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Biotic and physical forces as determinants of Adélie penguin population location and size

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A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences, The University of Auckland, 2009.
Abstract
Adélie penguins (*Pygoscelis adeliae*) are among the most thoroughly studied wild animals, which is remarkable considering they are sea-ice obligates, living only in the Antarctic, one of the most remote regions on Earth. Building on several decades of research on the Ross and Beaufort Island metapopulation, I have focused on understanding the underlying mechanisms related to colony size and growth patterns. I have found that life for a penguin at a large colony is extremely competitive, and that the ultimate size of these colonies is determined by the trade-off between the needs of parents and chicks, with penguins at large colonies approaching an energetic limit not reached at smaller colonies. However, some individuals are consistently able to utilize the available resources within these limits more efficiently than others by diving more deeply and recovering more quickly, especially when environmental conditions are less favorable. It is likely that these individuals thereby exhibit increased fitness in terms of their genetic contribution to the population. At smaller colonies, this kind of advantage does not necessarily translate to increased fitness, since there appear to be ample resources for all, or for none, depending more closely on simple yet extreme physical environmental stochasticity. Finally, in the larger context of Adélie penguin life-history throughout the annual cycle, they are confronting large scale changes in their environment that have been occurring for millennia, but which are currently in an unusual state of flux. Ultimately a lack of sufficient daylight overlapping the region of sea ice that is accessible to them during the inter-breeding period may constrain their populations.
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Chapter I: Understanding coloniality in Adélie penguins

PLATE 1. A gathering storm at Cape Crozier. Two researchers start heading back to the 4 person US Antarctic program hut (1km up the hill), amidst thousands of nesting Adélie penguins (photo: G. Ballard).
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1.1 Introduction
Extensive variability exists in population sizes of organisms in general, and in colony sizes of group-living animals in particular, and the demographic processes within metapopulations have been the subjects of long interest in ecology (Andrewartha and Birch 1954, Cairns 1989, Brown et al. 1990, Brown and Brown 2001). Despite the useful reviews on the causes and consequences of colony size variation provided by Brown et al. (1990), Brown and Brown (2001), and Safran (2004), most of the questions about the large variability in population sizes of colonial nesting birds remain un-addressed. This is in part due to difficulties in finding unperturbed populations of varying sizes that face similar physical and biological circumstances, such that readily interpreted answers can be sought from them (cf. Leopold 1949, Ainley 2002b). It is also due in part to the scale required of a project in which these questions can be addressed: investigating metapopulations of several colonies simultaneously is something that most researchers lack the resources to undertake.

MacArthur and Levins (1964) described the general theory of how species are allocated among habitat types, and proposed that fewer species should occupy habitats with unpredictable climates. However, they did not connect the idea of species-niche occupation with a potential parallel: that populations of single species should be smaller in habitats with unpredictable climates. They did specify that in the absence of competition for a given resource (e.g. food or nesting sites) a population should grow until it exceeds the capacity of that resource to sustain the population, at which point population growth should stabilize (cf. Malthus 1798). This effect should be more readily apparent in highly synchronous breeders, a common trait in colonial species. In the absence of nest site limitations, the amount and quality of the foraging habitat should ultimately limit colony size (Storer 1952, Ashmole 1963, Diamond 1978). Brown et al. (1990) proposed four non-mutually-exclusive explanations for variation in colony size within avian species: (1) habitat quality (2) social costs/benefits (3) random, based on lack of ability to choose; and (4) some individuals are
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forced to occupy sub-prime locations by dominant individuals occupying prime locations.

More recently, Brown and Brown (2000) added a fifth component by showing that colony size in Cliff Swallows (Hirundo pyrrhonota) has a genetic basis – individuals from large colonies are more likely to recruit to large colonies and vice versa (subsequently confirmed in Barn Swallows Hirundo rustica and Lesser Kestrels Falco naumanni; Möller 2002, Serrano and Tella 2006, respectively).

1.2 A study to understand coloniality in Adélie penguins

Since 1996 I have sought to understand the factors involved in determining population size and distribution in Adélie penguins (Pygoscelis adeliae) in an unusually apt natural laboratory, the Southern Ross Sea (Wilson et al. 2001, Ainley et al. 2004, Ballance et al. 2009, Lescroël et al. 2009). Ainley et al. (1995) described the pattern of distribution of Adélie penguin colonies for all of Antarctica, noting that colonies were clustered, with several small colonies often occurring in proximity to a very large colony. There are only six very large colonies (>120,000 breeding pairs) in Antarctica, whereas there are ~150 smaller colonies (Ainley et al. 1995, Ainley 2002a; Fig. 1.1). This structuring, however, may be changing because Adélies live in a part of the world in which climate change is affecting the ocean as well as prospective nesting areas in profound ways (Parkinson 2002, Stammerjohn et al. 2008, Ainley et al. in press; Fig. 1.2). Antarctica in general is warming (Steig et al. 2008) and (1) causing glaciers to retreat, potentially exposing new nesting areas; (2) loosening pack ice in areas previously inaccessible to foraging penguins; but (3) reducing sea ice habitat in some areas, thus causing the sea-ice obligate Adélie penguin to decline (Fig. 1.2; Ainley 2002a, Ainley et al. in press).
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FIGURE 1.1. Distribution of colony sizes of Adélie penguins (from Ainley et al. 1995).

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We designed the project that provides the broader theoretical and empirical context for my individual contributions that comprise this dissertation to explain why (1) colonies in the Ross Sea (which includes the southern-most portion of the Adélie penguin range) increased in size rapidly during the 1970-80s and then plateaued (Fig. 1.3); (2) the rate of increase and variability has been highest at smaller colonies (Fig. 1.3); and (3) adjacent colonies vary greatly in size (Ainley et al. 1995). Several factors combine to make the southern Ross Sea the ideal study location for this work. An isolated cluster of four penguin colonies of dramatically different size (and home to 8% of the world population for this species) is relatively easily accessible thanks to the U.S. and New Zealand Antarctic programs. A long history of scientific investigation of these colonies provides context, including a 40-yr, annual record of colony-size variation (Fig. 1.3; Ainley 2002a). The study area has a relatively intact food-web, especially when compared to 99% of the Earth’s bioregions – the Ross Sea is the least altered stretch of ocean on the planet (Halpern et al. 2008, Ainley in press) and the area of highest primary productivity in the southern ocean (Arrigo et al. 2008). And finally, dynamic environmental conditions provide natural experiments that can be exploited in ways typically only possible with traditional experimental manipulations, which are impossible or unethical at the scale necessary to address the large-scale ecological questions we are investigating (Shepherd et al. 2005, Ainley et al. 2006).
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**FIGURE 1.3.** Relative changes in population size of Adélie penguins at three of four colonies in the Beaufort/Ross Island metapopulation, 1960-2007 (compared with 1970). Colonies differ in number of breeding pairs by successive orders of magnitude: Royds smallest (~2000), Bird (~50,000), Crozier largest (~150,000). Beginning in the early 1980s, colony growth rate and variability differed by colony size. (unpublished data courtesy of Landcare Research, New Zealand).

My specific role in the project began as a field biologist in 1996 and evolved to co-Principal Investigator 2002 - 2009 (David Ainley is the lead investigator). As a co-PI I co-wrote 2 consecutively-funded proposals to the National Science Foundation, with a third submitted in June 2009. My contributions to the work have focused on motivating, inventing and refining methods for investigating the foraging tactics of Adélie penguins. Additionally, I personally conducted or oversaw all data collection at the largest colony (Cape Crozier) beginning in 1999. Foremost among the hypotheses that I constructed and evaluated was the idea that large colonies are large because they are in the most suitable physical locations, and are ultimately limited by biological (competitive) constraints rather than physical ones. By contrast, small colonies are small because they are situated in sub-optimal physical locations, but can grow rapidly during phases when physical conditions become favorable. Within this context, I have also developed and begun to evaluate the hypothesis that heterogeneity in quality of individuals plays an important role in population structuring, and that natural
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selection is continuously active in the most competitive situations (i.e., in the largest populations).

To assess these hypotheses, I helped to develop the computerized weighbridge (WB), from which, using implanted passively-interrogated transponder tags (PIT tags) to identify individual penguins, I could assess adult mass, meal size fed to chicks, and feeding frequency. WB’s were deployed at each of 3 colonies for 9-13 seasons (Chapters 3 & 4), and I personally tagged and monitored all of the Cape Crozier penguins included in our studies. I developed the techniques and software for compiling and analyzing all the WB-derived data that our project has produced. Another large part of my contribution to the work was the development of methods and software for processing and analyzing time-depth-recorder (i.e., penguin diving) data specifically in the context of Adélie penguin behavior (Chapter 4). I have also become expert in methods of device attachment to penguins, and co-invented a method for an over-winter attachment that allowed me to document for the first time the migration routes and wintering areas of Adélie penguins (Chapter 6). In my work I have had to become highly proficient in conducting spatial analyses of sea-ice concentration and iceberg movements and penguin foraging locations utilizing remotely-sensed data from several sources and Geographic Information Systems (GIS; Chapters 3 & 6). Working with longitudinal data collected in an unbalanced design, where many individuals were repeatedly sampled within and among years, and recognizing the huge amount of individual variation in penguin behavior, I have been among the first to apply generalized linear mixed models to analyses of penguin foraging ecology (Chapters, 3, 4, 6). Finally, the relatively long period of study and the extremely rare opportunity to capitalize on a large-scale natural experiment (see below), I have developed and applied expertise in the use of an information theoretic approach to elucidate complex patterns in penguin ecology (Chapters 3-6).
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Combining these methods, I found that penguins acted like optimal foragers as long as feeding-trips were $\leq 2 \text{ d}$ (food loads returned increased with trip length) but as trip length increased ($> 2 \text{ d}$), meal size, adult body condition and chick growth decreased (Ainley et al. 1998, 2004, Ballard et al. 2001; see also Chapter 3). Also, trip times and meal sizes differed between sexes, but were closely related to parent mass at the start of chick feeding; heavy birds subsequently lost mass but lighter ones foraged longer for themselves, rather than their chick, and gained mass (Chapter 3). Trip times were consistently longest, adult mass lightest, and energy expenditure greatest at the largest colony, indicating intra-specific competition at large colonies but not at smaller ones (Ainley et al. 1998, 2004, Ballance et al. 2009, Chapter 5). Trip times and foraging behavior were related to a bird’s breeding quality (“BQI”: an index related to propensity to breed successfully; Lescroël et al. 2009, Chapter 4). Trip times were also related to sea-ice conditions (Ainley et al. 1998, Ballard et al. 2001, Chapters 3, 4), and to the number of minke and killer whales present, because of inter-specific competition for food (more whales = longer penguin foraging trips; Ainley et al. 2006, 2007, 2009).

During all summers we also assessed breeding effort, measuring factors including chick growth, breeding success, numbers of breeding pairs, and survival of breeders (Ainley et al. 1998, 2004, Ballard et al. 2001, Dugger et al. 2006, Lescroël et al. 2009, Dugger et al. in prep). Chick growth was consistently greatest at the small colony and least at the large one. Overall breeding success did not vary among colonies. Breeding numbers were lowest at all colonies during summers when spring sea ice was more concentrated, thus hindering migration, a finding facilitated by a “natural experiment” (see below). Survival of breeding adults was lower at Cape Royds compared to Cape Bird and Cape Crozier (Dugger et al. in prep) which may reflect the different wintering post-breeding journeys or migration chronologies between the Royds breeders and birds breeding at the other two sites (Chapter 6).
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We quantified diet at each colony throughout the chick provisioning period every year, showing that diet composition and quality did not vary geographically (Ainley et al. 2003a). We did not directly assess prey availability because logistic support was not available, but there was indirect evidence for equal availability of foraging habitat, since the area offshore of colonies was thoroughly utilized by penguins (see below; cf. Cairns 1989). We also showed that penguin diet was affected by the presence of cetaceans (Ainley et al. 2006, 2007, 2009).

