions. The Cape Colbeck colony demonstrates that a large colony can be sustained at the most southerly ice edges of nearly 78° S. What I do not yet know is what the ultimate carrying capacity will be if emperor penguins are forced to relocate further south, or if the rate of such range contraction can keep pace with the rate of sea ice loss.

Table 2.1. Summary of the comparison of counts of adult Weddell seals derived from high-resolution satellite imagery and ground counts in Erebus Bay, Antarctica. Image type was the satellite platform upon which the image was acquired. The image and ground count dates represent the local date the image was acquired and date(s) that ground counts were conducted at directly comparable locations in Erebus Bay. The locations compared were the haul-outs within Erebus Bay, defined in Figure 2.2, where ground counts and suitable images overlapped entirely. The percent detected was the number of seals identified in the imagery divided by the number of adult Weddell seals counted on the ground in each of the overlapping areas for comparable date(s).

Image Type	Image Date	Ground Count Date(s)	Locations Compared	Count on Images	Ground Count of Adults	% Detected
WorldView-1	22 Nov 2009	17, 21, 25 Nov 2009	TH, TP, NB, TR, HC	340	385	88.3
QuickBird-2	10 Dec 2007	4 Dec 2007	TI, BR, II, TR	367	443	82.8
QuickBird-2	12 Nov 2006	12 Nov 2006	TI, TP, BR, HC, TR	204	330	61.8
QuickBird-2	9 Nov 2005	9, 13 Nov 2005	TH, NB, HC	57	130	43.8
QuickBird-2	19 Nov 2004	18 Nov 2004	TH, SB, HC, TR	32	106	30.2
<i>TOTAL</i>			<i>21</i>	<i>1000</i>	<i>1394</i>	<i>71.7</i>

Table 3.1. Colony year, date of image analyzed, calculated area of current-season guano stain, number of breeding pairs counted during aerial and ground surveys (BP), and number of breeding pairs from the model, including lower confidence interval (LCI) and upper confidence interval (UCI) at Adélie penguin colonies in Antarctica.

Colony	Image Date	Area (m ²)	BP	Modeled BP (LCI, UCI)
Cormorant 2007	16-Jan-08	125.5	94	82 (65, 105)
Humble2007	16-Jan-08	299.0	178	198 (155, 252)
Torgerson 2007	16-Jan-08	528.8	246	351 (275, 448)
Christine 2007	16-Jan-08	430.4	329	286 (224, 364)
Beaufort North 2010	12-Dec-10	1,134.1	957	758 (594, 967)
Wood Bay 2006	16-Dec-06	3,485.4	2,468	2,355 (1,846, 3,005)
Royds 2010	20-Jan-11	6,320.9	2,513	4,309 (3,377, 5,497)
Bird Middle 2011	8-Feb-12	3,716.4	2,534	2,512 (1,969, 3,204)
Royds 2009	13-Jan-10	4,662.6	2,609	3,160 (2,477, 4,032)
Royds 2011	30-Dec-11	5,200.1	2,887	3,529 (2,766, 4,502)
Bird Middle 2007	15-Dec-07	4,478.8	3,443	3,033 (2,377, 3,869)
Bird Middle 2009	16-Dec-09	5,008.6	4,333	3,397 (2,663, 4,334)
Bird South 2007	15-Dec-07	16,604.8	12,516	11,456 (8,980, 14,615)
Bird South 2011	8-Feb-12	20,687.8	14,481	14296 (11206, 18238)
Bird South 2009	16-Dec-09	15,871.9	16,716	10,957 (8,588, 13,978)
Hallett 2006	23-Nov-06	45,938.8	19,744	33,437 (26,209, 42,657)
Crozier East 2006	11-Jan-07	27,260.9	21,374	19,346 (15,164, 24,680)
Crozier East 2004	4-Dec-04	31,680.9	24,775	22,578 (17,698, 28,803)
Crozier East 2011	12-Dec-11	27,786.0	27,786	20,210 (15,842, 25,783)
Crozier East 2009	7-Dec-09	51,551.7	32,062	36,618 (28,703, 46,715)
Crozier East 2010	18-Dec-10	38,293.9	33,220	27,172 (21,299, 34,665)
Bird North 2007	15-Dec-07	55,772.6	34,636	40,047 (31,391, 51,090)
Bird North 2011	8-Feb-12	60,744.3	42,860	44,075(34,548, 56,228)
Bird North 2009	16-Dec-09	61,201.1	46,073	46,837 (36,714, 59,753)
Beaufort 2010	12-Dec-10	83,147.8	63,760	60,501 (47,424, 77,185)
Crozier West 2004	4-Dec-04	208,289.1	157,717	181,474 (142,249, 231,516)
Crozier West 2011	12-Dec-11	263,275.6	233,585	235,177 (184,344, 300,027)
Crozier West 2010	18-Dec-10	250,418.3	245,708	216,953 (170,059, 276,777)
Crozier West 2009	7-Dec-09	268,378.0	250,453	329,355 (187,619, 305,357)

Table 3.2. Mean densities (of either nests or breeding pairs/m²) of Adélie penguin colonies in the published literature.

Location	Mean Density	Method	Reference
Peninsula	2.13	Nests	Stonehouse (1975)
Cape Crozier	1.46	Nests	Stonehouse (1975)
Cape Royds	0.82	Breeding pairs	Taylor (1961)
Wilkes Station	0.75	Nests	Penney (1968)
Ross Sea & Peninsula	0.73	Breeding Pairs	This study
Mawson Region	0.63	Breeding pairs	Woehler and Riddle (1998)
Beaufort Island	0.49	Breeding pairs	LaRue et al. (2013)

Table 4.1. Total available habitat (m²), number of breeding pairs (BP) counted from independent air photos, and calculated density (breeding pairs/m²) of the Adélie penguin colony at Beaufort Island, Antarctica, during November/December each year.

Year	Total Available Habitat (m ²)	Breeding Pairs	Density (BP/m ²)
1958	75670.3	--	--
1983	107571.2	34588	0.32
1993	104637.3	--	--
2005	127603.4	52335	0.41
2010	129029.5	63760	0.49

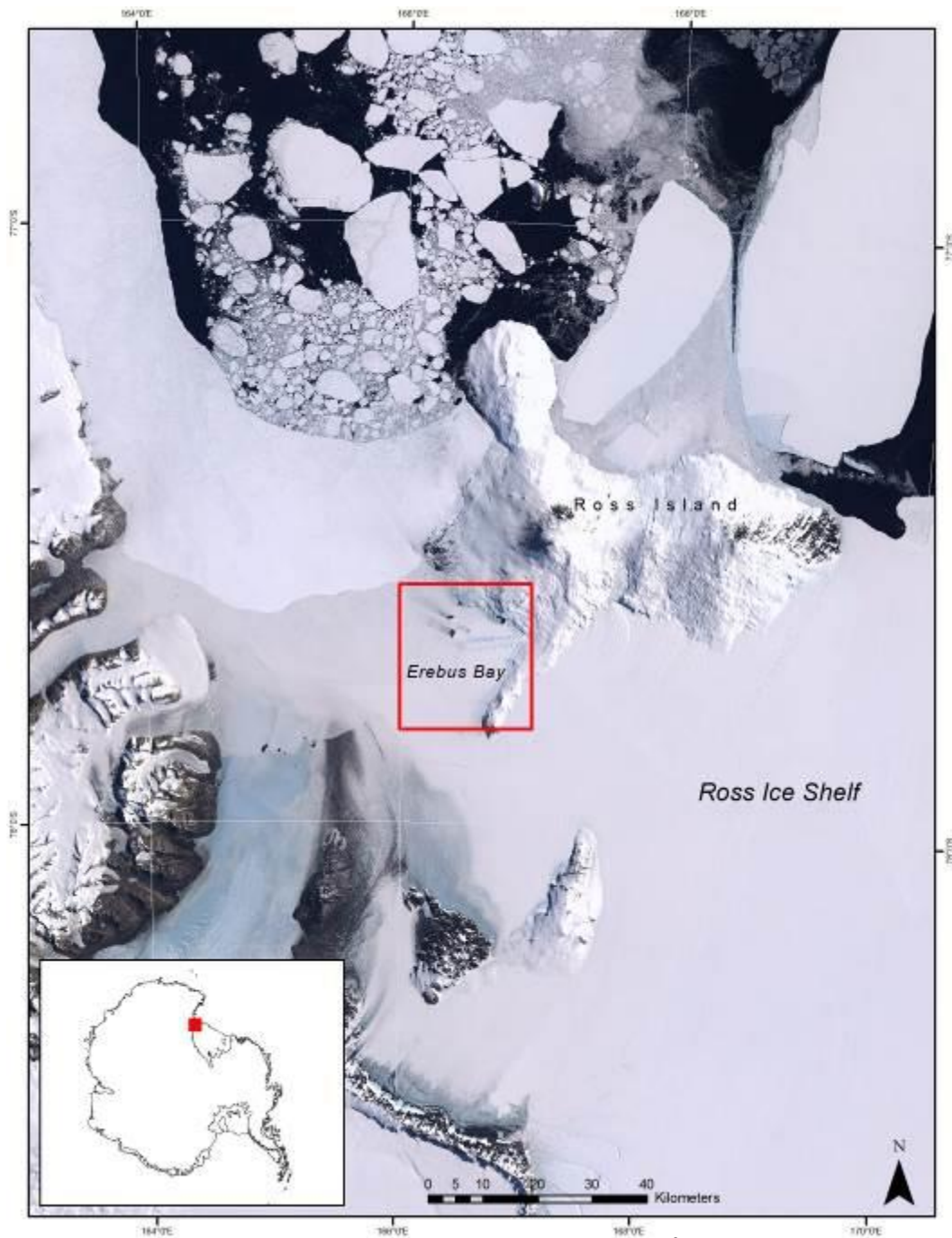


Figure 2.1. Study area in Erebus Bay, Antarctica (420 km²) outlined in red, to compare ground counts of Weddell seals to counts derived from high-resolution satellite imagery (0.6m resolution; QuickBird-2 and WorldView-1 satellite imagery) during November 2004-2006 and 2009 and December 2007. Background image is 15m Landsat Image Mosaic of Antarctica (LIMA) imagery courtesy NSF, BAS, USGS, and NASA.