1.3 Effects of intraspecific trophic competition
In his “hinterland” model, Cairns (1989) found support for the earlier hypotheses of Storer (1952) and Ashmole (1963), showing a positive correlation between the amount of foraging area available to seabirds and their colony size and showing that adjacent colonies should have abutting, non-overlapping foraging areas. Similarly, Furness and Birkhead (1984) showed that intra-specific competition for food among colonies in close proximity would limit their size, but that foraging areas might overlap to some extent. In all years (1996-2008) of our study, radio and satellite telemetry provided information on foraging-area size and degree of overlap among the four colonies (Fig. 1.4; Ainley et al. 2004, Chapter 3). We found up to 50% overlap among the three smaller colonies (Beaufort, Bird, Royds), but minimal (if any) overlap with the large colony (Crozier). The foraging area of the three smaller colonies together was equivalent in size to that of the largest colony, but the density of foraging penguins in the common area was half that in the foraging area of the large colony. At the two largest colonies foraging by parents was at first nearby, but then became progressively farther away and deeper, effectively expanding the total foraging volume utilized as the chick-provisioning period advanced (larger chicks demanding more food; Fig. 1.4, 1.5; Chapters 3 & 4, Ballard et al. in review 2, Lescroël et al. in review).
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**FIGURE 1.4.** Foraging locations (clusters of 3 or more locations within 2km and 4hr) of Adélie penguins as determined by satellite telemetry, 2000-2004. Green locations are early season (guard stage), orange locations are late season (crèche stage). Effect of day within season on trip distance significant for largest colony, not for smaller colonies (ANOVA for effect of day on max distance to colony by individual for Cape Crozier, controlling for year effect: $\beta = 0.071 \pm SE 0.014$, $F_{2,100} = 5.85$, $P = 0.004$, partial $r^2 = 0.085$). Base map layers from British Antarctic Survey (1998; land and ice shelves) and Davey (2004; bathymetry).
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**Figure 1.5.** Mean foraging depth of penguins from colonies of 3 different sizes related to time within season (days since 50% of nests in the colony had hatched; results for 2003-2004 shown). Foraging depth increased dramatically at the largest colony, Cape Crozier, but not at the smaller colonies (ANOVA for effect of day on depth at Cape Crozier controlling for year effect, 1999 - 2003: \( \beta = 0.009 \pm \text{SE} 0.003, F_{2,92} = 9.69, P = 0.003, \text{partial } r^2 = 0.084; \) see Chapter 4 for methods).

Near the end of the chick period at Cape Crozier, penguins foraged as far as the eastern shores of Beaufort Island, at which time Beaufort birds no longer foraged there (Beaufort birds then foraged only to the west of the island). These results suggest that intraspecific competition is important in metapopulation structuring, with the large colony affecting the size and location of foraging areas of smaller colonies located within foraging range (Ainley et al. 2004).

1.4 A “natural experiment” reveals effects of plasticity in philopatry

After the end of the 2000-01 season, two very large icebergs (C-16, 10 x 45 km; B-15, 40 x 160 km) grounded between Cape Crozier and Beaufort Island (Arrigo et al. 2002; Fig. 1.6), thus providing a “natural experiment” to test our hypotheses about population structuring and resource competition.
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**Figure 1.6.** Southern Ross Sea showing penguin colonies (black dots) and the position of mega-icebergs C16 and B15A in relation to Ross Island. The large arrow shows the usual migration route of Adélie penguins during spring (October). Upon reaching B15A, penguins attempting to reach Cape Bird or Cape Royds had to turn in either direction to round B15A. Graphs show intercolony visitation levels before (2000-2001) and after (2001-2002) the icebergs lodged in the position shown. This natural-color satellite image from the National Aeronautics and Space Administration’s Multiangle Imaging SpectroRadiometer was acquired during two polar overpasses of the Terra satellite on Dec. 9, 2001. Details of the satellite image are available at www.misr.jpl.nasa.gov. (From Shepherd et al. 2005).

Crozier birds were physically restricted from foraging close to Beaufort Island, an area from which Beaufort birds no longer retreated. This supports the hypothesis of Ainley et al. (2004), that the large population at Cape Crozier normally displaced foraging birds from Beaufort Island (and Cape Bird), and indicates that intra-specific competition is a likely factor involved in geographic structuring of colonies (Ainley et al. 1995, 2004; Figs. 1.6, 1.7).
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FIGURE 1.7. Satellite positions for Ross and Beaufort Island penguins in 2005-06 (left) and 2006-07 (right) showing effect of giant icebergs on foraging locations. Base map layers from Antarctic Digital Database (land and ice shelves; British Antarctic Survey 1998).

At the onset of our project, we proposed to study the demographic causes of population increase, in contrast to a 1960-70s study that investigated population decrease (Ainley and DeMaster 1980). After 5 years of data collection, the large icebergs arrived, forcibly separating the large Crozier colony from the others (Fig. 1.6). The icebergs formed a barrier 165 km long (~1.5° latitude) and 50 m high, abruptly stemming the flow of potential recruits from Crozier to the smaller colonies (artificially increasing philopatry at Crozier), and increasing the flow of potential recruits among the other colonies (artificially decreasing philopatry at Royds, Bird, and Beaufort; Fig. 1.6). We have documented the short-term demographic effects of increased immigration (Dugger et al. in prep), poor reproductive success, decreased breeding population size and decreased breeding propensities at Royds, Bird and Crozier. Before the icebergs’ arrival, appreciable numbers of birds produced at Crozier were sighted elsewhere, a flow of individuals that has subsequently been reduced. In addition, the extensive fast ice that required 20-50 km over-ice treks by breeding Royds penguins has encouraged them to recruit to Bird, closer to open water. In general, the icebergs increased movement probabilities for established breeders at all three colonies but
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these movements were strongest from Royds to Bird (Fig. 1.8). At the fourth colony (Beaufort), the extensive ice discouraged movement from there to Royds, a pattern that previously had been significant. Therefore, when faced with challenging conditions, penguins can forgo what earlier was assumed to be an extremely high degree of breeding and natal philopatry (Ainley et al. 1983). Adélies abandon colonies in favor of ones where sea ice is more dispersed and where less breeding and foraging effort is required.

We thus had an unparalleled “natural experiment,” showing how penguins coped with a rapid climate change event (i.e., substantially increased sea ice). Our results provided insights into causes for the previously enigmatic genetic homogeneity (because of presumed philopatry there should have been more divergence) of Adélie penguins throughout their current range (Roeder et al. 2001, Lambert et al. 2002) and provided a measure of the rate of microevolution of their nuclear DNA over the past 6,000 years, which we previously attributed primarily to mutational processes rather than selection (Shepherd et al. 2005). The frequency with which such large icebergs occur is high enough during interglacial periods (twice per millennium; D. Macayeal, pers. comm.) and the resulting mixing of individuals from different colonies is substantial enough to explain the relative lack of genetic variation in the species. This dissertation provides support for the idea that selection is actively affecting this metapopulation, posing an alternate (and not mutually exclusive) hypothesis for the genetic changes we showed previously.
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**Figure 1.8.** Differences in movement probabilities for three colonies of breeding, adult Adélie penguins in the Ross Sea during years with (2002-2005) and without iceberg influences (1996-2001, 2006; Dugger et al. in prep).

In addition to the obvious impacts of the mega-icebergs, we have hypothesized (Wilson et al. 2001) that increasing winter temperatures and winds during the 1970-90s, as a result of a shift in the Southern Annular Mode, led to more open water near shore (earlier-forming, larger, and more persistent Ross Sea and McMurdo Sound polynyas), a hypothesis supported by Parkinson (2002; Fig. 1.2) and by Turner et al. (2009). These physical processes have contributed to the increasing size of the smaller penguin colonies (Royds and Bird). In addition to the evidence for intraspecific competition summarized above, however, our finding that cetaceans are a direct competitor of the penguins (Ainley et al. 2006), has led us to surmise further that the coincident industrial extraction of 15,000 minke whales from the Ross Sea area has also played an important role, contributing to the growth of penguin populations during the 1970-80s (Ainley et al. 2007; 2009 Fig. 1.9).
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FIGURE 1.9. Minke whales (x 100) removed from the Ross Sea sector by decade compared to percent differences relative to 1960s numbers of Adélie penguins breeding at capes Royds and Bird, Victoria Land, and Emperor penguins at Pt Géologie, Adélie Land. These penguins and whales spend the late summer to early winter in the same habitat and region; both have the same diet (Ainley 2002b). Data on penguins are from Wilson et al. (2001) and Weimerskirch et al. (2003); those for whales from Brown and Brownell (2001) (from Ainley et al. 2007).

1.5 Effects of plasticity in foraging behavior
Harsh environmental conditions can select breeding individuals on the basis of their foraging ability (e.g. Grant and Grant 1993), and wild animal populations can be demographically heterogeneous (e.g. Grant 1999, Fox et al. 2006); some populations are composed of groups of individuals with a permanent hierarchy in fitness components (e.g. survival, fecundity) among individuals. Thus, understanding the determinants of individual heterogeneity is crucial for comprehension of a population’s response to environmental change. Interindividual differences in energy acquisition may affect both breeding output and survival rates (Annett and Pierotti 1999). Especially in the context of the short Antarctic summers, foraging efficiency is a key parameter to investigate for central-place foraging seabirds since it ultimately determines the amount of energy that can be invested in the other components of life history. How successful a marine predator is during its foraging trips, and the associated benefit to reproductive performance, is not only influenced by prey availability but also by
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individual attributes (Grant 1999). We have shown (Lescroël et al. 2009) that variation in adult survival in Adélie penguins is largely explained by heterogeneity in individual quality; individuals have different performance levels that are consistent throughout life, independent of environmental conditions.

Furthermore, higher quality individuals, or “Better Breeders” (BB) can mitigate costs of reproduction even under demanding environmental conditions (e.g., heavy pack ice of iceberg years 2001-2005, Lescroël et al. 2009, Chapters 3 & 4). A closer examination of the foraging tactics used by BB revealed that they dive deeper at the end of the season when intra-specific competition is high and they are more efficient foragers (return to their offspring more catch per unit effort) than lower quality individuals. These differences were exaggerated during heavy ice years when foraging conditions were more demanding (Chapter 4). This suggests that “harsh” environmental conditions might favor individuals on the basis of their foraging ability, but it remains to be determined whether BB are better able to maintain their own condition during breeding, whether they begin the breeding season in better condition, and under what circumstances (of physical condition) high-quality individuals invest “too much” in breeding effort, thereby risking their own survival (i.e., the point in Fig. 1.10 at which survival begins to decrease).

Therefore, Adélie penguins show important phenotypic plasticity, suggesting that some portion of the population is able to cope with variability in their physical and biological environment. Such variability is likely to be associated with climate change and, ultimately, the species’ evolution (Shepherd et al. 2005). Given the relatively rapid changes in the Ross Sea physical environment now projected by climate models (Ainley et al. in press), this plasticity in Adélie penguins will likely be tested in the near future. Therefore, I predict that the capabilities of BB will become increasingly prevalent in the overall population. In fact, the consistently harsher (more competitive) conditions at the largest colonies (Ainley et al.
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2004, Ballance et al. 2009) may serve as a facultative mechanism, encouraging prevalence of higher foraging performance across the entire metapopulation of four Ross Sea colonies (Chapter 4).

**FIGURE 1.10.** Relationship between survival and breeding quality (and 95% confidence interval) in Adélie penguins (from Lescroël et al. 2009).

![](image)

1.6 Toward a more complete understanding
In spite of ongoing, large-scale anthropogenic resource extraction from the world’s oceans (Pauly et al. 1998, Myers and Worm 2003), most studies seeking explanations for variation in the populations of marine vertebrates in the Southern Ocean have focused almost exclusively on links between climate variability and demographic parameters of species (e.g. Barbraud and Weimerskirch 2001, Jenouvrier et al. 2003, 2005, 2009, Laidre et al. 2008; but see Ainley et al. 2007, Ainley and Blight 2009). Although these studies have demonstrated that climate-induced changes to the environment can trigger population change, the mechanisms underlying such patterns, whether driven by physical or biological processes, occur on an individual level, since each individual animal must deal with changing environmental conditions. The inability of an individual to adjust to fluctuations in resource availability
1. Understanding coloniality in Adélie penguins

due to stochastic environmental variability will ultimately lead to low reproductive success and/or low adult survival and, thus, may contribute to population decline if many individuals in a population face similar conditions. Hence, studying the behavioral, physiological and life-history responses of individuals is key to understanding adaptive phenotypic plasticity that might allow these marine predators to cope with environmental changes.

In this dissertation I present an overview of Adélie penguin natural history in the context of my ongoing research (Chapter 2 & DVD: Return To Penguin City) and four detailed analyses of components that directly relate to individual responses to environmental change, either in the form of variability in the physical environment due to icebergs and sea ice, or in the biological environment due to colony size, numbers of chicks being provisioned, or time within season (increasing chick needs and prey depletion). Chapter 3 describes trade-offs between parents and offspring to assess to what extent Adélies have the capacity to sacrifice their own condition for the benefit of their chicks. Chapter 4 investigates the role of variability in individual quality in the ability of Adélies to successfully raise young in difficult circumstances, and documents the links between quality and foraging efficiency. Chapter 5 shows the relationship between colony size and energetics, providing a model by which an ultimate size limit to Adélie penguin populations can be projected. In Chapter 6 I move away from breeding season dynamics to consider the role of migration and wintering habitat and timing, addressing whether different winter sea-ice conditions and colony-specific wintering areas could explain the population dynamics I am seeking to understand. In Chapter 7 I summarize the most important results of my work, its limitations, and the implications for future research.
1. Understanding coloniality in Adélie penguins

1.7 Overview of thesis structure and contributions
Chapters 1 & 2 are solely my original work (100%), incorporating customary minor comments on content and style by my thesis supervisor on the final drafts.

Chapter 3 is based on material by Grant Ballard, Katie M. Dugger, Nadav Nur, and David G. Ainley, formatted for Ecological Monographs. My contribution to this chapter (~85% of the total effort) was to generate the primary research questions, design the study, write the full draft, conduct all analyses, and incorporate comments from co-authors. Additionally, I collected all the data included with help from field assistants and oversaw or conducted all techniques for processing the weighbridge data, and co-designed the weighbridge itself (with Ainley, Mike Beigel, Nat Polish, and Peter R. Wilson). Funding for this work resulted from proposals that I co-wrote with Ainley.

Chapter 4 is based on material by Grant Ballard, Amélie Lescroël, Viola Toniolo, Kerry J. Barton, Peter R. Wilson, Phil O’B. Lyver and David G. Ainley, formatted for Ecology. My contribution to this chapter (~50% of the total effort) was to co-design the study (with Ainley), collect (or supervise collection of) all the data, co-invent the Breeding Quality Index (with Lescroël), analyze all the weighbridge and TDR data, co-write the full draft, and incorporate comments from co-authors. Funding for this work resulted from proposals that I co-wrote with Ainley and Lescroël.

Chapter 5 is based on material by Lisa T. Ballance, David G. Ainley, Grant Ballard, and Kerry J. Barton, formatted for Journal of Avian Biology. My contribution to this chapter (~50% of the total effort) was to co-design the study (with Ainley and Ballance), conceive and conduct the central analyses of effects of colony size on Field Metabolic Rate and Total Energy Expenditure, conceive and create the theoretical model (Figure 5.4) and co-write the
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full draft. Additionally, I participated in all aspects of data collection at one of the two colonies (Cape Crozier). Funding for this work resulted in part from proposals that I co-wrote with Ainley.

Chapter 6 is based on material by Grant Ballard, Viola Toniolo, David G. Ainley, Claire L. Parkinson, Kevin R. Arrigo, and Phil N. Trathan formatted for Ecology. My contribution to this chapter (~75% of the total effort) was to co-write the full draft, and incorporate comments from co-authors. I co-designed the study (with Ainley following his earlier discussions with Trathan), co-invented the technique for attaching Geolocation Sensors to penguins, and supervised collection of all field data. I also conducted all statistical analyses and supervised or conducted all GIS work. Funding for this work resulted from proposals that I co-wrote with Ainley.

Chapter 7 is solely my work (100%), outlining considerations of the implications, shortcomings, and directions for future research based on my thesis. It incorporates customary minor comments on content and style by my thesis supervisor on the final draft.

“Return To Penguin City” (DVD) was produced by Lloyd Fales, David G. Ainley, Grant Ballard, Ian Gaffney, Viola Toniolo, and Katie M. Dugger. I co-wrote the script (with David G. Ainley and Lloyd Fales), was interviewed extensively, and shot ~33% of the video. I also participated in editing and reviewing earlier versions.
Chapter II: A species copes with rapid, large-scale environmental change

2. A species copes with rapid, large-scale environmental change

When you first set foot in the enormous Adélie penguin colony at Cape Crozier, you are inundated by a rush of noise and of smell, of life and of death. If you have not experienced penguins before, you will probably first focus on the life. Even among penguins, Adélies are especially entertaining – very busy, often mischievous (stealing neighbors’ rocks for their own nests), and quite boisterous – constantly defending their space by bill-gaping, ecstatically vocalizing, flipper-bashing, and chewing on any transgressors of their carefully-defined personal space (about 0.5 m in any direction). But there is also something hypnotic about the experience of seeing so many of them together, with their formal color scheme (one of nature’s most reliable for an ocean predator: black above and white below) completely appropriate in the austere landscape of rock, ice, and windswept ocean. Scanning the few hundred thousand of them that I see every day during the majority of their breeding season, November 15th to January 25th, I am often entranced by the homogeneity – countless little black-and-white bipedal beings, without anything human for scale. This seems an ancient and unchanging scene, innocent of the anthropogenic perturbations so characteristic of the rest of the world.

Eventually, despite all the Adélies’ life energy, your attention is drawn to the dead — to the thousands of little penguin mummies that litter the ten square kilometers of the colony. They are everywhere, most of them dried and yellow — carcasses partially buried in stones or guano, small remains, many with penguins nesting on top of them. On my first visit to Crozier, in 1996, I asked David Ainley (40-year veteran leader of Antarctic expeditions) why there were so many dead penguins there — strikingly more dead than I had seen in other seabird colonies around the world. He explained that, at high latitudes, the extreme cold temperatures keep the processes of decay at near standstill. So, after thousands of years of occupation, a penguin colony at 77° south accumulates quite a pile of dead bodies.
2. A species copes with rapid, large-scale environmental change

But why hadn’t skuas scavenged all the dead chicks? Crozier is also home to the world’s largest population of South Polar skuas, who make brutally short work of any penguin chicks that die or wander from their home territory, even briefly.

My original questions have persisted over the subsequent 13 Austral breeding seasons that I have spent working mostly with the living — tagging them with transponders and making them travel across weighbridges, resighting individual penguins banded as chicks, attaching satellite transmitters to some that we track on their foraging journeys, making diet observations, and measuring chicks. We are investigating the processes that determine why penguin colonies exist where they do, why some grow very large, why some disappear, why some fluctuate wildly, and how they respond to climate change. Some of the answers were found literally right under our feet, in the dead penguins themselves: with colleagues from New Zealand and Italy we have documented the rate of micro-evolution in DNA of penguins, comparing 10,000 year old DNA, in tissue samples preserved that long in this environment, to that from current populations occupying the same sites (Shepherd et al. 2005).

After a few years, having gained a bit more experience with high-latitude Adélie colonies, I asked David why so many of the dead, at Cape Crozier in particular, were about the same age: a high percentage are crèched chicks (out of the nest but still dependent on their parents for food), about three weeks old, that appear to have died in a single season rather than representing accumulated mortality over the centuries. He then speculated that perhaps a giant iceberg had broken off of the adjacent Ross Ice Shelf when most of the parents were out foraging, blocking access to and from the colonies, with subsequent mass starvation of the chicks. Another explanation was offered by Steve Emslie (a paleo-ornithologist and professor at University of North Carolina), who visited our study site during the 2000-2001 season to ascertain the dates of the original occupation of the Cape Crozier colony. He was also astonished by the numbers of bodies; he guessed that most of the ones near the surface were
2. A species copes with rapid, large-scale environmental change between 100 and 200 years old, affirmed that most of them appeared to have come from a single event, and suggested that perhaps a massive snow storm one year had buried all the chicks alive.

At the time neither explanation seemed particularly likely, given that I had never seen either a giant iceberg or a massive snow storm (Antarctica is by far the driest continent on Earth), and the scene I had been observing then for several years seemed both primordial and permanent. Hadn’t the Crozier colony always been there, and hadn’t it always been huge? If such things could happen, might it mean that the colony was not as old as it seemed, or that it might someday vanish?

Since then, events have shown that both hypothetical explanations are plausible. We have seen giant icebergs break off the Ross Ice Shelf (most notably in 2001 – at 160 kilometers long, ‘B15’ was the biggest ever observed by humans) and crash into Cape Crozier, blocking almost all access to not just one colony but four of them simultaneously (at Cape Royds, Cape Bird, Beaufort Island, and Cape Crozier). This resulted in the deaths of many thousands of adults and chicks. We have also seen, in the same years (especially December 2001 and January 2005), the biggest snowfalls anyone can remember and some of the highest winds, depositing up to three meters of densely packed snow over scores of subcolonies in a single day, burying thousands of nests, adults, eggs (2001), and chicks (2005) – and skuas, too. Several years have since passed, and many of those dead birds have yet to emerge. I feel amazingly lucky to have observed such spectacles first-hand, events never seen before by scientists (or anyone else) and thought to have happened only once in the past thousand years (D. Macayeal, pers comm.).

The resilience of the penguins to such rapid and drastic environmental change is amazing. In the big blizzards, most of the parents were able to literally eat their way out of the snow that buried them, and they also learned how to navigate labyrinthine passageways through
2. A species copes with rapid, large-scale environmental change

iceberg-jumbled fast ice so they could get back to the open ocean and food, returning to find the scene constantly re-scrambled because of further collisions between the bergs and the island. Adults subsequently moved among colonies at unprecedented rates, to find ice-free nesting habitat and to improve their access to food. In the course of a single year, Adélies abandoned locations that had been occupied for centuries.

And once the giant icebergs moved north and broke apart in 2006, the penguins returned to business as usual. Though several thousand more adults than usual were killed by storms and icebergs between 2001 and 2005, the breeding population appears in 2008 to be as large as it has ever been in the 39 year period for which there are data. Apparently the penguins can cope with massive environmental change – so far.

The penguins will keep trying as hard as they can – that is the nature of Adélies. After a 48-hour foraging trip, having made thousands of essentially consecutive dives to 45 m or more, returning with a stomach stretched to the point of bursting with fish or krill, they will take a moment to pause briefly to pick up (or steal) a pebble on the way up the hill to bring to their mate at the nest; an act that can seem heartbreakingly romantic. They are remarkably resilient. There is bound to be a lot of new nesting habitat available to them on a warming Earth – at least for several decades to come – since there are still hundreds of kilometers of future coastline to emerge from under Antarctica’s ice-sheets. What is less certain is whether the ocean will continue to provide the apparently endless quantities of fish and krill that these birds rely on – especially now that industrial fishing ships are tempted into the Ross Sea’s pristine waters by the collapse of the world’s remaining fisheries.
Chapter III: Parental foraging and chick provisioning strategies of Adélie penguins in response to body condition and environmental variability

PLATE 3. An Adélie crosses the weighbridge, getting weighed and identified on its way out to find food for its chicks (photo: V. Toniolo).
3. Parental foraging and chick provisioning strategies

3.1 Introduction
Among central-place foraging species (Orians and Pearson 1979), parents are challenged to provide for nutrient needs of rapidly growing young and simultaneously meet their own energetic requirements while foraging at a distance (Williams 1966, Stearns 1976, Ydenberg et al. 1994). In all species, if young are inadequately fed, their immediate (pre-departure) or subsequent (post-departure) survival may be at risk; but, if parents do not adequately feed themselves, they risk their own survival and residual reproductive success (Goodman 1974, Charlesworth 1980, Costa 1991, Boyd et al. 1994, 1997, Golet et al. 1998, 2004, Erikstad et al. 1998, Weimerskirch et al. 2001). For long-lived species, even small reductions in adult survival as a trade-off for elevated breeding effort can have large impacts at the population level (Goodman 1974, Wooller and Coulson 1977). Therefore, the frequency and duration of feeding trips, as well as food load size, are critical for both parent and young.

Among birds, more feeding trips generally imply more food for offspring, but at greater energetic cost to the parent (Nur 1984a). Parents may use longer feeding trips to replenish their own reserves, but possibly at the expense of the chick(s) (Chaurand and Weimerskirch 1994b, Weimerskirch et al. 1994, 2003, Catard et al. 2000). However, some flying birds may voluntarily sacrifice some of their own mass in order to decrease travel costs to foraging areas, thereby optimizing foraging efficiency (Freed 1981, Norberg 1981, but see Nur 1984b, Moe et al. 2002). The dilemma for the parent is particularly acute when environmental conditions or other factors reduce access to prey. Goodman (1974) was first to present a formal argument that, when faced with the trade-off between self-maintenance and chick provisioning, seabirds in general will favor their own survival at the expense of the chick, particularly in food-poor years (see also Drent and Daan 1980, Weimerskirch et al. 2000, 2001, Golet et al. 2004). The idea that parents will adjust their reproductive tactics depending on their own condition and environmental factors has been referred to as the “individual optimization hypothesis” (Nur 1986) and has been described for volant landbirds as well as
3. Parental foraging and chick provisioning strategies

seabirds (Perrins and Moss 1975, Nur 1988, Charaund and Weimerskirch 1994b, Erikstad et al. 1997). A model of optimal investment of parents feeding their young has been developed, predicting that as prey availability or quality decreases, parents will partially compensate by working harder, but cannot afford to fully compensate; thus the quantity and/or quality of food delivery to the chick(s) is reduced, exemplifying a parent-offspring trade-off (Nur 1987). Parents in good condition have been shown to deliver more food to chicks than parents in poor condition for several seabird species (Weimerskirch et al. 1994, Erikstad et al. 1997, Tveraa et al. 1998) and can do so while making shorter duration foraging trips than parents in worse condition (Varpe et al. 2004).