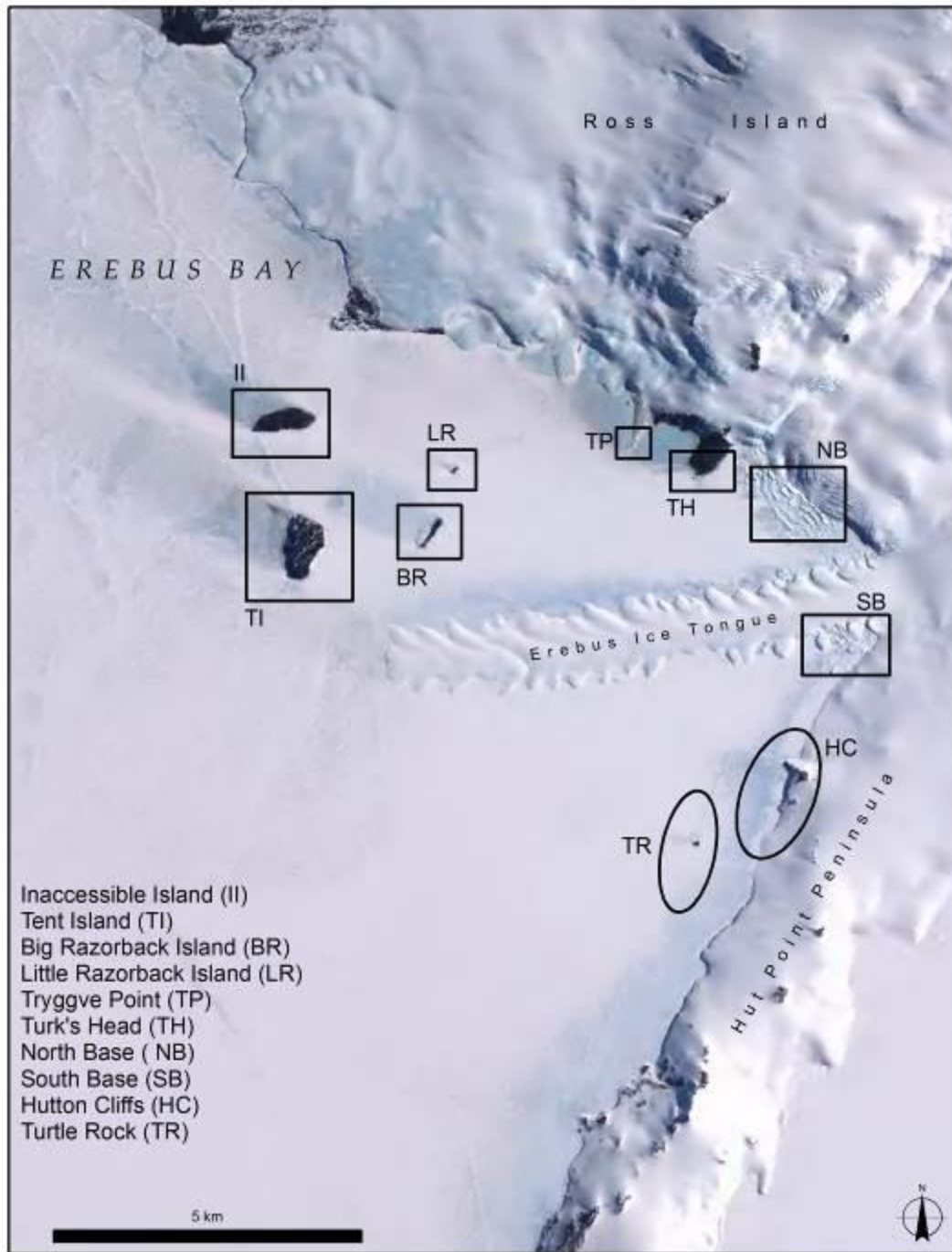


Figure 2.2. Specific haul-out locations within the Erebus Bay study area used for direct comparisons of counts of adult Weddell seals derived from satellite images to ground counts conducted during the same time. Background image is 15m LIMA, courtesy NSF, USGS, NASA, and BAS.



Figure 2.3. WorldView-1 image (0.6m resolution) of Weddell seals hauled out east of Inaccessible Island, Erebus Bay, Antarctica at 1:2,000 scale. This is an example of a suitable satellite image for use in counting seals. Image copyright DigitalGlobe, Inc., provided by National Geospatial-Intelligence Agency (NGA) Commercial Imagery Program.

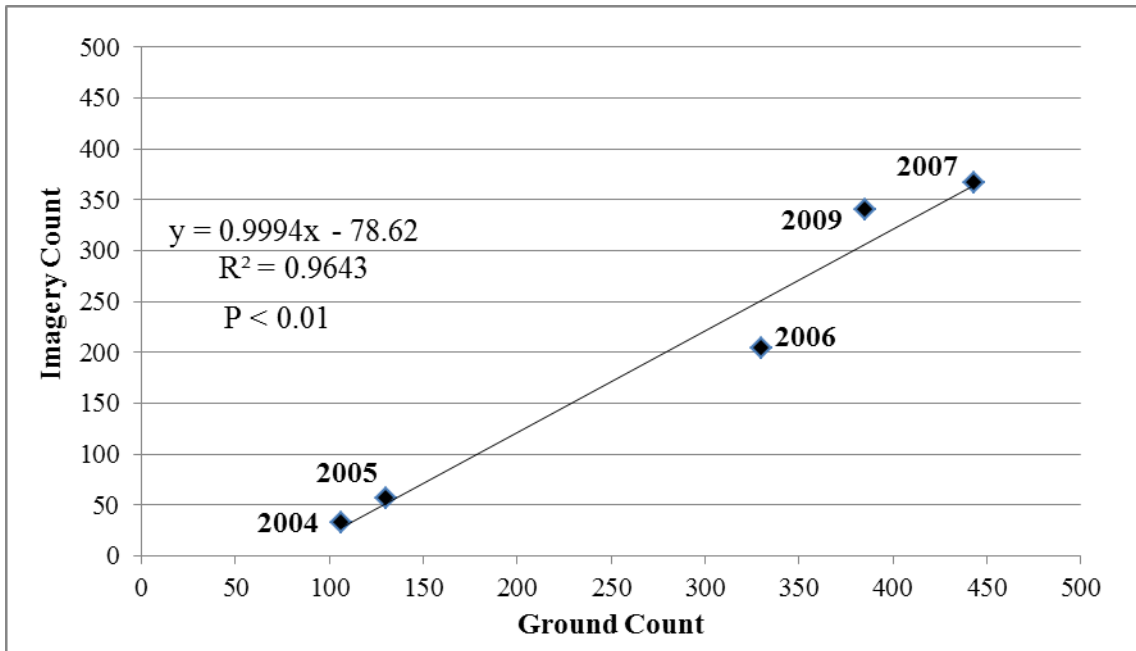


Figure 2.4. Count of seals on the sea ice from satellite imagery versus ground counts of adult Weddell seals on the sea ice in Erebus Bay, Antarctica, conducted the same day.

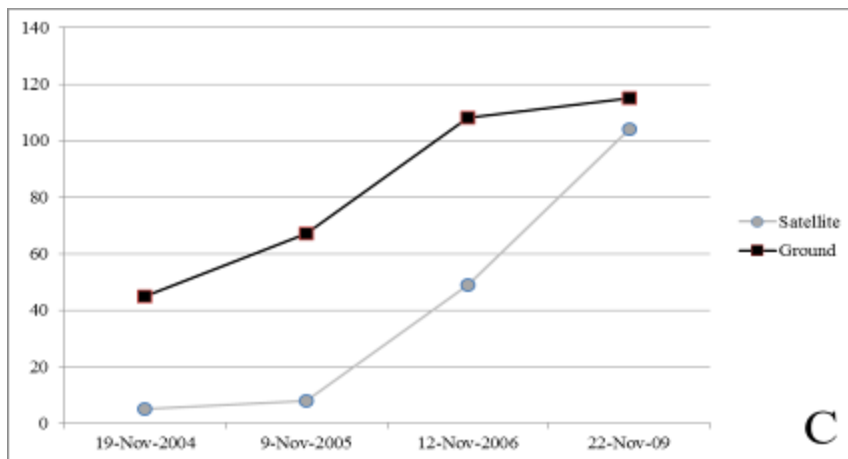
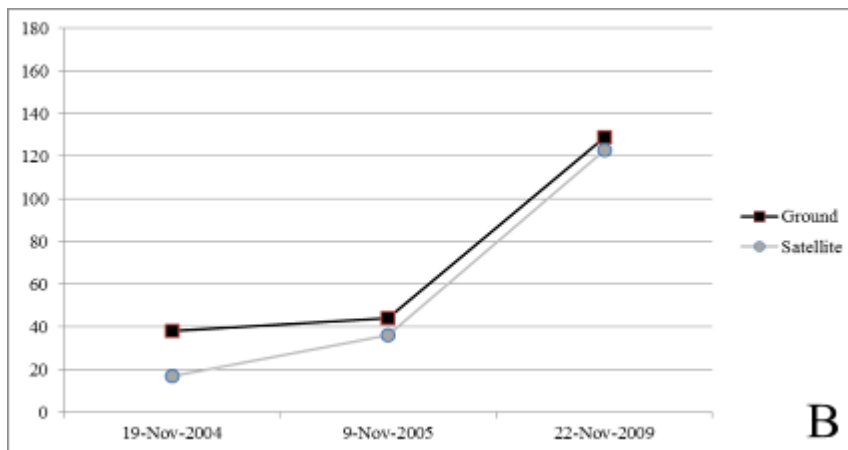
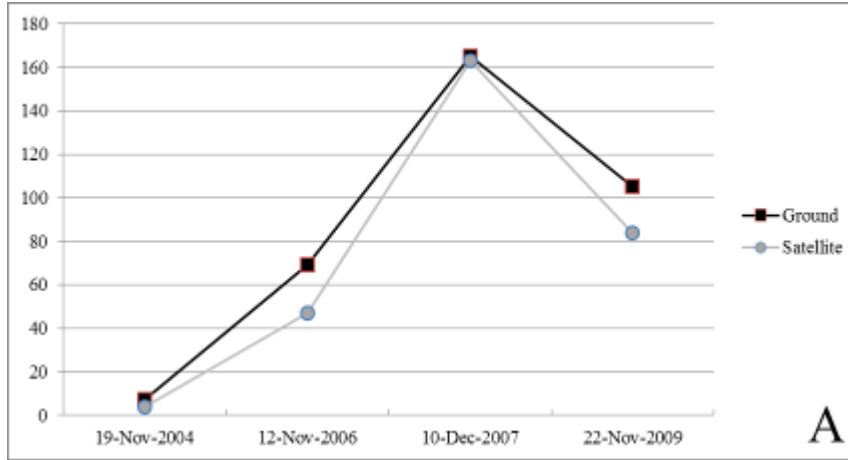