A large body of work specific to these factors in long-lived seabirds has focused on Laridae (genera Rissa, Sterna), Procellaridae and Diomedeidae, flying species of high mobility, with morphology adapted towards maximizing flight efficiency (e.g. Pennycuick et al. 1984). These seabirds are renowned for long-distance movements during migration and while foraging during breeding, including in some cases patterns of very long versus short foraging trips depending on whether parents needed to recover condition (e.g. Chastel et al. 1995a, b, Weimerskirch et al. 1997, 2000, 2001, Becker et al. 2001, Golet et al. 1998, 2004). A bimodal pattern in foraging trip duration, with parents making long self maintenance trips and shorter chick-provisioning trips has been described for several seabirds (Granadeiro et al. 1998, Weimerskirch 1998, Booth et al. 2000), and in some cases, long and short trips alternated consecutively (Chaurand and Weimerskirch 1994a, Weimerskirch et al. 1994). Bimodality in foraging trip durations has been linked to habitat availability because in cases where only one habitat is available, species do not show bimodality (Weimerskirch et al. 1994). Environmental conditions also affect foraging trip patterns, with parents adopting a bimodal strategy when food was less accessible (Granadeiro et al. 1998) and potentially to types of prey available (Ropert-Coudert et al. 2004, Angelier et al. 2008). Further, longer
3. Parental foraging and chick provisioning strategies

Trips appear to be triggered by lower adult body condition, and the presence of a threshold body mass triggering longer trips has been posited for blue petrels (Chaurand and Weimerskirch 1994a) and for sooty shearwaters (Weimerskirch 1998).

As a contrast to all the work on flying species, penguins generally, and Adélie penguins (Pygoscelis adeliae) specifically, are informative species with which to investigate relationships among parental condition, provisioning behavior, and chick growth (Clarke 2001, Takahashi et al. 2003, Ropert-Coudert et al. 2004). Adélies, because they must swim or walk to find food, are more reliant than flying species on predictable access to and availability of prey that are only a comparatively short distance from the colony (Ainley 2002a, Ainley et al. 2004). Further, the Adélie penguin is the only migratory penguin that lays two viable eggs and commonly rears both to fledging; as such, the species may be particularly sensitive to variability in body condition or prey accessibility. Other migratory penguins, and also most pelagic seabirds, lay just one viable egg (in some species two are laid, but the second never produces a chick; Williams 1995). Among the ecologically similar Alcidae, species that lay two eggs either feed on abundant food found within minutes of the nest site (e.g. genus Cepphus) or bring semi-precocious chicks to where food is available soon after hatching (e.g. Synthliboramphus; Sealy 1973). The more mobile seabirds, which generally lay a single egg per breeding attempt, have been shown to have an energetic “cushion” to allow for variation in prey availability as well as variation in foraging strategies, whereby they can temporarily reduce their own condition in order to deliver sufficient food to their offspring (Lack 1968, Chaurand and Weimerskirch 1994b, Weimerskirch et al. 1994).

It remains unclear to what extent penguins have such a cushion, and under what conditions they reach a limit such that their chicks’ survival is at risk. Watanuki et al. (2004) hypothesized that penguins might be constrained from adjusting (i.e., increasing) investment in their chicks in the face of challenging environmental conditions. A contrasting conclusion,
3. Parental foraging and chick provisioning strategies

consistent with flexible investment, has been postulated based on examination of diving behavior and foraging models for Adélie penguins (Ropert-Coudert et al. 2004). Furthermore, at least three empirical studies have found that Adélies alternate long, relatively low-activity, self-maintenance trips with short, high-activity chick-provisioning trips (Clarke 2001, Clarke et al. 2006, Angelier et al. 2008).

As a major habitat variable, sea ice can affect penguin foraging and reproductive effort in diametrically opposing ways, depending on whether there is too much or not enough ice (Ainley 2002a, Clarke et al. 2006, Emmerson and Southwell 2008). Given the choice, Adélie penguins feed in close proximity to sea ice, presumably because their preferred prey is associated with the sea ice habitat, but potentially also because it offers a resting platform and easy source of drinking water (summarized in Ainley 2002a). When sea ice becomes far distant from breeding colonies the penguins’ foraging efficiency decreases, foraging effort increases, or both; parents undergo a severe loss in mass and less food is returned to chicks (Ainley et al. 1998). Alternatively, if there is too much sea ice or insufficient open-water between floes, sea ice can present a physical barrier (Massom et al. 2006, Emmerson and Southwell 2008), though not always (Lescroël et al. in review, Ballard et al. in review 1).

Previous studies on Adélie penguins found that foraging trip duration was longest, and breeding success lowest, in seasons when ice extent (as opposed to concentration; defined as the distance between the coast and the outer edge of the large-scale ice pack offshore) was greatest, but mechanistic linkages were not proposed (Clarke et al. 2002, Watanuki et al. 2002, 2004).

Here we report results of ten years’ investigation of the foraging behavior of 216 Adélie penguins at one of the largest Adélie breeding colonies in the world (Ainley 2002a), during a period of unprecedented (for human observers, at least) environmental variability. We test two primary hypotheses: (1) the poorer the condition of a parent, the more it invests in its
3. Parental foraging and chick provisioning strategies

own self-maintenance with negative consequences to how much food is delivered to the young and (2) under conditions of lower prey accessibility (higher energetic cost to parents per g of food delivered) parents will make more investment in their own self-maintenance. To evaluate these hypotheses we made the three following predictions:

1.) Parents beginning a breeding season with more mass are more likely to lose mass during chick provisioning; conversely, those that began the season with lower mass are more likely to gain mass during chick rearing.

2.) Adult penguins in worse condition make longer foraging trips and deliver less food to young than penguins in better condition (or less food than they themselves deliver when in better condition) because of a need to maintain or regain their own condition; this results in a bimodal distribution of long and short trips, which might be consecutive.

Environmental conditions varied dramatically during the study period, due in part to the presence of two very large icebergs (B-15 and C-16; as much as 175km long) in the foraging area for half the study (2001 – 2005; Fig. 3.1; Arrigo et al. 2002, Ainley et al. 2004, Shepherd et al. 2005). During their presence, these icebergs restricted the normal movements of pack ice, resulting in 1) higher spring/summer sea ice concentration that induced a regional, 40% reduction in primary productivity (Arrigo et al. 2002), and 2) significantly less open water, thus reducing access, requiring more walking, for penguins on foraging trips (as reviewed in general by Ainley 2002a).

3.) Reduced access to prey due to higher than optimal sea-ice concentration and/or presence of icebergs results in longer foraging trips and less food carried to young, with parents gaining mass for themselves instead, representing higher investment in parental condition especially when there are two chicks instead of one chick and when chicks were older.
3. Parental foraging and chick provisioning strategies

Here we contrast the five iceberg years with the non-iceberg years (1997-2000; 2006) with respect to Adélie penguin foraging behavior, especially the balance between self maintenance and chick provisioning.

**Figure 3.1.** Study area in the southern Ross Sea, Antarctica. Cumulative penguin foraging area (containing 95% of all foraging positions) as determined from radio and satellite telemetry 1997 – 2006 and positions of giant icebergs (fragments of original B15 and C16) in 2003-2004 are indicated. Base map layers are from British Antarctic Survey (1998).

### 3.2 Materials and methods

**Data collection**
The study was conducted at Cape Crozier, Ross Island, Antarctica, during ten breeding seasons (October - February), with fieldwork for this portion of the study beginning in December of each year and ending in late January of the next. We refer to each season by its initial year, i.e. 1997 = 1997-98. Our study included all of the “guard” breeding stage (at least one parent always present) and approximately three-fifths of the “crèche” stage (young can
3. Parental foraging and chick provisioning strategies

be left by both parents), 11 December to 20 January 1997 to 2006. The study area (Fig. 3.1) is in 24 h per day of daylight throughout the breeding season.

One subcolony of about 200 (range 160 - 259) pairs in the Cape Crozier colony of ~140,000 pairs was encircled by a plastic fence, the only avenue in or out being over a weighbridge (WB; Ballard et al. 2001). The WB subcolony generally increased in size over the course of the study, coincident with increases in the overall Cape Crozier breeding population (G. Ballard unpublished data). The WB consisted of a scale, direction indicator (coupled photocells), and a radio-frequency-identification reader connected to a data logger (Kerry et al. 1993, Clarke et al. 1998, Ainley et al. 1998, Ballard et al. 2001). In the WB subcolony, we implanted 216 penguins with a passively-interrogated-transponder (PIT tag), which uniquely identified the bird each time it passed over the WB. All individuals were also banded with one stainless steel flipper band on the left flipper (description in Dugger et al. 2006). We attempted to have at least 30 actively breeding pairs tagged each season (range 20 – 36 pairs, 40 – 75 individuals), but because variable numbers of pairs failed early in chick rearing, actual sample sizes used for analyses ranged from 15 to 49 per year (Table 3.3). Sex was primarily determined by copulatory position, but we also employed a combination of size (especially head and bill; Ainley and Emison 1972) and behavior cues to discriminate sexes (e.g. timing of arrival to the colony, Ainley et al. 1983, Kerry et al. 1992). From the WB data we could determine foraging trip duration, feeding frequency, food load mass, parental mass, and change in parental mass (to 10g) during the season and within specific foraging trips.

**Definition of parameters** (summarized in Table 3.1):

*Foraging trip duration and number of trips.* We measured foraging trip durations (FTD; ± 0.01 h) of birds known to be actively provisioning chicks. Visual inspection of the distribution of trip durations revealed that 95% of all trips were longer than 6 h. In order to avoid including penguins that were simply carrying rocks to nests or making other non-
3. Parental foraging and chick provisioning strategies

Foraging excursions away from the subcolony (Ballard et al. 2001), we excluded the 5% of shortest duration trips. The number of trips is simply the number of foraging trips by a given individual between 21 December and 15 January, which is the period in which approximately 95% of all breeding penguins observed were provisioning chicks.

**Table 3.1. Acronyms and brief descriptions of parameters measured and included in models describing foraging strategies of Adélie penguins at Cape Crozier.**

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>brstage</td>
<td>breeding stage: guard or crèche</td>
</tr>
<tr>
<td>FM</td>
<td>Fledging Mass - mass of chicks at 5 weeks (kg)</td>
</tr>
<tr>
<td>foodload</td>
<td>Mass of food delivered to chicks, measured on each foraging trip (kg)</td>
</tr>
<tr>
<td>FTD</td>
<td>Foraging trip duration (h)</td>
</tr>
<tr>
<td>IC</td>
<td>Sea ice concentration (% of foraging area covered by sea ice)</td>
</tr>
<tr>
<td>iceberg</td>
<td>Y/N - whether giant icebergs were present</td>
</tr>
<tr>
<td>IM</td>
<td>Initial Mass – mass as measured in early guard stage (kg)</td>
</tr>
<tr>
<td>n_chick</td>
<td>number of chicks in nest (1 or 2)</td>
</tr>
<tr>
<td>RMCi</td>
<td>Relative Mass Change as a proportion of IM, measured upon initiation of each foraging trip, negative values indicate mass gain</td>
</tr>
<tr>
<td>RMCr</td>
<td>Relative Mass Change as a proportion of IM, measured upon return from each foraging trip, after feeding chicks, negative values indicate mass gain</td>
</tr>
<tr>
<td>sex</td>
<td>female or male</td>
</tr>
<tr>
<td>TFD</td>
<td>Total mass of food delivered to chicks for full season (kg)</td>
</tr>
<tr>
<td>WTMC</td>
<td>Within Trip Mass Change - difference between mass at return of trip after feeding chicks compared with mass at beginning of trip, as a proportion of IM</td>
</tr>
<tr>
<td>yr</td>
<td>year; 1997 – 2006 (e.g. 1997 refers to the 1997 – 1998 breeding season)</td>
</tr>
</tbody>
</table>

*Food loads (meals) to chicks.* The mass of food delivered to chicks (± 0.01 kg) was calculated as the difference between individual parents’ out-weight after food delivery and their most recent in-weight. This does not take into account any food used by the adult while attending their chick(s) during the guard stage, but we assume this was negligible, and this assumption is supported by previous analyses comparing weighbridge meal size estimates to results from stomach-flushing (Clarke et al. 2002). During the crèche stage parents normally fed chicks and departed within a few hours. We were unable to assess the effect of differential amounts of water content or digestion on our calculated meal sizes, which may have varied with foraging trip duration or prey type. We calculated approximate total food.
3. Parental foraging and chick provisioning strategies

delivered to chicks by each parent for the guard and crèche stages separately by using the
mean meal size delivered for each individual multiplied by the number of trips made by that
individual. We were unable to use the actual value of food delivered because meal sizes were
not always calculable, (the WB scale was subject to error due to multiple penguins on the
scale at once, for example), while numbers of trips was assessed accurately. Only parents that
made > 1 feeding trip during each breeding stage (guard and crèche) were included in the
food load analysis.

*Initial mass.* For each individual we calculated their “initial mass” (IM; ± 0.01 kg) during the
season as the mean mass during the early guard period (on average Dec. 16 – Dec. 25: crèche
date minus 15 to crèche date minus 6 days, where crèche date is date when 50% of nests in
the subcolony entered crèche).