Figure 2.5. Abundance of adult Weddell seals present on the sea ice counted on the ground and from satellite imagery per image date at 3 haul-out locations within Erebus Bay: A). Turtle Rock ($r = 0.98$, $df = 2$, $P < 0.01$); B). Turks Head ($r = 0.99$, $df = 1$, $P < 0.05$); and C). Hutton Cliffs ($r = 0.89$, $df = 2$, $P < 0.05$).

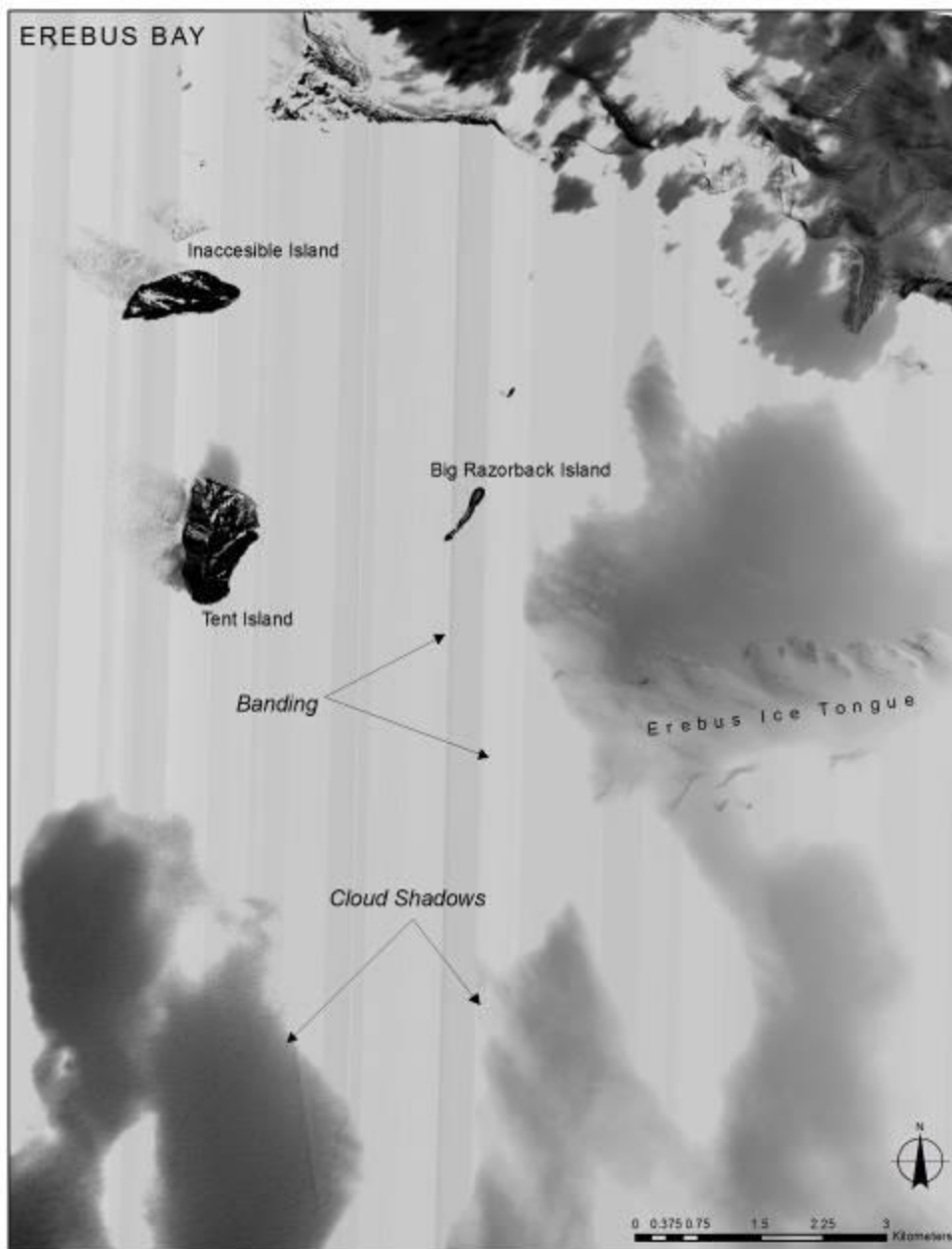


Figure 2.6. Panchromatic QuickBird-2 image (0.6m resolution) of a portion of Erebus Bay, Antarctica, acquired 1 December 2009. This image demonstrates some potential problems (e.g., banding, cloud cover, over-exposure) that could interfere with accurately counting Weddell seals using high-resolution satellite imagery. Image copyright DigitalGlobe, Inc., provided by National Geospatial-Intelligence Agency (NGA) Commercial Imagery Program.

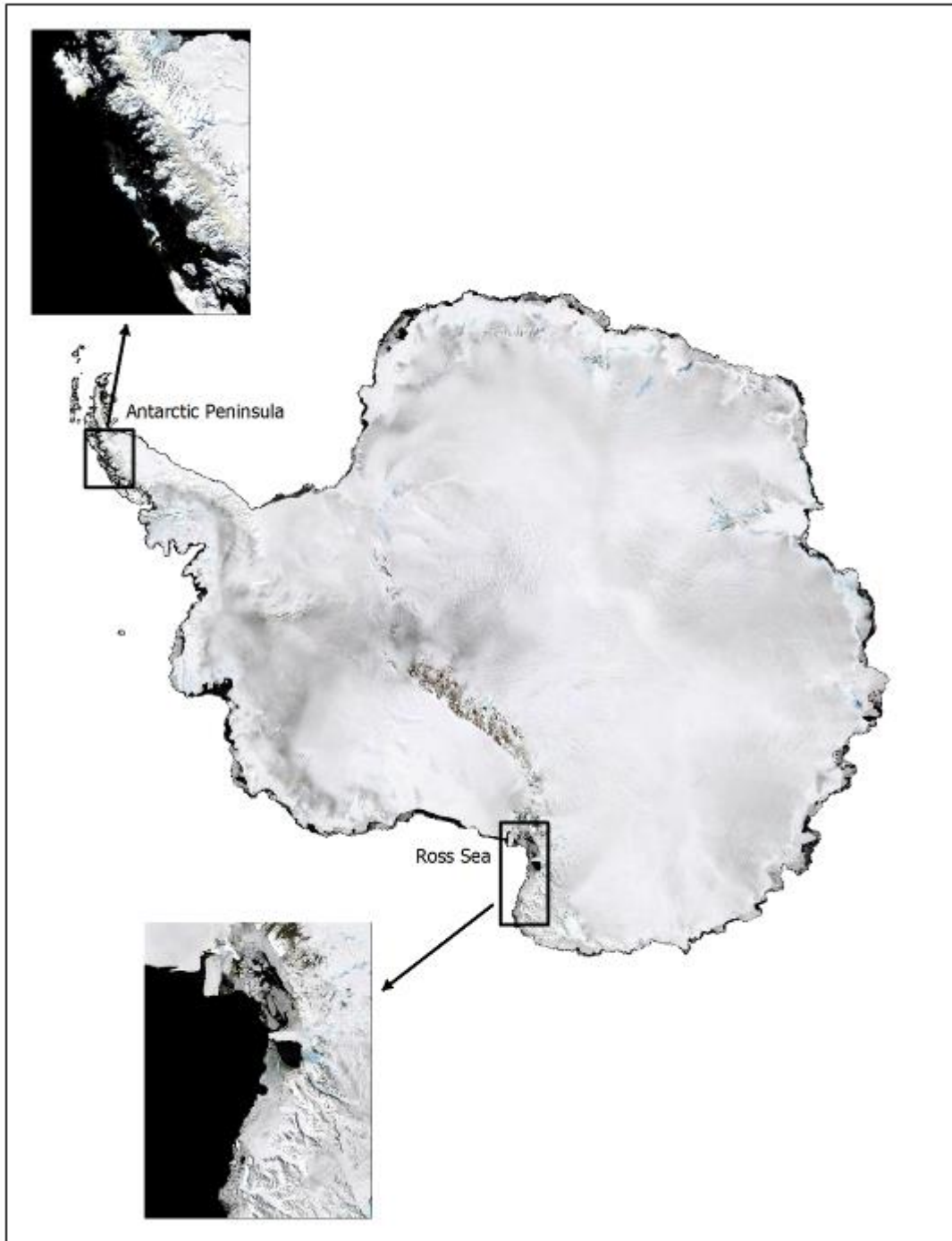


Figure 3.1. Study areas in the Ross Sea and the Antarctic Peninsula for testing the relationship between guano area (m^2) and population size (number of breeding pairs) of Adélie penguins in Antarctica.