*Within trip mass change of adults.* Adult mass change within each foraging trip (WTMC; ±
0.01 kg) was calculated as the outbound weight of a parent (after feeding the chick(s)) minus
the previous outbound weight of the parent. WTMC was divided by IM for all analyses, since
the same absolute mass change for a large individual may be less consequential than for a
smaller individual.

*Relative Mass Change.* We calculated a potential proxy for change in adult condition that we
call “relative mass change” (RMC). RMC was assessed at two times for each foraging trip
(i.e., many times per individual per season): as RMCi (mass change at the time an individual
initiated a trip) or RMCr (mass change at the time a foraging trip was completed, after chicks
had been fed; i.e., at the time of departure for the subsequent foraging trip). Both were
calculated as a proportion of IM. Before transformation (see below), positive values indicated
that mass had been gained since early in the guard stage, and negative values that mass had
been lost. We posit that individuals improve condition when initial condition is poorest;
3. Parental foraging and chick provisioning strategies

therefore a gain in mass is associated with poor initial condition. To make the index more readily interpretable, and because Adélies usually lost mass during chick provisioning, as reported previously (e.g. Clarke 2001, Takahashi et al. 2003), we multiplied RMC values by negative 1, so that positive RMC values are associated with good parental condition and negative values poor condition.

*Chick fledging mass.* On average, chicks crèche at 23 d and fledge at 51 d (Ainley 2002a: 171 ff). We assessed fledging mass by weighing 50 chicks (± 0.025 kg), selected randomly from subcolonies near the WB subcolony (minimizing disturbance to any single subcolony) in week 5 (30-34 d past the colony’s median hatch date), the age of heaviest mass (Ainley 2002a).

*Sea ice concentration and icebergs.* We calculated the percent of the Crozier foraging area covered by sea ice (ice concentration) as measured by weekly passive microwave imagery (SSMI; Cavalieri et al. 1996). The foraging area was determined as the polygon that contained 95% of at sea positions of provisioning parents as determined by using radio and satellite telemetry, 1997-2006 (Ainley et al. 2004, 2006, and unpublished data). Image resolution was 25km pixel⁻¹. Higher resolution (12.5 km pixel⁻¹) microwave imagery (AMSR-E; Cavalieri and Comiso 2004) is available for only part of the study period (2002 onward), and values for these five years were very highly correlated with the SSMI derived values (r = 99.4%). Visual imagery at varying resolution (250m to 1.5km pixel⁻¹) is available but impossible to use consistently due to discontinuous availability of cloud-free images. In order to assess consistent periods among years we used sea-ice concentration values for the same seven dates each year (Dec. 17, 23, 29, Jan. 4, 10, 16, 22). All penguin foraging trips within the week centered on each of those dates were considered to have confronted the same sea ice concentration, which is the case at the scale that these measurements were taken (pers.
3. Parental foraging and chick provisioning strategies

Iceberg size was calculated using visual (MODIS, 250m pixel\(^{-1}\); NASA 2007) imagery on the same weekly basis as sea ice concentration, and the portion of the foraging area occupied by icebergs was considered unavailable for foraging penguins. Image analyses and foraging area polygon calculations were performed with ArcGIS 9.2 (ESRI 2006). We evaluated two iceberg variables – presence/absence and amount of foraging area covered (km\(^2\)). In all tests, the presence/absence of icebergs performed better than the iceberg area variable, so this is what we used in all results presented here. However, the presence/absence variable only performed well as an explanatory variable if the 2000-2001 season was labeled as a “no iceberg” year (the icebergs arrived late in that breeding season, but were present within the potential foraging area of the penguins during the crèche stage; thus 2000-2001 was labeled “no iceberg” in all analyses).

**Analyses**

*Outline of analyses:*

We used generalized linear mixed models (GLMMs) fitted using maximum likelihood, with individual treated as a random effect, allowing us to use unbalanced repeated measures within and between years (Bolker et al. 2009). We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate which of several competing models best predicted each dependent variable (linked to specific predictions and defined below). All covariates that were included were ones that we either had specific predictions about, or which we have previously shown to importantly effect the dependent variable in the given model (Ballard et al. 2001, Dugger et al. 2006, Lescroël et al. in review). Sex was included as a main effect because parental roles of Adélie penguins are distinctive by sex (Ainley et al. 1983, Chappell et al. 1993a, Clarke et al. 1998, 2002, Clarke 2001, Ballard et al. 2001, Watanuki et al. 2004) and because there is ample evidence that, in birds in general, reproductive strategies of the sexes often differ (Lessells 1991). Residuals from models were normally distributed after
3. Parental foraging and chick provisioning strategies

specified (below) transformations of the dependent variable, so Gaussian link functions were employed throughout. Each candidate model was ranked against the others in the set, examining each dependant variable separately using differences in the corrected Akaike’s Information Criterion (AICc), and relative model weights (Burnham and Anderson 2002). All models within 2 \( \Delta \)AICc of the best model or contributing to 90% of the summed model Akaike weights were considered as potentially relevant and examined further for implications of alternative interpretations. Reported effect sizes are estimates from the best model (the one contributing the highest Akaike weight) since our goal was not to find the best possible estimate for a given parameter but rather to evaluate which combination of parameters best predicted the dependent variable, with the expectation that different combinations would have different ecological implications (Burnham and Anderson 2002). Standard errors and 95% confidence intervals were bootstrap-derived with 1000 repetitions, bias corrected (Rabe-Hesketh and Skrondal 2008). We present means and coefficients ± SE unless otherwise specified. All statistical calculations were performed using STATA (version 10.1; Stata Corp. 2008).

Below we elaborate on the predictions that we evaluated, with specific reference to the model sets we developed in each case (also see Table 3.2 for all predictions, including predicted direction of each effect evaluated).

**Predictions**

**Prediction 1 – parents beginning a season with higher mass lose more mass during chick provisioning.** We evaluated whether RMCr at the two breeding stages during chick rearing was positive when parents started with higher IM and negative when parents had lower IM. The two stages were (1) guard: crèche date minus 20 to crèche date minus 1 and (2) crèche: crèche date to crèche date plus 20. We expected that parents would begin to regain some
3. Parental foraging and chick provisioning strategies

mass during crèche, as reported previously (Clarke 2001), that females would be able to
afford to lose proportionally less mass than males (presumably having invested more in
breeding during the egg laying stage), and that there would be substantial annual variation.
Thus, the covariates considered included IM, breeding stage, year, and sex, with individual
treated as a random effect.

**Prediction 2.1 – parents in worse condition make longer foraging trips and carry
smaller food loads while gaining mass for themselves.** We evaluated two model sets, one
with natural log-transformed foraging trip duration (ln FTD; 2.1.1), and the other with food
load (2.1.2) as dependent variable. For each, we considered the same set of potential
explanatory variables including condition at the beginning of the given foraging trip (RMCi),
WTMC, breeding stage (guard or crèche), sex, and season, with individual treated as a
random effect. We expected that trip duration would be longer during the crèche stage, that
females would make longer trips, and that there would be substantial annual variation
(Ballard et al. 2001, Dugger et al. 2006). We hypothesized that the number of chicks being
fed would positively affect trip duration because it might take longer to find food sufficient
for two chicks compared to one. We also expected that food loads would be larger during
crèche because of larger chicks requiring more food, larger for 2 chicks compared to 1 chick
broods, and that females might carry less food because of their generally smaller size.

**Prediction 2.2 – parents exhibit a bimodal distribution in trip duration.** Negative
correlation between present trip duration and previous trip duration would indicate a pattern
of consecutively alternating trip duration, whereas positive correlation would indicate that the
longer a trip was, the longer the previous trip had been, and vice versa. Using the best model
predicting ln(FTD) from prediction 2.1 (above), we added ln(previous FTD) as a covariate.
We also evaluated whether there was any general bimodal pattern to, not necessarily
3. Parental foraging and chick provisioning strategies

sequentially, by visually inspecting the distributions of (untransformed) trip duration for each individual each season, and for all individuals within a season.

*Prediction 2.3 – a proportional mass threshold exists, below which a parent will usually make a self-provisioning trip.* We assessed whether WTMC on each trip as an indication of whether the trip was self-provisioning or not, i.e., did the adult gain mass for itself (i.e., not including the food delivered to chicks) on the trip or not? Individual was treated as a random effect and with WTMC on the trip as the dependent variable, we looked for best predictors among the following covariates: adult condition (RMCi) and non-linearity’s (which would reveal changes in the magnitude of the effect) in the effect of adult condition by including the quadratic (RMCi^2) and cubic (RMCi^3) structure of the RMCi covariate. The rationale for inclusion of these non-linear structures was that the relationship between WTMC and RMCi may reflect threshold(s) in the amount of mass that could be gained or lost by an individual. We predicted that the cubic term in particular might be important because we posited that WTMC could reach both an upper and lower limit, above or below which no more mass could be gained or could be lost on a given trip. Because we expected that this effect might be stronger in females than in males (i.e., that a female in the same relatively poor condition might be more likely to make a self provisioning trip than a male in the same relative condition; cf. Clarke 2001) we added the interaction of sex with the highest order polynomial of RMCi that was retained during modeling to see if it improved the model. We also expected that individuals starting with higher IM would have lower WTMC because they presumably had more reserves to trade against, so IM was included as a covariate.

*Prediction 3.1 – high sea ice concentration and/or presence of giant icebergs result in longer foraging trips and parents returning from foraging trips in poorer condition, especially when there were two chicks to feed or when chick needs were greater, later in the season.* We evaluated two model sets for two dependent variables: one for ln(FTD)
3. Parental foraging and chick provisioning strategies (prediction 3.1.1) and one for RMCr (prediction 3.1.2). For both we evaluated the individual and combined additive effects of sea ice concentration, presence of icebergs, breeding stage (guard, crèche), number of chicks, and sex, with individual treated as a random effect. Predicted effects for 3.1.1 were as for previous FTD models and for 3.1.2 were as for the previous RMCr model (1) except we excluded season because sea ice concentration and iceberg presence/absence did not vary much (or at all) within year, compared with interannual variation. We also added the number of chicks being fed to model 3.1.2 because we were interested in the effect of challenges to parents on their condition, predicting that having 2 chicks would have negative consequences. In both model sets we included the potential for non-linear effects in sea ice cover by evaluating the quadratic term (sea ice concentration$^2$). In other words, we predicted that both too much and too little sea ice could have negative effects on foraging trip duration and condition of adult Adélie penguins. For the RMCr models we included IM as a covariate, and for both models individual was treated as a random effect.

Prediction 3.2 – high sea ice concentration and/or presence of giant icebergs result in less food delivered to chicks and lower fledging mass. We evaluated two model sets, one for total food delivered (only included parents who crèched at least one chick in a given season) (3.2.1) and another for fledging mass (3.2.2). For each, we examined the individual and additive effects of sea ice concentration and the presence of icebergs. As previously, the quadratic sea ice concentration$^2$ was included in both models because we expected that a certain amount of sea ice should be beneficial to amount of food delivered and fledging mass, but that too much sea ice could be detrimental. Individual was included as a random effect in model 3.2.1 since most individuals were present in at least two of the ten years. Additionally, we expected food delivery to be higher to 2 chick broods than 1 chick broods, and that females might bring less total food than males due to their smaller size.
3. Parental foraging and chick provisioning strategies

TABLE 3.2. Predictions regarding relationships between foraging parameters and co-variates for Adélie penguins at Cape Crozier, Ross Island, Antarctica, 1997-2006. Primary (P) effects are ones which we were most interested in evaluating relative to the given prediction. Ancillary (A) effects were ones which we expected to be influential but for which the outcomes did not bear directly on our main predictions.