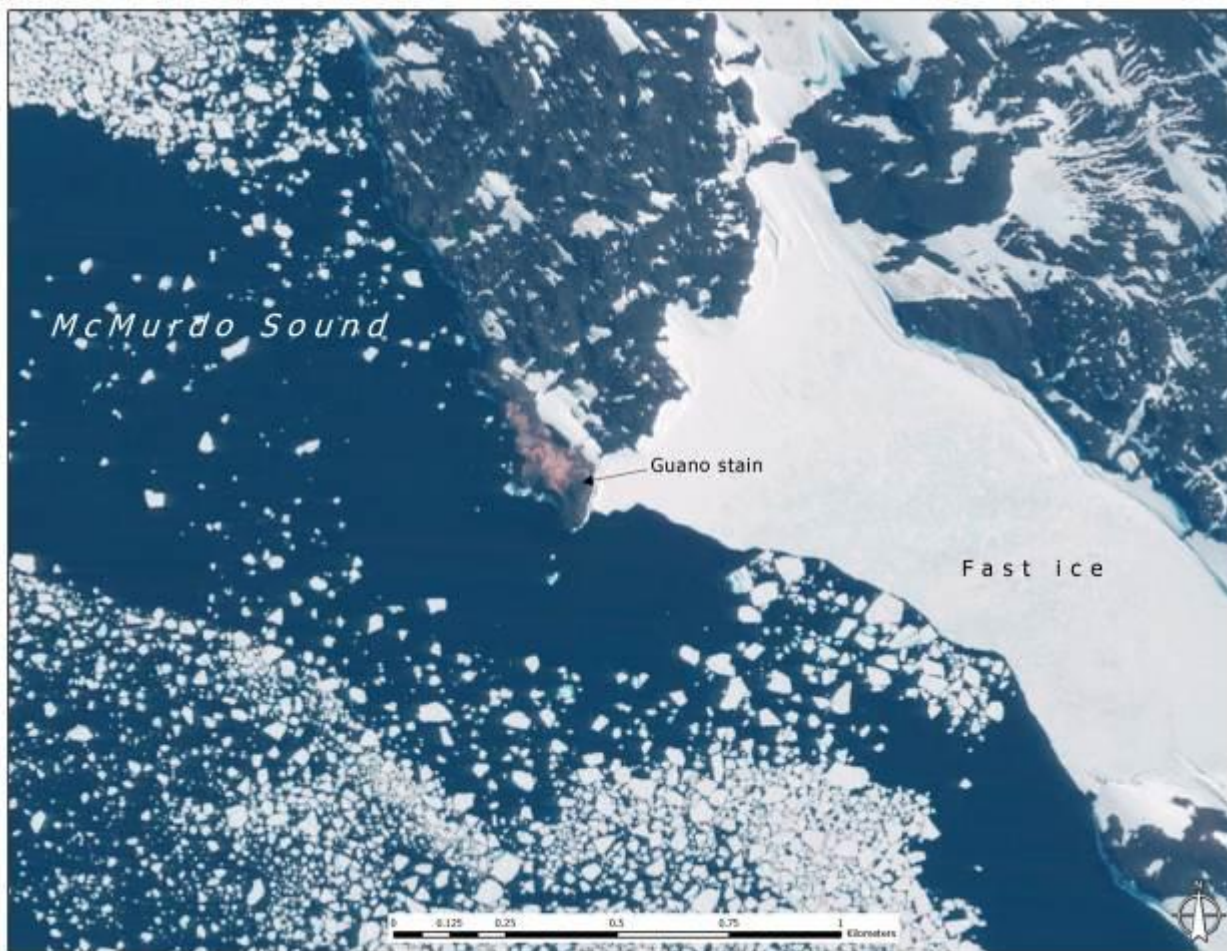


Figure 3.2. VHR image, with color-infrared band combination, of Cape Royds colony on Ross Island, Antarctica. The “new” guano stain is darker pink and its area is used in the supervised classification to estimate abundance; whereas the “residual” guano stain from previous years is located between the current-year guano and is lighter in color. Note Shackleton’s historic hut, near the top of the image, just right of center. Image date is January 20, 2011; copyright DigitalGlobe, Inc.

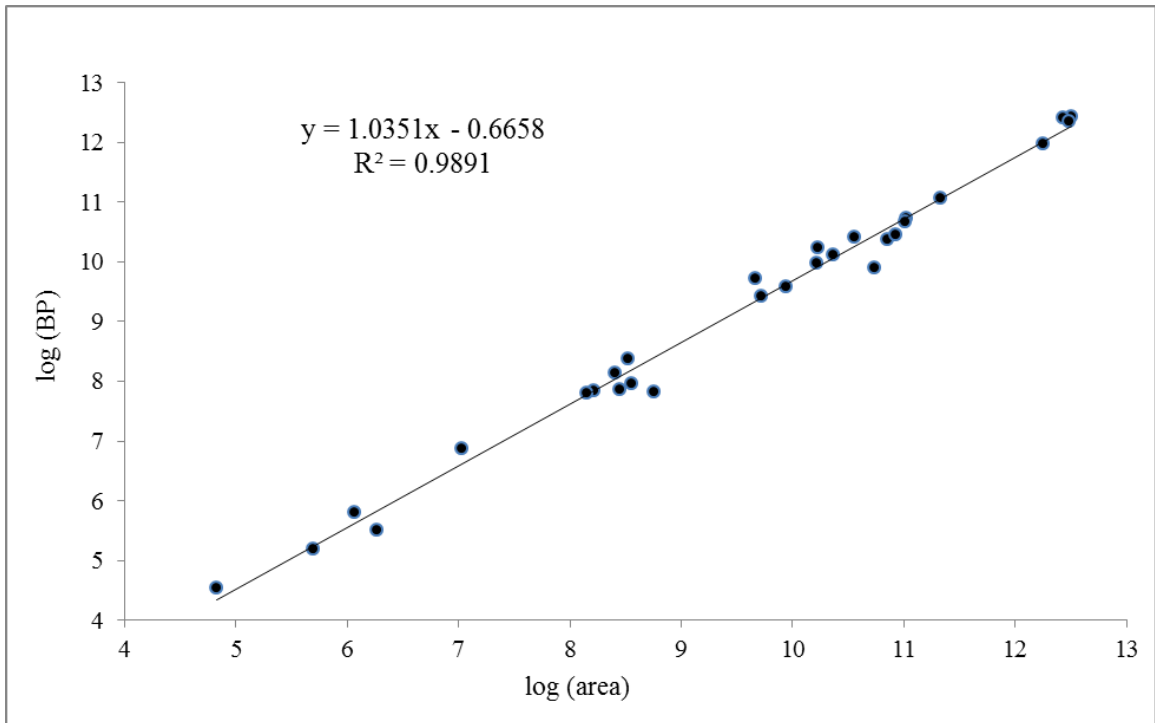


Figure 3.3. Log relationship between guano area (m^2) and population size (number of breeding pairs of Adélie penguins) for 14 colony locations in Antarctica. Note that $n = 29$, as I compared population size and guano area in >1 season for colonies on Ross Island.