<table>
<thead>
<tr>
<th>General Prediction</th>
<th>Dependent Variable</th>
<th>Structure of predicted effects</th>
</tr>
</thead>
</table>
| 1. Parents beginning a season heavier lose more mass during chick provisioning. | RMCr | $P: \beta_{RMCr} > 0$  
$A: \beta_{RMCr} < 0, \beta_{sex(f)} < 0, \beta_{year}$ (variable) |
| 2.1.1 Parents in worse condition make longer foraging trips. | Ln(FTD) | $P: \beta_{RMCi} < 0$, $\beta_{WTMC} > 0$  
$A: \beta_{RMCi} > 0, \beta_{sex(f)} > 0, \beta_{n.chick} > 0, \beta_{year}$ (variable) |
| 2.1.2 Parents in worse condition bring less food while gaining mass for themselves. | Foodload | $P: \beta_{RMCi} < 0$, $\beta_{WTMC} < 0$  
$A: \beta_{RMCi} > 0, \beta_{sex(f)} < 0, \beta_{n.chick} > 0, \beta_{year}$ (variable) |
| 2.2 Parents exhibit a bimodal distribution in trip duration. | Ln(FTD) | $P: \beta_{prevFTD} < 0$  
$A: \beta_{RMCi} < 0, \beta_{WTMC} > 0, \beta_{brstage} > 0, \beta_{sex} > 0, \beta_{n.chicks} > 0, \beta_{year}$ (variable) |
| 2.3 A proportional mass threshold exists, below which a parent will usually make a self-provisioning trip. | WTMC | $P: \beta_{RMCi} > 0, \beta_{sex(f)} < 0, \beta_{n.chick} < 0, \beta_{RMCi} < 0$  
$A: \beta_{RMCi} < 0, \beta_{WTMC} > 0, \beta_{brstage} > 0, \beta_{sex} > 0, \beta_{n.chicks} > 0, \beta_{year}$ (variable) |
| 3.1.1 High sea ice concentration and/or presence of giant icebergs resulted in longer foraging trips. | Ln(FTD) | $P: \beta_{iceberg} > 0, \beta_{IC} < 0, \beta_{IC2} > 0$  
$A: \beta_{sex(f)} > 0, \beta_{brstage} > 0, \beta_{n.chick} > 0$ |
| 3.1.2 High sea ice concentration and/or presence of giant icebergs resulted in parents in poor condition. | RMCr | $P: \beta_{iceberg} < 0, \beta_{iceconc} > 0, \beta_{iceconc2} > 0$  
$A: \beta_{RMCr} > 0, \beta_{brstage} < 0, \beta_{sex(f)} < 0, \beta_{n.chick} < 0$ |
| 3.2.1 High sea ice concentration and/or presence of giant icebergs resulted in less food delivered to chicks | TFD | $P: \beta_{iceberg} < 0, \beta_{IC} > 0, \beta_{IC2} > 0$  
$A: \beta_{sex(f)} < 0, \beta_{n.chick} > 0$ |
| 3.2.2 High sea ice concentration and/or presence of giant icebergs resulted in lower fledging mass. | FM | $P: \beta_{iceberg} < 0, \beta_{IC} > 0, \beta_{IC2} > 0$ |
3. Parental foraging and chick provisioning strategies

3.3 Results

**Prediction 1 - Parents beginning a season with higher mass lose more mass during chick provisioning.** Mean IM varied from 3.22 ± 0.08 kg (1997) to 3.86 ± 0.07 kg (1999) and females were lighter than males in every year (Table 3.3). The best model predicting RMCr included the covariates IM, sex, year, and breeding stage (Table 3.4). For every kilogram of extra IM, individuals on average lost an extra 20.0 ± 1.8 % of their initial body mass during chick provisioning. Females lost 5.4 ± 1.2% more proportional weight than males (counter to our expectation), and parents measured during crèche stage had regained 0.99 ± 0.51% of the mass they had lost during the guard stage (Table 3.5). RMCr as measured during the crèche stage was positive in nine out of ten seasons, meaning that parents usually lost mass during chick rearing. However, in 1997, when IM was lowest for both sexes, RMC values (before controlling for IM in the model) were negative, meaning that adults gained mass during chick provisioning (Table 3.3).

**Table 3.3.** Average body mass (kg ± SE) of breeding Adélie penguin parents beginning chick-provisioning (IM; mean for d-15 to d-6 relative to median crèche date) and percent change in Mass (± SE) between IM and crèche stage (d0 – d20). Bold indicates estimates for which 95% CI did not overlap zero. Sample size (n) is individuals per season.

<table>
<thead>
<tr>
<th>Year</th>
<th>Females</th>
<th></th>
<th></th>
<th></th>
<th>Males</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean IM</td>
<td>% change</td>
<td>n</td>
<td>Mean IM</td>
<td>% change</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>2.97 ± 0.06</td>
<td>+8.3 ± 1.0</td>
<td>12</td>
<td>3.40 ± 0.11</td>
<td>+5.1 ± 1.0</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>3.41 ± 0.06</td>
<td>-0.2 ± 1.0</td>
<td>20</td>
<td>3.80 ± 0.07</td>
<td>-2.8 ± 1.0</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>3.58 ± 0.05</td>
<td>-3.5 ± 1.0</td>
<td>21</td>
<td>4.18 ± 0.08</td>
<td>-10.1 ± 1.0</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>3.50 ± 0.08</td>
<td>-1.0 ± 1.0</td>
<td>17</td>
<td>4.00 ± 0.07</td>
<td>-5.5 ± 0.9</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>2001</td>
<td>3.55 ± 0.10</td>
<td>-4.6 ± 1.4</td>
<td>8</td>
<td>3.97 ± 0.16</td>
<td>-7.6 ± 1.5</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>2002</td>
<td>3.70 ± 0.12</td>
<td>-9.7 ± 1.3</td>
<td>10</td>
<td>3.97 ± 0.10</td>
<td>-9.6 ± 1.3</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td>3.35 ± 0.12</td>
<td>-0.8 ± 1.7</td>
<td>5</td>
<td>3.85 ± 0.14</td>
<td>-3.9 ± 1.7</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>3.58 ± 0.11</td>
<td>-6.0 ± 1.5</td>
<td>16</td>
<td>4.00 ± 0.07</td>
<td>-9.1 ± 1.4</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>2005</td>
<td>3.41 ± 0.09</td>
<td>-2.5 ± 1.1</td>
<td>12</td>
<td>3.86 ± 0.09</td>
<td>-6.1 ± 1.0</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>3.56 ± 0.07</td>
<td>-3.2 ± 1.0</td>
<td>12</td>
<td>4.00 ± 0.11</td>
<td>-6.8 ± 1.0</td>
<td>11</td>
<td></td>
</tr>
</tbody>
</table>

**Prediction 2.1 – parents in worse condition make longer foraging trips and carry smaller food loads while gaining mass for themselves.** Parents who made longer trips and...
3. Parental foraging and chick provisioning strategies

brought back smaller food loads gained more weight (had higher WTMC), and parents with lower RMC brought back less food (Fig. 3.2 & 3.3, Table 3.5). However, parents in worse condition did not make longer trips, as we predicted they would. While RMCi was retained in the 3rd strongest model, the 95% CI around the estimate of its effect included zero, and therefore was a very weak effect (Δ; 2.06, 15.0% AICc weight; β = -0.020 95% CI: -0.495 – 0.455; Table 3.4).

TABLE 3.4. Model selection results for each prediction as evaluated by comparing differences and weights as determined using Akaike’s conservative Information Criterion (AICc). All models that contributed to 90% of the summed AICc model weights, as well as intercept only models are shown. All possible combinations of term that were included in the each model set (different for each prediction) were evaluated. Number of estimated parameters per model (K) and number of observations (n) are shown for each. All models except 3.2.2 included individual as a random effect.

<table>
<thead>
<tr>
<th>Prediction</th>
<th>Term Inclusion</th>
<th>Log Likelihood</th>
<th>K</th>
<th>Δ AICc</th>
<th>AICc weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. RMCr (n = 1321)</td>
<td>IM + yr + sex + brstage</td>
<td>1568.122</td>
<td>15</td>
<td>0.000</td>
<td>0.738</td>
</tr>
<tr>
<td></td>
<td>IM + yr + sex</td>
<td>1565.880</td>
<td>14</td>
<td>2.439</td>
<td>0.218</td>
</tr>
<tr>
<td></td>
<td>Intercept only</td>
<td>1300.284</td>
<td>3</td>
<td>511.327</td>
<td>0.000</td>
</tr>
<tr>
<td>2.1.1 Ln(FTD) (hr) (n = 986)</td>
<td>WTMC + sex + yr + brstage + n_chick</td>
<td>-674.308</td>
<td>16</td>
<td>0.000</td>
<td>0.421</td>
</tr>
<tr>
<td></td>
<td>WTMC + sex + yr + brstage</td>
<td>-675.656</td>
<td>15</td>
<td>0.631</td>
<td>0.307</td>
</tr>
<tr>
<td></td>
<td>WTMC + sex + yr + brstage + n_chick + RMCi</td>
<td>-674.304</td>
<td>17</td>
<td>2.064</td>
<td>0.150</td>
</tr>
<tr>
<td></td>
<td>WTMC + sex + yr + brstage + RMCi</td>
<td>-675.654</td>
<td>16</td>
<td>2.692</td>
<td>0.110</td>
</tr>
<tr>
<td></td>
<td>Intercept only</td>
<td>-785.518</td>
<td>3</td>
<td>195.885</td>
<td>0.000</td>
</tr>
<tr>
<td>2.1.2 Foodload (kg) (n = 754)</td>
<td>RMCi + WTMC + yr + n_chick</td>
<td>-84.880</td>
<td>15</td>
<td>0.000</td>
<td>0.268</td>
</tr>
<tr>
<td></td>
<td>RMCi + WTMC + yr + n_chick + sex</td>
<td>-84.018</td>
<td>16</td>
<td>0.362</td>
<td>0.224</td>
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<tr>
<td></td>
<td>RMCi + WTMC + yr</td>
<td>-86.598</td>
<td>14</td>
<td>1.353</td>
<td>0.136</td>
</tr>
<tr>
<td></td>
<td>RMCi + WTMC + yr + sex</td>
<td>-85.677</td>
<td>15</td>
<td>1.593</td>
<td>0.121</td>
</tr>
<tr>
<td></td>
<td>RMCi + WTMC + yr + n_chick + brstage</td>
<td>-84.755</td>
<td>16</td>
<td>1.836</td>
<td>0.107</td>
</tr>
<tr>
<td></td>
<td>RMCi + WTMC + yr + n_chick + brstage + sex</td>
<td>-83.868</td>
<td>17</td>
<td>2.156</td>
<td>0.091</td>
</tr>
<tr>
<td></td>
<td>Intercept only</td>
<td>-165.511</td>
<td>3</td>
<td>138.643</td>
<td>0.000</td>
</tr>
</tbody>
</table>
3. Parental foraging and chick provisioning strategies

(Table 3.4, continued from previous page)

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Log Likelihood</th>
<th>K</th>
<th>Δ AICc</th>
<th>AIC weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.3 WTMC (n = 1068)</td>
<td>1449.209</td>
<td>8</td>
<td>0.000</td>
<td>0.705</td>
</tr>
<tr>
<td>sex + IM + RMCI + RMCI² + RMCI³</td>
<td>1449.216</td>
<td>9</td>
<td>2.021</td>
<td>0.257</td>
</tr>
<tr>
<td>Intercept only</td>
<td>1301.857</td>
<td>3</td>
<td>284.590</td>
<td>0.000</td>
</tr>
<tr>
<td>3.1.1 Ln(FTD) (hr) (n = 2388)</td>
<td>-1687.135</td>
<td>9</td>
<td>0.000</td>
<td>0.505</td>
</tr>
<tr>
<td>iceberg + IC + IC² + sex + brstage + n_chick</td>
<td>-1688.161</td>
<td>8</td>
<td>0.038</td>
<td>0.495</td>
</tr>
<tr>
<td>Intercept only</td>
<td>-1807.120</td>
<td>3</td>
<td>227.904</td>
<td>0.000</td>
</tr>
<tr>
<td>3.1.2 RMCr (n=1321)</td>
<td>1564.984</td>
<td>7</td>
<td>0.000</td>
<td>0.257</td>
</tr>
<tr>
<td>IM + sex + brstage + iceberg</td>
<td>1565.719</td>
<td>8</td>
<td>0.553</td>
<td>0.194</td>
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<tr>
<td>IM + sex + brstage + iceberg + IC</td>
<td>1565.674</td>
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<td>0.644</td>
<td>0.186</td>
</tr>
<tr>
<td>IM + sex + brstage + iceberg + n_chick + IC</td>
<td>1566.588</td>
<td>9</td>
<td>0.843</td>
<td>0.168</td>
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<tr>
<td>IM + sex + iceberg</td>
<td>1562.876</td>
<td>6</td>
<td>2.195</td>
<td>0.086</td>
</tr>
<tr>
<td>IM + sex + brstage + iceberg + n_chick + IC + IC²</td>
<td>1565.739</td>
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<td>2.541</td>
<td>0.075</td>
</tr>
<tr>
<td>Intercept only</td>
<td>1300.284</td>
<td>3</td>
<td>521.332</td>
<td>0.000</td>
</tr>
<tr>
<td>3.2.1 TFD (kg) (n=187)</td>
<td>-437.865</td>
<td>6</td>
<td>0.000</td>
<td>0.733</td>
</tr>
<tr>
<td>n_chick + iceberg + IC + IC²</td>
<td>-437.887</td>
<td>7</td>
<td>2.204</td>
<td>0.243</td>
</tr>
<tr>
<td>Intercept only</td>
<td>-458.100</td>
<td>3</td>
<td>34.135</td>
<td>0.000</td>
</tr>
<tr>
<td>3.2.2 FM (kg) (n=501)</td>
<td>-3927.530</td>
<td>3</td>
<td>0.000</td>
<td>0.728</td>
</tr>
<tr>
<td>iceberg IC</td>
<td>-3927.497</td>
<td>4</td>
<td>1.967</td>
<td>0.272</td>
</tr>
<tr>
<td>Intercept only</td>
<td>-4003.179</td>
<td>1</td>
<td>147.257</td>
<td>0.000</td>
</tr>
</tbody>
</table>

1 Minimum AICc for each analysis: 1: -3105.877, 2.1.1: 1381.177, 2.1.2: 200.411, 2.3: -2882.282, 3.1.1: 3392.345, 3.1.2: -3115.882, 3.2.1: 888.196, 3.2.2: 7861.108
3. Parental foraging and chick provisioning strategies

**TABLE 3.5.** Estimated coefficients of effects, bootstrapped standard errors and confidence intervals for the selected model for each prediction.