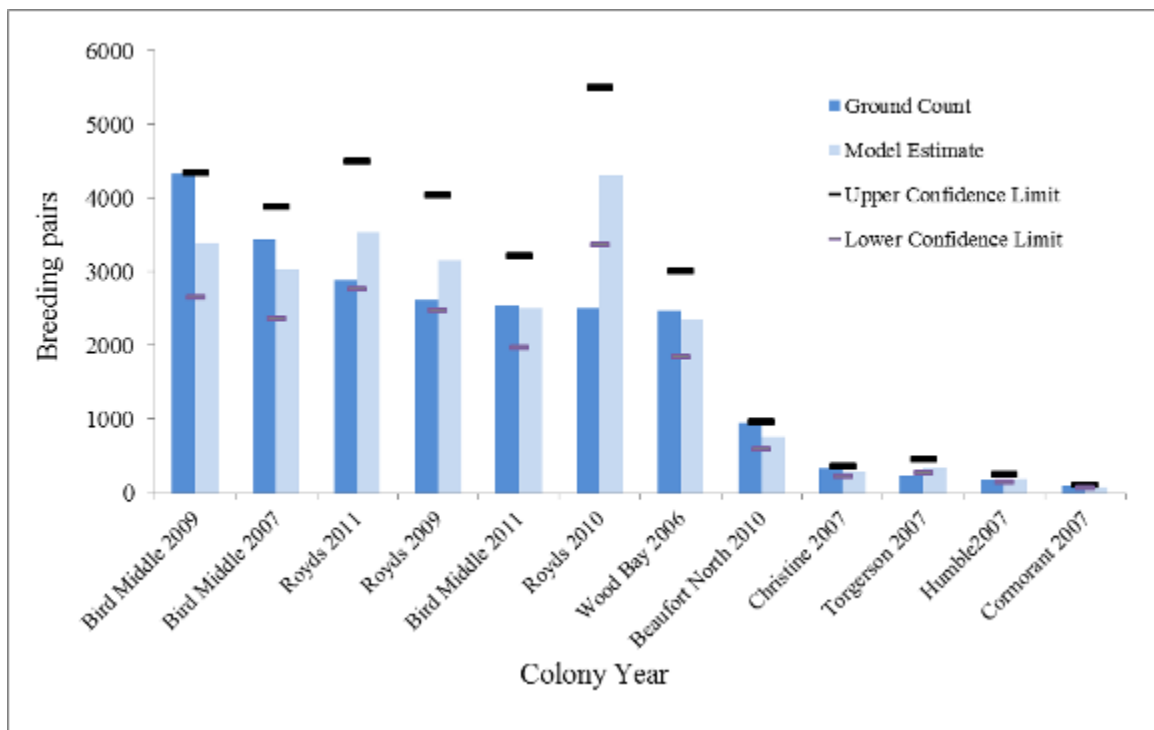
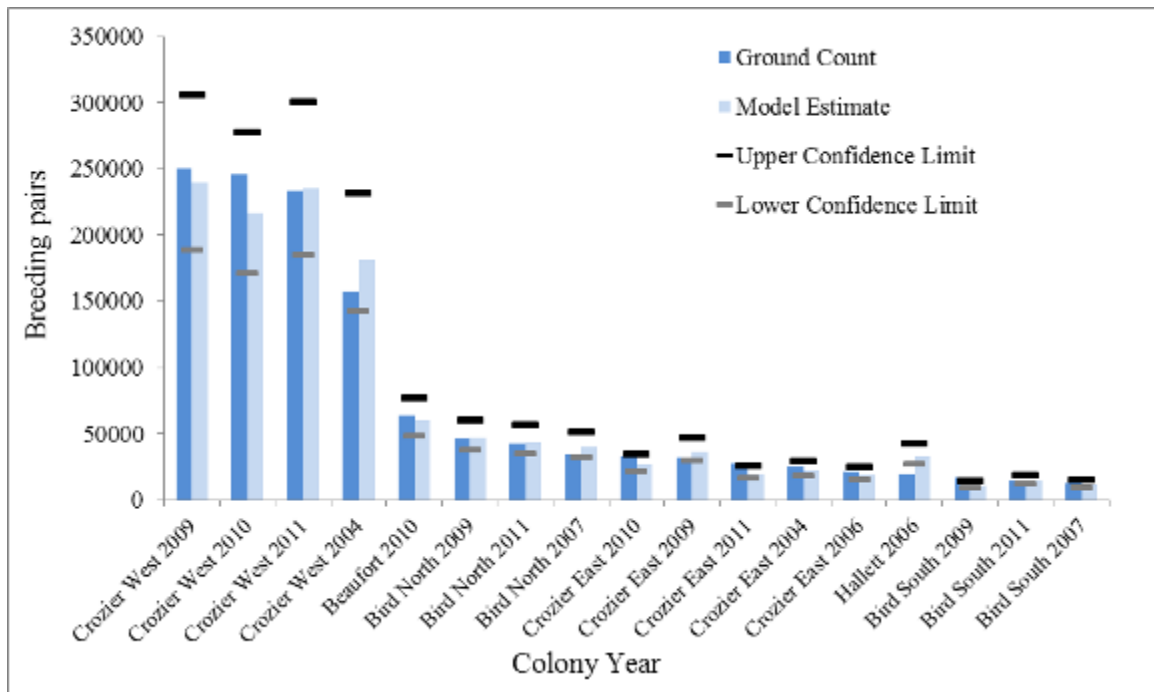


Figure 3.4. Modeled estimates of number of breeding pairs at large colonies (top) and small colonies (bottom) of Adélie penguin colonies on Ross Island and the Antarctic Peninsula and ground counts of penguins during the same season. Note different scale on Y axis between top and bottom.

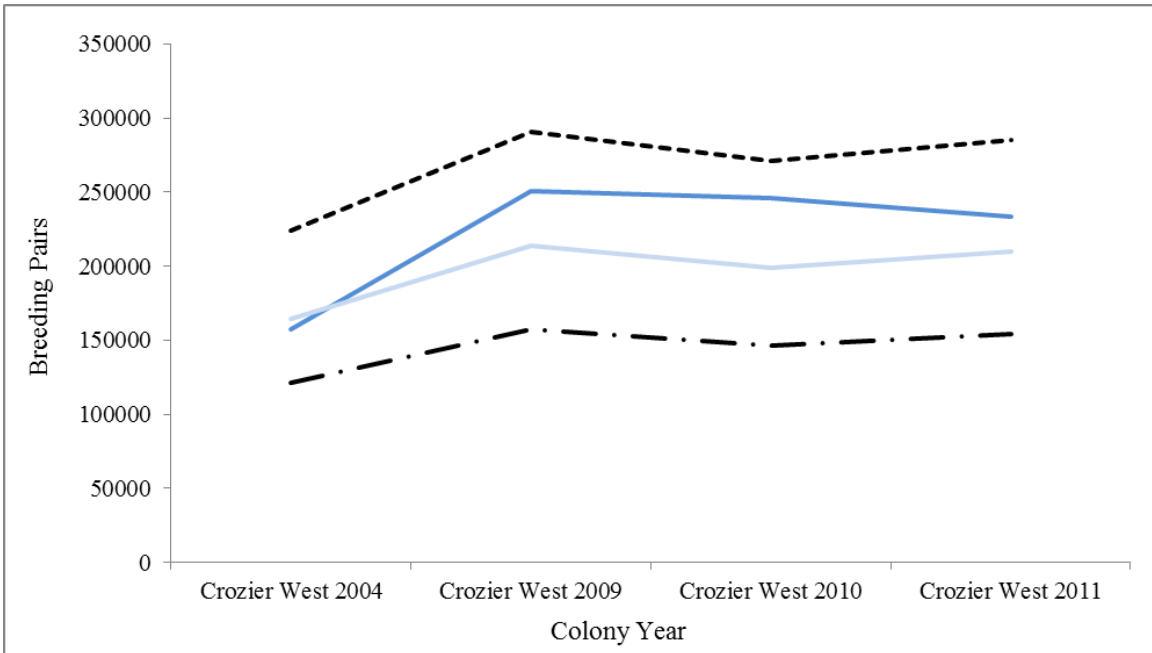
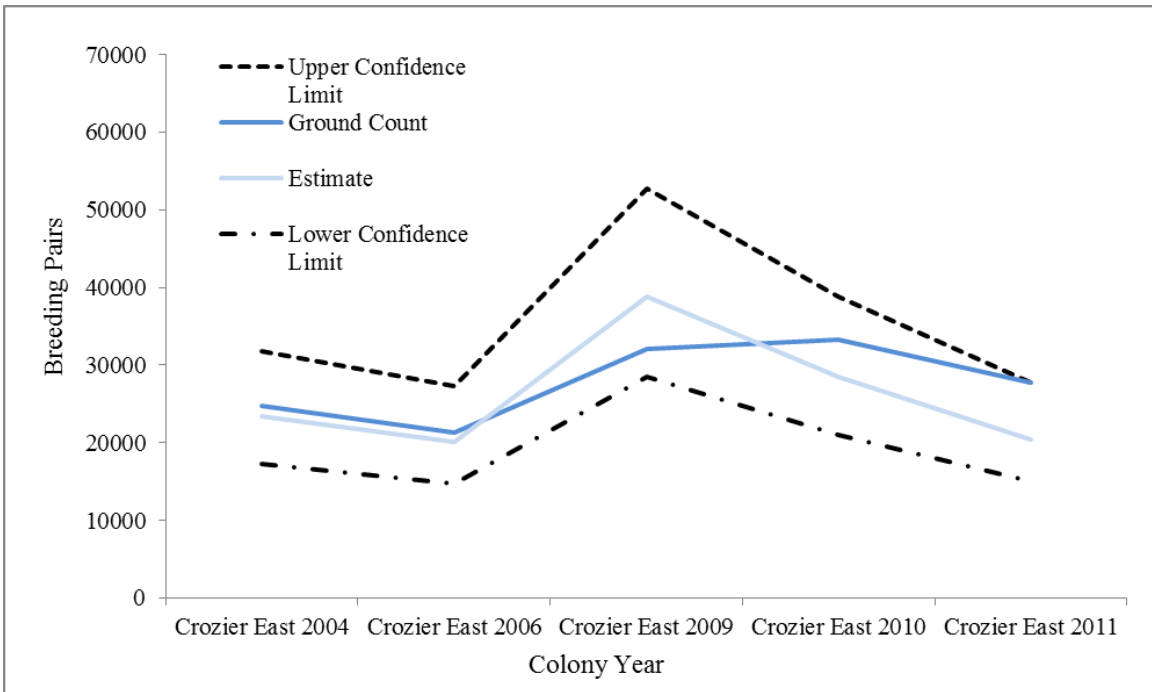


Figure 3.5. Predicted number of breeding pairs of Adélie penguins from my model, and number of observed breeding pairs from ground counts during the same breeding season, with upper and lower confidence intervals, at Cape Crozier East (top) and West (bottom) during 2004-2011. Note different scale on Y axis between top and bottom graphs.

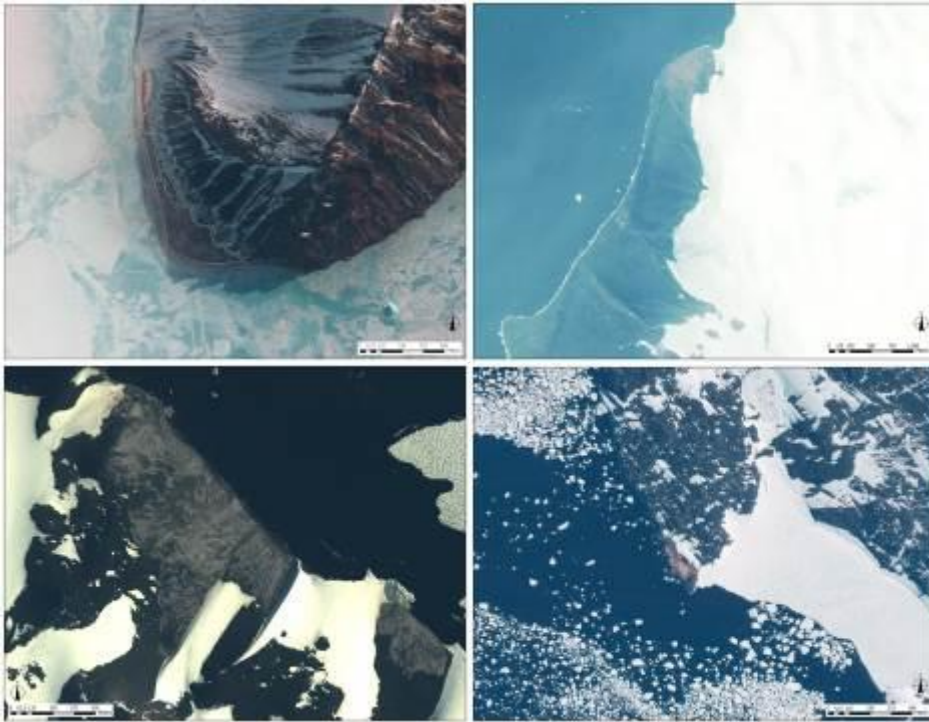


Figure 4.1. Satellite images of each Adélie penguin colony within the 4-colony metapopulation in the southern Ross Sea showing colony area at each location. Clockwise from top left: Beaufort, which has been habitat-limited by steep moraines to the east, a glacier to the north, and the ocean to the west and south; Bird, with a glacier to the east; Royds, with fast ice to the southeast; and Crozier colonies, both east and west, that are separated by a glacial field. Images are QuickBird-2, courtesy Digital Globe, Inc.

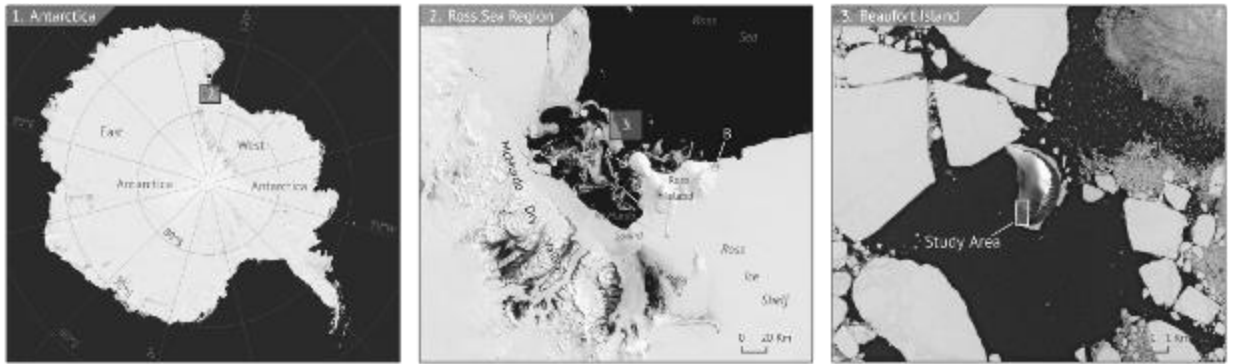


Figure 4.2. Locator map for our study area at Beaufort Island, Ross Sea, Antarctica. Left, the location of the Ross Sea region; middle, the location of Beaufort Island and the locations of other Adélie penguin colonies on nearby Ross Island (A. Cape Bird, B. Cape Crozier, C. Cape Royds) and, right, the location of the main Adélie penguin colony on Beaufort Island.

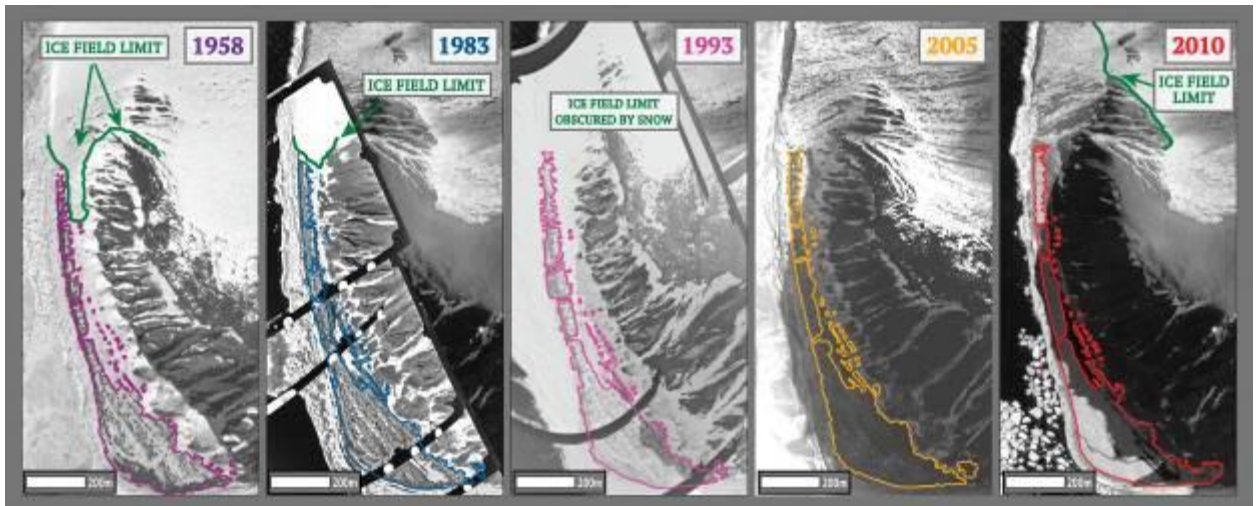


Figure 4.3. Changes in snow and ice cover and spatial extent of the Adélie penguin colony at the southern end of Beaufort Island, Antarctica, from 1958-2010 using air photos and high-resolution (0.6 m) satellite imagery (copyright DigitalGlobe, Inc). During the early years, best seen in the 1958 and 1993 image, snow covered the area, with penguins nesting on bare mounds and ridges.

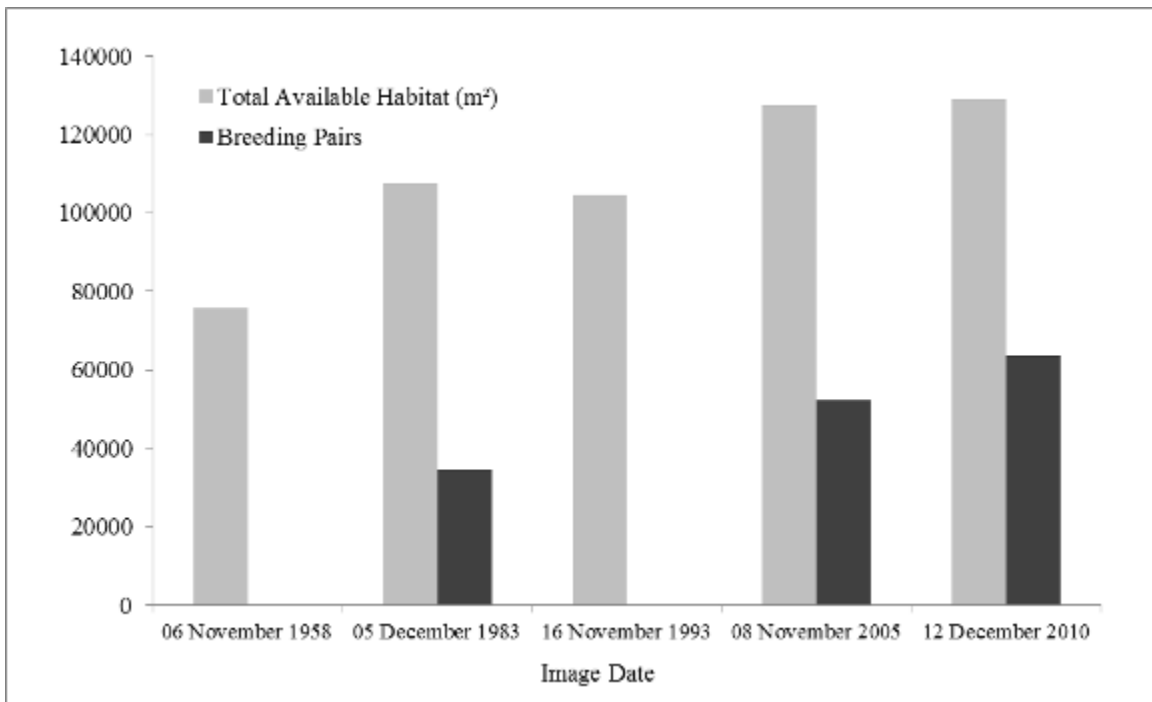


Figure 4.4. Available habitat (m²) and breeding pairs of Adélie penguins at the main Beaufort Island colony during 1958-2010. Available habitat was defined as the maximum extent of the guano stain of the colony minus the snow cover (i.e., unsuitable habitat) within the colony boundary.