<table>
<thead>
<tr>
<th>Prediction</th>
<th>Model</th>
<th>Parameter</th>
<th>Coefficient</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 RMCr</td>
<td>IM (kg)</td>
<td>0.200</td>
<td>0.165</td>
<td>0.235</td>
</tr>
<tr>
<td></td>
<td>Breeding Stage</td>
<td>-0.010</td>
<td>-0.020</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>sex = F</td>
<td>0.054</td>
<td>0.030</td>
<td>0.077</td>
</tr>
<tr>
<td></td>
<td>yr (9 estimates)</td>
<td>-0.710</td>
<td>-0.823</td>
<td>-0.596</td>
</tr>
<tr>
<td>2.1.1 Ln(FTD) (hr)</td>
<td>WTMC</td>
<td>0.724</td>
<td>0.342</td>
<td>1.107</td>
</tr>
<tr>
<td></td>
<td>sex = F</td>
<td>0.220</td>
<td>0.121</td>
<td>0.319</td>
</tr>
<tr>
<td></td>
<td>Breeding Stage</td>
<td>0.152</td>
<td>0.079</td>
<td>0.226</td>
</tr>
<tr>
<td></td>
<td>n_chick</td>
<td>-0.076</td>
<td>-0.192</td>
<td>0.040</td>
</tr>
<tr>
<td></td>
<td>yr (9 estimates)</td>
<td>3.230</td>
<td>3.019</td>
<td>3.441</td>
</tr>
<tr>
<td>2.1.2 Foodload (kg)</td>
<td>RMCi</td>
<td>1.308</td>
<td>0.866</td>
<td>1.749</td>
</tr>
<tr>
<td></td>
<td>WTMC</td>
<td>-1.841</td>
<td>-2.259</td>
<td>-1.424</td>
</tr>
<tr>
<td></td>
<td>n_chick</td>
<td>0.057</td>
<td>-0.002</td>
<td>0.117</td>
</tr>
<tr>
<td></td>
<td>yr (9 estimates)</td>
<td>0.530</td>
<td>0.408</td>
<td>0.653</td>
</tr>
<tr>
<td>2.2 Ln(FTD) (hr)</td>
<td>ln(prev FTD)</td>
<td>0.239</td>
<td>0.113</td>
<td>0.365</td>
</tr>
<tr>
<td></td>
<td>WTMC</td>
<td>0.850</td>
<td>0.369</td>
<td>1.330</td>
</tr>
<tr>
<td></td>
<td>sex = F</td>
<td>0.164</td>
<td>0.083</td>
<td>0.246</td>
</tr>
<tr>
<td></td>
<td>Breeding Stage</td>
<td>0.165</td>
<td>0.078</td>
<td>0.252</td>
</tr>
<tr>
<td></td>
<td>n_chick</td>
<td>-0.122</td>
<td>-0.211</td>
<td>-0.033</td>
</tr>
<tr>
<td></td>
<td>yr (9 estimates)</td>
<td>2.527</td>
<td>2.076</td>
<td>2.977</td>
</tr>
<tr>
<td>2.3 WTMC</td>
<td>sex = F</td>
<td>-0.030</td>
<td>-0.046</td>
<td>-0.015</td>
</tr>
<tr>
<td></td>
<td>IM</td>
<td>-0.122</td>
<td>-0.147</td>
<td>-0.097</td>
</tr>
<tr>
<td></td>
<td>RMCi</td>
<td>0.671</td>
<td>0.555</td>
<td>0.786</td>
</tr>
<tr>
<td></td>
<td>RMCi²</td>
<td>-0.264</td>
<td>-0.704</td>
<td>0.176</td>
</tr>
<tr>
<td></td>
<td>RMCi³</td>
<td>-1.913</td>
<td>-3.926</td>
<td>0.100</td>
</tr>
<tr>
<td></td>
<td>intercept</td>
<td>0.438</td>
<td>0.345</td>
<td>0.530</td>
</tr>
<tr>
<td>3.1.1 Ln(FTD) (hr)</td>
<td>sex = F</td>
<td>0.224</td>
<td>0.138</td>
<td>0.310</td>
</tr>
<tr>
<td></td>
<td>Breeding Stage</td>
<td>0.112</td>
<td>0.058</td>
<td>0.166</td>
</tr>
<tr>
<td></td>
<td>Sea Ice Concentration</td>
<td>-0.051</td>
<td>-0.074</td>
<td>-0.028</td>
</tr>
<tr>
<td></td>
<td>Sea Ice Concentration²</td>
<td>0.002</td>
<td>0.001</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Iceberg = T</td>
<td>0.396</td>
<td>0.239</td>
<td>0.553</td>
</tr>
<tr>
<td></td>
<td>intercept</td>
<td>3.164</td>
<td>3.064</td>
<td>3.263</td>
</tr>
<tr>
<td>3.1.2 RMCr</td>
<td>sex = F</td>
<td>0.195</td>
<td>0.175</td>
<td>0.215</td>
</tr>
<tr>
<td></td>
<td>IM</td>
<td>0.052</td>
<td>0.031</td>
<td>0.073</td>
</tr>
<tr>
<td></td>
<td>Breeding Stage</td>
<td>0.010</td>
<td>0.000</td>
<td>0.020</td>
</tr>
<tr>
<td></td>
<td>Iceberg = T</td>
<td>0.024</td>
<td>0.012</td>
<td>0.036</td>
</tr>
<tr>
<td></td>
<td>intercept</td>
<td>-0.697</td>
<td>-0.617</td>
<td>-0.777</td>
</tr>
</tbody>
</table>
3. Parental foraging and chick provisioning strategies

(Table 3.5, continued from previous page)

<table>
<thead>
<tr>
<th>Prediction</th>
<th>Model</th>
<th>Parameter</th>
<th>Coefficient</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.2.1 TFD (kg)</td>
<td></td>
<td>n Chicks</td>
<td>1.814</td>
<td>1.045 – 2.584</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Iceberg = T</td>
<td>-2.056</td>
<td>-2.910 – -1.202</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sea Ice Concentration</td>
<td>0.332</td>
<td>0.106 – 0.558</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sea Ice Concentration²</td>
<td>-0.013</td>
<td>-0.021 – -0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>intercept</td>
<td>1.373</td>
<td>0.205 – 2.540</td>
</tr>
<tr>
<td>3.2.2 FM (kg)</td>
<td></td>
<td>Iceberg = T</td>
<td>-0.783</td>
<td>-0.898 – -0.669</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sea Ice Concentration</td>
<td>0.018</td>
<td>0.011 – 0.025</td>
</tr>
<tr>
<td></td>
<td></td>
<td>intercept</td>
<td>3.205</td>
<td>3.128 – 3.282</td>
</tr>
</tbody>
</table>

**Figure 3.2.** Relationship between trip duration (ln(FTD); note log scale) and adult mass change on a given trip (WTMC) as predicted by a mixed model controlling for random effects of individual identity and fixed effects of season and breeding stage; males and females compared. Dashed lines are 95% confidence intervals. See prediction 2.1.1 in Table 3.5 for model.

The best model for FTD suggested that females made 1.25 (95% CI: 1.13 – 1.38) h longer trips than males, there was substantial annual variation in FTD, and trips were 1.16 (95% CI: 1.08 – 1.25) h longer during the crèche stage than during the guard stage (Table 3.5). In addition, for every 10% increase in WTMC, trip duration was extended by 1.08 (95% CI: 1.41 – 3.03) h. WTMC, sex, year, and breeding stage were included in both competitive FTD
3. Parental foraging and chick provisioning strategies

models, and the number of chicks being fed was included in the best model, but the confidence interval for this estimate included zero ($\beta = -0.076$, 95% CI: -0.193 – 0.042), so the strength of this effect was weak.

**FIGURE 3.3.** Relationship between food delivered to chick(s) on a given foraging trip to (A) adult condition upon initiating the trip (RMCi), and (B) within-trip mass change (WTMC), controlling for season and individual. Dashed lines are 95% confidence intervals. See prediction 2.1.2 in Table 3.5 for model.
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There were several competitive models relating the covariates of interest to food loads brought to chicks, however RMCi, WTMC, and year were always included in the top models, and together these 7 models accounted for 100% of the total model weight (Table 3.4). Every 10% decrease in relative mass (i.e., increase in RMCi) resulted in 130.8 ± 2.3 g more food brought to chicks (Fig. 3.3, Table 3.5), and every 10% increase in WTMC resulted in 184.1 ± 2.1 g less brought back to chicks. The effects of sex (in second best model $\Delta AICc = 0.36$, 22.4% AICc weight; $\beta$ (female) = 0.046, 95% CI:-0.022 – 0.114) and number of chicks ($\beta$ = 0.057, 95% CI: - 0.002 – 0.117) were weaker as confidence intervals for these effects included zero (although just barely for number of chicks).

**Prediction 2.2 – parents exhibit a bimodal distribution in trip duration.** FTD was positively correlated with previous trip duration (Table 3.5) and inclusion of ln(previous FTD) in the best FTD model improved model 2.1.1 substantially (decreased AICc by 338.561; Table 3.4), although the direction of effect was the opposite of what we predicted: FTD increased 0.47 ± 0.03 h for every hour increase in the previous trip, meaning that the longer a trip was, the longer the next trip would be. Over all ten years there was no consistent pattern of bimodality in trip duration within or among individuals within seasons. However, in two of the iceberg years (2002 and 2003), bimodal patterns across all individuals were evident (Fig. 3.4). So there was a consistent pattern of bimodality across individuals in 2 years (2 out of 5 iceberg years; 0 out of 5 non-iceberg years).

**Prediction 2.3 – a proportional mass threshold exists, below which a parent will usually make a self-provisioning trip.** The selected model included a cubic effect of parent condition and also a small effect of sex, with females averaging 3.0 ± 0.7% percent less mass gain per trip than males after controlling for a substantial effect of IM (Table 3.5, Fig. 3.4). Adding the interaction of sex and RMCi$^3$ did not improve the model, and the coefficient for the
3. Parental foraging and chick provisioning strategies

interaction term overlapped zero ($\beta = 0.14$, 95% CI: $-2.37$ – $2.66$). For every 10% heavier a parent began the season, it lost 1.2 ± 0.1 % more per foraging trip. On average, parents who made self-provisioning trips had lost 6.87 ± 0.27 % (males) to 8.81 ± 0.32 % (females) of their IM, with more mass gained per trip as a function of how much mass had been lost (Fig. 3.5). While the cubic term was retained in the strongest model, the bootstrapped 95% confidence intervals for the quadratic and cubic terms included zero, so we do not emphasize the non-linearity described by this model. The linear term (RMCi) reveals that for every 10% increase in RMCi, WTMC increased by 6.7 ± 0.58% (Table 3.5).

FIGURE 3.4. Distribution of foraging trip durations (h) of Adélie penguins 1997 – 2006. Icebergs (difficult foraging conditions) were present 2001 – 2005.

(continued next page)
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(Figure 3.4 continued from previous page)
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**Figure 3.5.** Relationship between within trip mass change of adults on a foraging trip (WTMC) and the condition (RMCi) of the individual, male and female Adélie penguins compared. Model predictions from a mixed linear model controlling for penguin initial mass (i.e., mass at beginning of breeding season). Despite different shapes of models fit independently by sex (shown), the model with common quadratic and cubic terms (but different intercepts) for the effect of RMCi on WTMC is better supported. See prediction 2.3 in Table 3.5 for model.

![Graph showing relationship between WTMC and RMCi for females and males](image)

**Prediction 3.1 – high sea ice concentration and/or presence of giant icebergs resulted in longer foraging trips and parents in poor condition.** Parents made longer trips when icebergs were present and shorter trips when sea ice concentration was higher (Table 3.5). The sea ice concentration effect was non-linear (i.e., the quadratic term was retained; Table 3.4) such that trip durations declined with increasing sea ice concentration until ice concentration reached ~15%, at which point trip durations increased (Fig. 3.6). As predicted, females made longer trips than males and trips were longer during crèche period than during the guard period (Table 3.5).