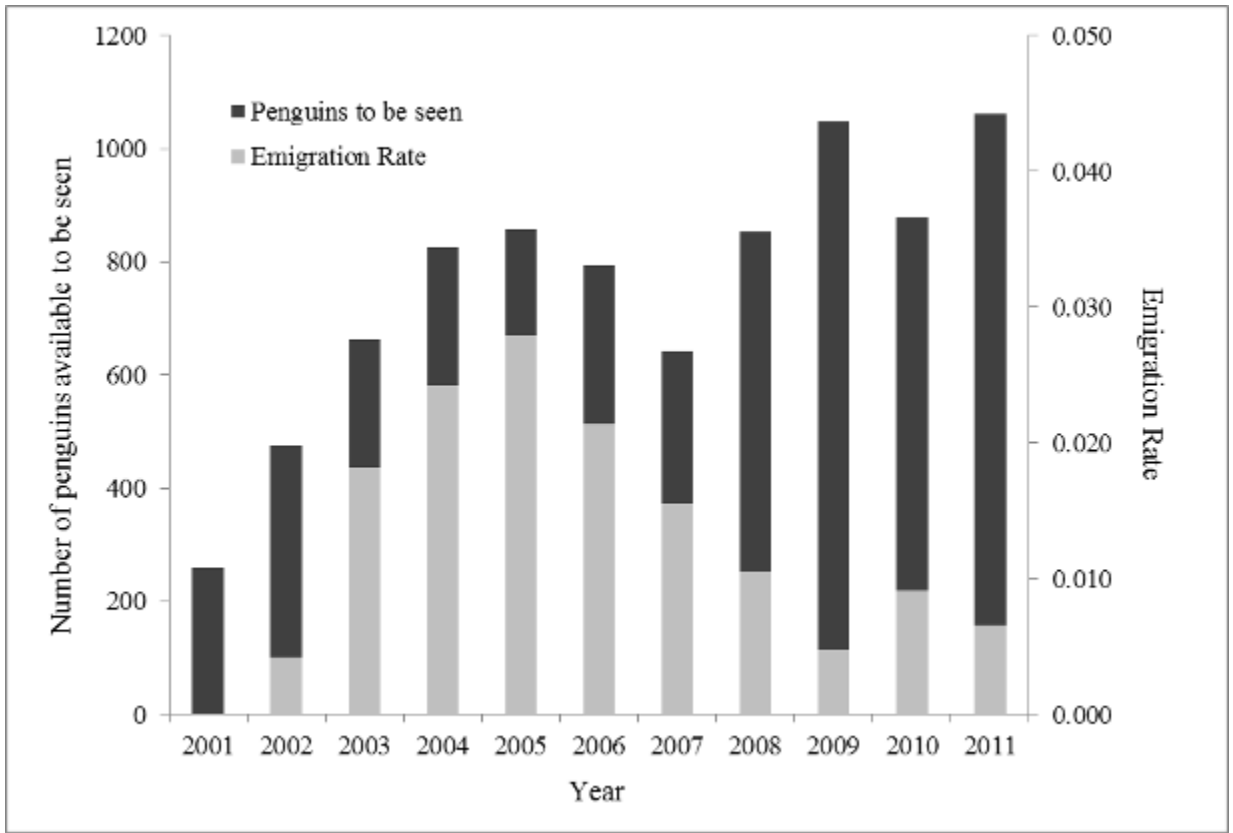


Figure 4.5. The proportion of banded Beaufort birds seen at one of the other three Ross Island colonies (Capes Royds, Bird, Crozier), relative to the total number of Beaufort banded birds potentially alive each year (“Emigration Rate”; light bars) and the total number of banded Beaufort birds potentially available (dark bars) during band searches. Except for 2005 and 2008, 400 chicks were banded at Beaufort Island per year from 1999-2010. Birds banded as chicks at the beginning of the study (1999) began returning to breeding colonies within the Ross-Beaufort island metapopulation in 2002.

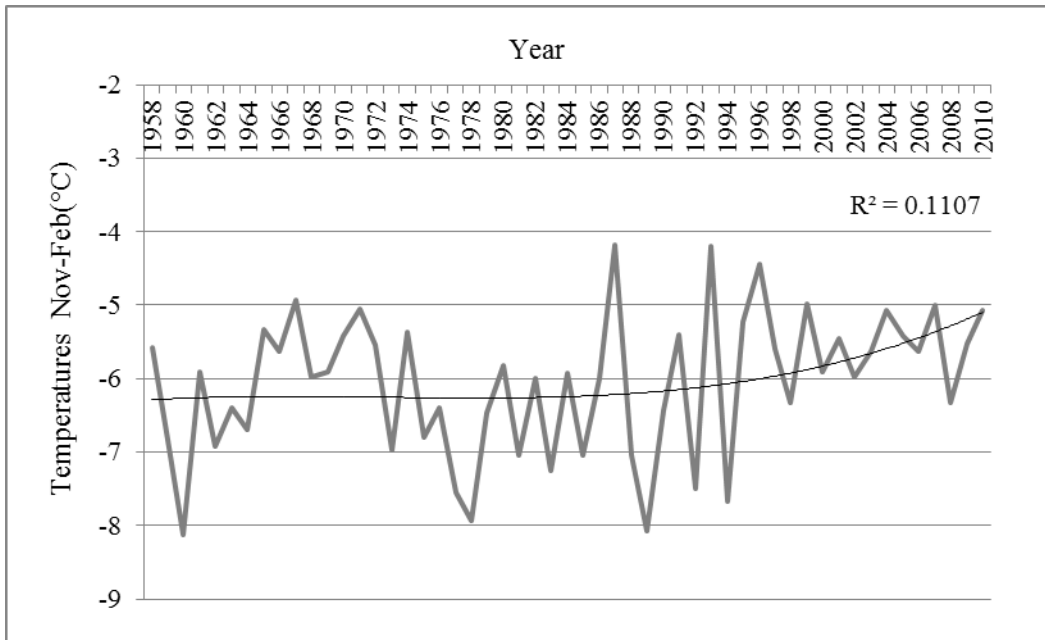


Figure 4.6. Average summer (November-February) temperatures in °C recorded at McMurdo Station, approximately 90 km south of Beaufort Island, Antarctica, during 1958-2010.

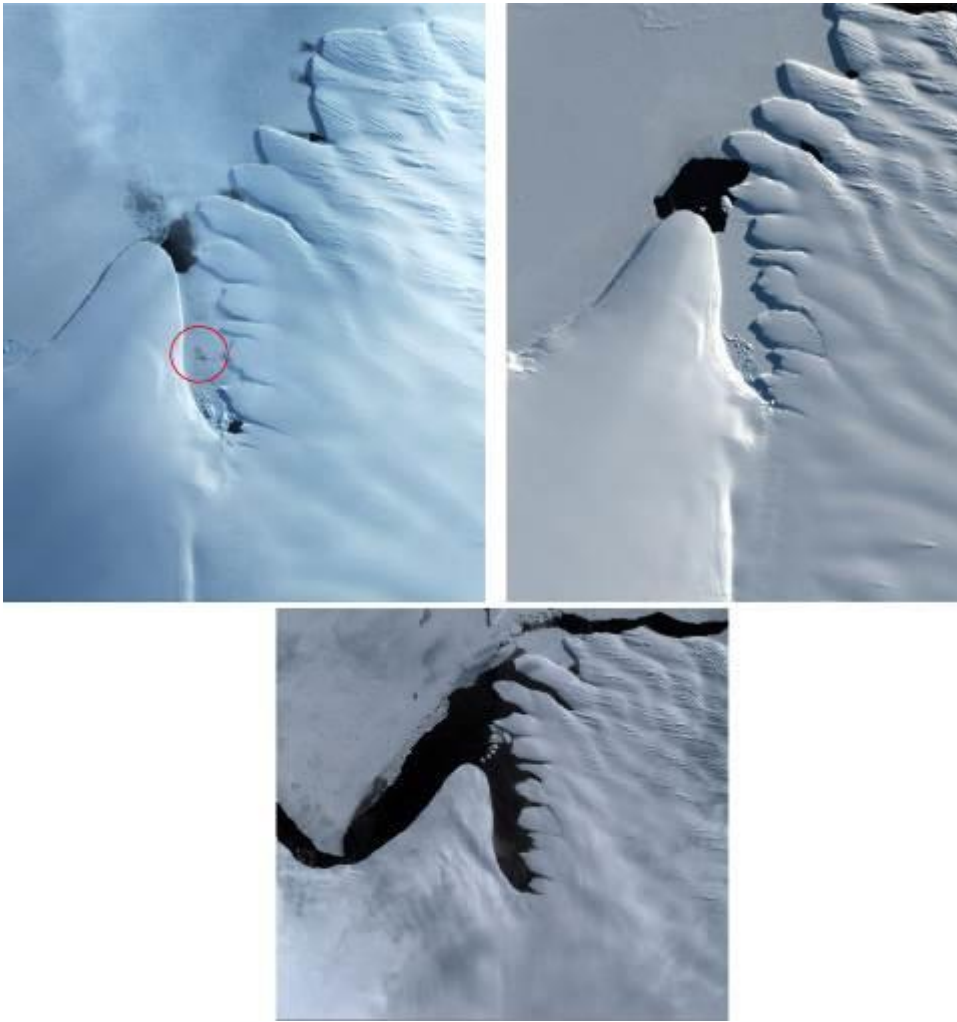


Figure 5.1. Ledda Bay emperor penguin colony (coordinates) on October 7, 2010 (within the red circle on the left image) and on September 23, 2011 (right image), where no guano stain is apparent. Bottom image shows the changes in sea ice at Ledda Bay during 2012, with no colony. Imagery courtesy DigitalGlobe, Inc.

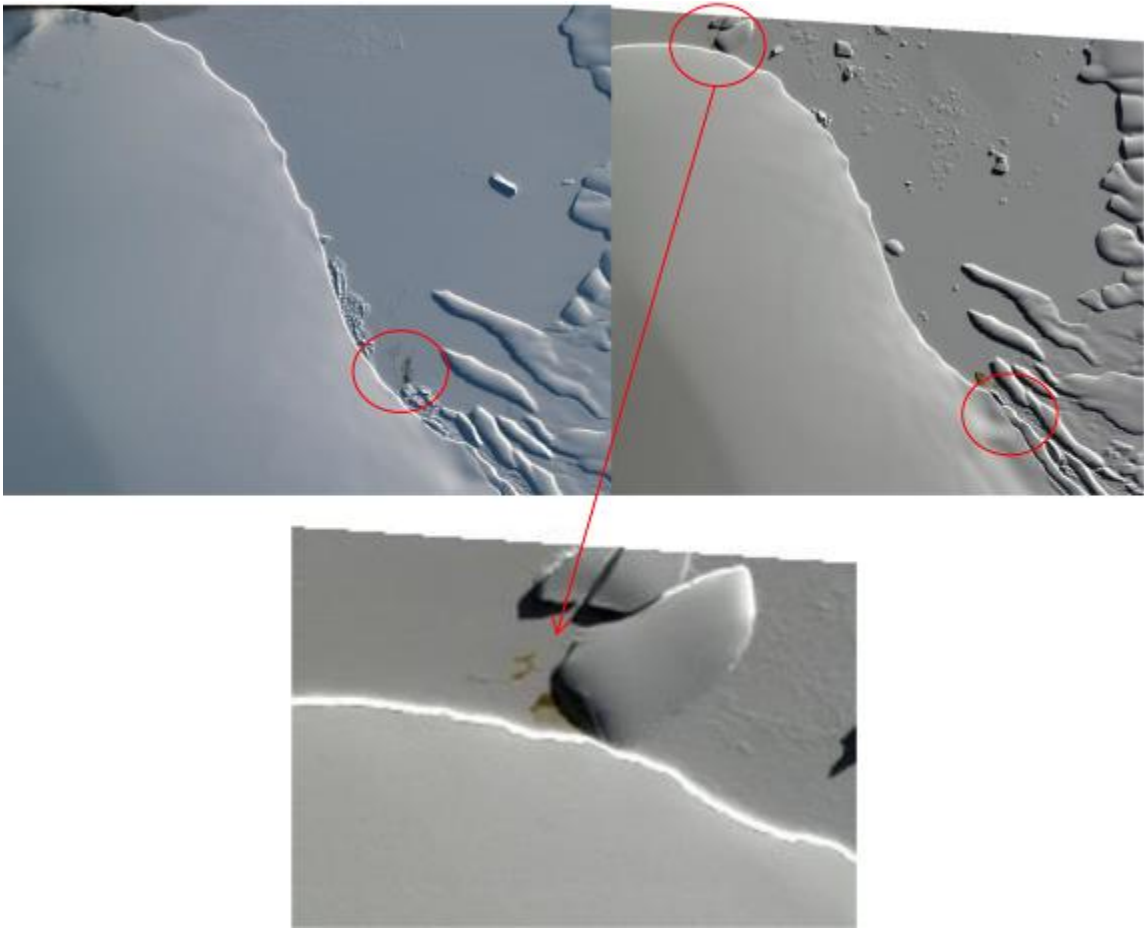


Figure 5.2. Cape Colbeck colony location on September 27, 2010 (left image), showing the normal location of the colony; and on September 23, 2011 (right image), showing the main colony and also the satellite colony to the north (guano stain on bottom picture). Imagery courtesy DigitalGlobe, Inc.

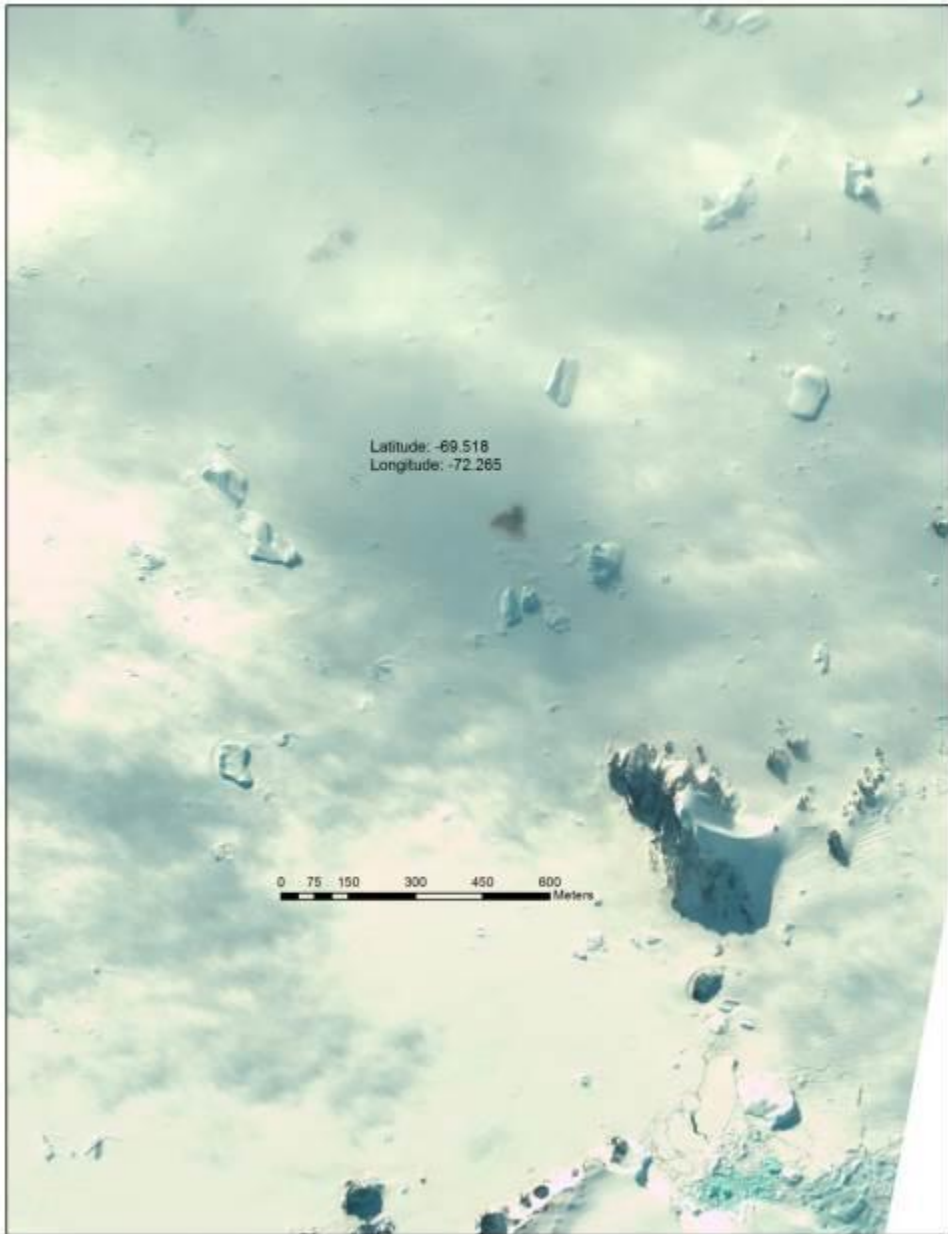


Figure 5.3. Location of newest emperor penguin colony on the Antarctic peninsula, on October 12, 2012. Image courtesy DigitalGlobe, Inc.

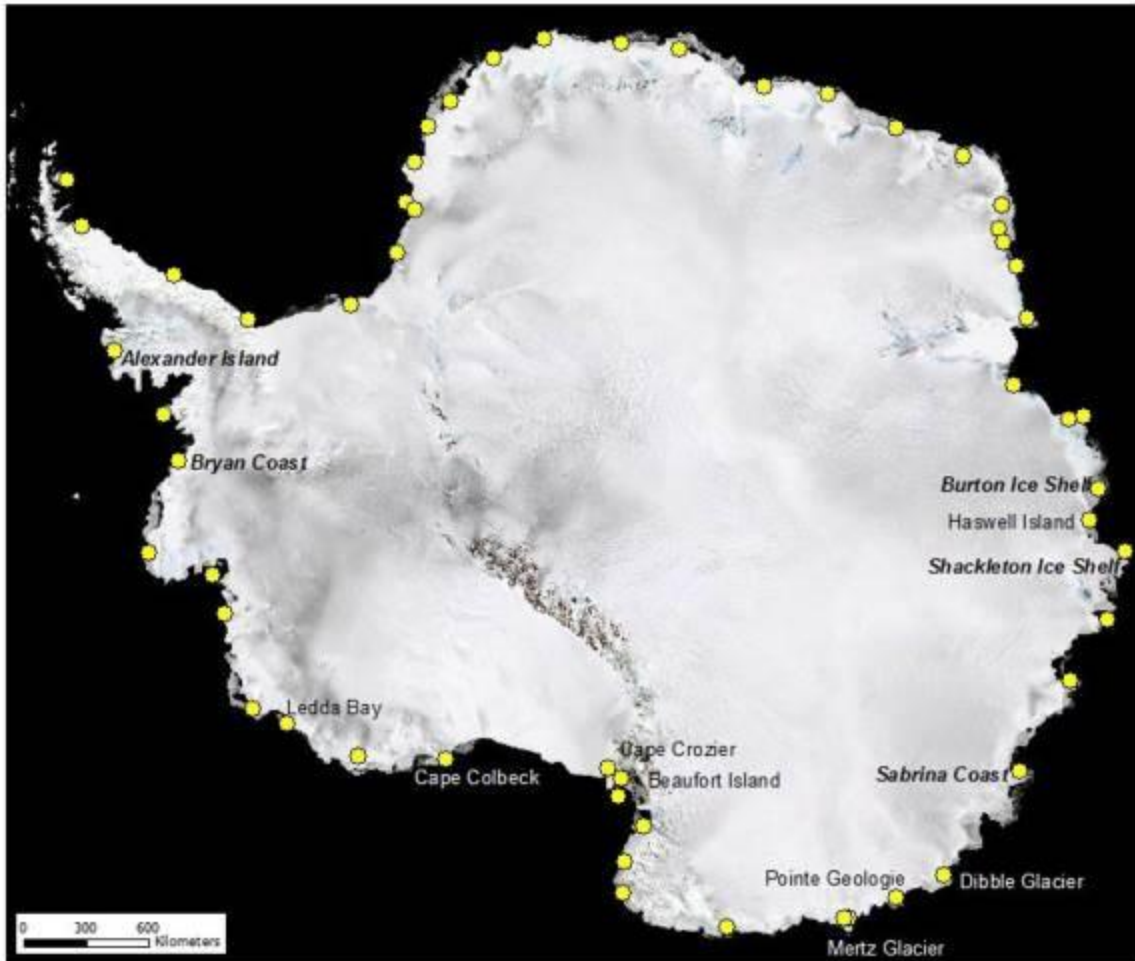


Figure 5.4. Emperor penguin locations (n=54) known as of December 2013, including the new colony discovered at Alexander Island on the Antarctic peninsula. Colonies in italic, bold font represent new colonies.

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