Contrary to our prediction, parents lost 2.4 ± 0.62% more of their IM (i.e., 2.4% higher RMCr) during iceberg years compared with non-iceberg years, controlling for a positive effect of IM, a positive effect of sex (RMCr more positive for females, also contrary to our expectation) and a negative effect of breeding stage, as in the best model for prediction 1
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(parents began to regain a small amount of mass during crèche; Table 3.5). The iceberg effect on RMCr was not altered when 1997 was excluded from the model (which we checked because 1997 was a non-iceberg year that had anomalously low RMCr values). The number of chicks being fed was included in the second most competitive model ($\Delta_i = 0.55$; Table 3.4), but was a relatively weak negative effect on RMCr ($\beta = -0.010$, 95% CI: -0.019 – 0.004). Ice concentration occurred in the third most competitive model ($\Delta_i = 0.644$, 18.6% AICc weight; $\beta = 0.00071$, 95% CI: -0.00005 – 0.00189; Table 3.4), but the 95% CI for this term included zero, so this was a relatively weak effect.

_Prediction 3.2 – high sea ice concentration and/or presence of giant icebergs resulted in less food delivered to chicks and lower fledging mass._ The total amount of food delivered to chicks was related to the presence/absence of icebergs, mean sea ice concentration and, as predicted, increased with the number of chicks (2 chick broods received 1.81 ± 0.39 kg more total food per parent than 1 chick broods; Table 3.5). Chicks received 2.06 ± 0.39 kg less food (per parent) overall during iceberg years than during non-iceberg years and sea ice had a positive, non-linear effect on total food delivered until ~12% cover, at which point higher sea ice concentration became negative during iceberg years and did not change during non-iceberg years (Fig 3.6, Table 3.5). Contrary to predictions, sex was not included in the strongest model, although it did occur in the second best one ($\Delta_i = 2.20$, 24% of AICc weight). The estimate of the effect of sex was negative (i.e., females predicted to bring less total food) but the 95% CI included zero ($\beta = -0.39$, 95% CI: -1.11 – 0.34).

Both the presence of icebergs and ice concentration had strong effects on chick fledging mass (Table 3.5). Chick fledging mass was 783 ± 58 g lower in iceberg years, and for every 1% more sea ice concentration, fledging mass increased 18 ± 4 g (Table 3.5). The quadratic term for sea ice concentration was retained in the second best model ($\Delta_i = 1.97$, 27% of AICc weight) but the effect was very weak ($\beta = -0.17$, 95% CI: -1.45 – 1.12).
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FIGURE 3.6. Effect of sea ice concentration on (A) foraging trip duration and (B) food delivery to chicks of Adélie penguins with and without icebergs present. Results from mixed-effects generalized linear model controlling for random effect of parent identity and (A) fixed effects of sex and breeding stage or (B) fixed effect of number of chicks being fed. Dotted lines are 95% confidence intervals. See prediction 3.2.1 & 3.2.2 in Table 3.5 for models.
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3.4 Discussion
We have shown that Adélie penguins operate with an energetic “cushion” at the outset of breeding, almost always beginning a breeding season with mass that they subsequently lose as they raise their chicks; the heavier an individual started, the larger a proportion of this mass it lost during the season. Later in the season, this “cushion” may be depleted. In fact, we observed that parents that had lost more than ~ 8% of their IM made longer foraging trips and gained mass for themselves while bringing their chicks less food. Generally there was not a bimodal pattern in trip duration; rather, trips increased in length as the season progressed and when demands of chicks were higher, supporting the inter- and intra-specific competition results reported previously (Ainley et al. 2004, 2006). The presence of the giant icebergs intensified these patterns – increased trip durations, made it more likely that parents would lose mass during chick rearing (i.e., more positive RMC), reduced the amount of food that chicks received and decreased their fledging mass. There was a more complex relationship with sea ice, with up to about 12% cover resulting in shorter trips and more food brought to chicks, and parents with two chicks brought more food back than those with one chick.

**Hypothesis one: adults in poor condition invest in self maintenance, which has negative consequences to chicks.** Our results confirm those of Chastel et al. (1995a, b), Weimerskirch et al. (1997, 2000, 2001), Takahashi et al. (2003), and Clarke et al. (2006) that relative body condition is part of the decision making process in avian parents on foraging, following the predictions of life history theory: penguins in poorer condition made longer foraging trips, carried less food to young, and gained more mass per foraging trip than those in better condition. While previous researchers have hypothesized that longer foraging trips were associated with smaller food loads for Adélie penguin chicks (Drent and Daan 1980, Clarke et al. 2002), ours is the first study to quantify this effect and the effect of adult body condition on this relationship.
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Clarke (2001) and Clarke et al. (1998, 2002) found that trip duration of females at Bèchervaise Island, MacRobertson Land, showed a bimodal frequency distribution of short (< 40 h) and long trips (> 40 h), feeding more food to chicks after long trips than they did after short trips, as subsequently predicted in a model developed by Ropert-Coudert et al. (2004). In addition, females departing on long trips had lower body mass than those making short trips, implying that females “decided” to satisfy both their own energetic demands as well as those of the chicks (Clarke et al. 1998, 2002). These kinds of foraging patterns were interpreted as responses to the greater energetic debt incurred by females during the early breeding season (Chappell et al. 1993b, Clarke et al. 1998, 2002). Clarke (2001) surmised that Adélie penguins, like petrels and albatrosses, made long trips when they had to recover condition (see also Ropert-Coudert et al. 2004, Angelier et al. 2008).

Our results support this pattern; however, we did not observe an alternating, bimodal strategy of long and short trips. We did not have structural or other physiological measures of these individuals with which to attempt to create alternative indices of condition, but mass alone has been shown to be nearly as good, just as good, or even better than any such indices (Schambler et al. 2009). This is borne out in several ways by our results, beginning with the fact that during the one season when adult masses were initially lowest RMC was negative. RMC was also negatively related to parents’ foraging trip durations and WTMC, and positively related to chicks’ meal sizes. All imply trade-off between parental self-maintenance and investment to the chick, possibly mediated in part by chick demands (see also Erikstad et al. 1997, Ropert-Coudert et al. 2004, Varpe et al. 2004).

Clarke et al. (1998) found no evidence for a bimodal distribution of trip durations at another site, Edmonson Point, Ross Sea. Nor was there any evidence for bimodal trip durations at three widely-spaced colonies in East Antarctica (Watanuki et al. 2002); at Torgerson Island (Chappell et al. 1993a); or in the present study in most years, though all
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found that males made shorter trips than females. The fact that bimodal trip durations were not seen in most years at Crozier, nor anywhere other than Bèchervaise implicates colony or season-specific factors related to prey availability. Ropert-Coudert et al. (2004) did observe bimodality in trip durations in a single season study, but they did not study the effect of sex, and only one foraging trip per individual was observed. The years we did observe bimodality were ones of extremely difficult environmental conditions, and may reflect the distribution of trips made by high quality individuals (i.e., those that were able to forage efficiently) vs. trips made by low quality individuals (Lescroël et al in review).

In all study locations other than Bèchervaise Island, penguins foraged principally or entirely in neritic or continental slope waters, those being among the richest portions of the Southern Ocean (Arrigo et al. 2003, and references therein). The extremely narrow shelf in the vicinity of Bèchervaise Island, therefore, may contribute to the penguins’ foraging tactics, offering two distinct foraging habitats. Longer trips during the crèche period compared to the guard period were reported for Adélie penguins at Bèchervaise Island (Clarke et al. 1998), consistent with prey depletion as argued by Ainley et al. (2004) for the large colony at Cape Crozier (see also Clarke et al. 2006, Ballance et al. 2009).

**Hypothesis two: lower prey accessibility increases parents’ investment in self-maintenance.**

In years of high sea ice concentration, foraging habitat is reduced because penguins can only exploit the water column within breath-holding distance of floe edges. Moreover, if there is a great deal of ice, penguins spend much time and energy walking over its surface, rather than swimming to forage more efficiently. Therefore, even if prey is superabundant, prey availability, in effect, is reduced (see further discussions in Smith et al. 1999, Ainley 2002a, Ainley et al. 1998, 2004). In the absence of extremely expensive efforts to quantify the abundance and distribution of marine prey in the Antarctic, quantifying ice conditions
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provides a proxy to prey availability, a method used by a number of researchers (e.g. Watanuki et al. 2002, 2004; Takahashi et al. 2003).

The effects of sea ice extent on Adélie foraging behavior and breeding success, have been previously evaluated (Clarke et al. 2002, Watanuki et al. 2002, 2004). These studies found that foraging trips were longest and breeding success lowest in years when ice extent was greatest. With the very narrow shelf near Bèchervaise Island, extensive coastal fast ice would limit penguin access to the presumably richest (neritic) waters (Clarke et al. 2006, Emmerson and Southwell 2008), but other aspects of the penguin-sea ice-prey relationship may also have been involved. In one study comparing the small colony at Hukuro Cove, which had extensive fast ice (sea ice attached to land, with access to prey only available via sparse cracks; i.e., potentially very challenging conditions) to colonies with more “normal”, loosely distributed pack ice conditions at the (also small) Biomar colony and at a larger colony (17,200 pairs) at Magnetic Island, Adélies were shown to make longer trips to maintain their own condition while feeding their chicks less frequently at Magnetic Island, a site with (theoretically) much higher prey availability than Hukuro Cove (Watanuki et al. 2002). It is possible that Hukuro Cove had far lower competition for prey and consequently Adélies there were able to maintain their condition and feed young without confronting a trade-off. By contrast, penguins at Magnetic Island may have encountered some prey depletion effects (cf. Ainley et al. 2004). Additionally, Watanuki et al. (2004) proposed that long distances or difficult access to food might limit Adélie penguins’ investment in their young, even for adults in relatively good condition, though they did not observe a sufficient range in foraging trip durations to test this idea and, therefore hypothesized that Adélie penguins might not be able to regulate their own condition; a conclusion that is opposite from what we found in this study.
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In our study, there was a high degree of variability in trip durations, with longest ones far in excess of those previously reported (e.g. Watanuki et al. 2004, Ropert-Coudert et al. 2004). Our results suggest a clear relationship between foraging parameters and pack-ice concentration, which had a positive effect on trip duration and a negative effect on food loads when sea ice concentration exceeded ~12%. We did not assess relationships to sea-ice extent, because in summer the inner Ross Sea is ice free and the outer edge of the large-scale ice pack offshore is hundreds of kilometers away and not accessible to parents foraging from Ross Island. However, ice extent and ice concentration, at least in the Ross Sea, are highly correlated at the large scale (Wilson et al. 2001). Thus, assuming that the latter relationship is wide spread, our results help to explain the relationships to ice extent found by Clarke et al. (2002) and Watanuki et al. (2002).

In 1996, the year before we began the present study, when pack ice was especially distant from Cape Crozier, trip durations were long and penguins lost body mass and brought back smaller loads on foraging trips > 48 h (Ainley et al. 1998), similar to the situation for the longest foraging trips reported by Watanuki et al. (2002, their Fig. 2.3). Apparently, on long trips, penguins begin to digest their food loads (see Wilson and Culik 1991, Ropert-Coudert et al. 2004 and references therein), with less food getting to the chick.

It is interesting that 2000 did not act as an “iceberg year,” despite the fact that the icebergs were making their way into the foraging area of Crozier penguins during that breeding season. This and the fact that the iceberg presence/absence variable performed far better than the “iceberg area” variable implies that it was more the actual barrier that the icebergs eventually presented (2001 – 2005) that affected adult condition than the fact that the icebergs occupied potential foraging habitat. Additionally, negative effects on in situ primary productivity were observed only once the icebergs became grounded in 2001 (Arrigo et al. 2002), which could have impacted penguins’ ability to maintain or regain condition.
3. Parental foraging and chick provisioning strategies

after winter. Further work is required to link over-winter sea-ice dynamics and penguin behavior to their condition upon return to the breeding colony (Chapter 6; Ballard et al. in review 1).

3.5 Conclusion

Given the importance of RMC in this study, the similar negative correlation between parent mass and trip duration found previously (Clarke 2001, Watanuki et al. 2002), and the consequences of parental body condition found in several flying species by others (Charaund and Weimerskirch 1994b, Weimerskirch et al. 1997, 2001, Erikstad et al. 1997, Tveraa et al. 1998), it is evident that researchers need to account for the condition of individual breeding birds in order to best understand measures of parental investment in young, such as foraging trip duration and meal sizes delivered to chicks. Researchers should also consider whether the range of conditions presented during their study revealed the full range of the animals’ foraging strategies when interpreting results (Weimerskirch et al. 2001), especially since a flexible investment strategy may be defined by the worst conditions likely to be encountered by a species (Ricklefs and Schew 1994, Lescroël et al. in review). In that context, it would be useful to investigate relationships between individual quality, condition in varying environmental conditions, and potentially confounding effects of age and experience.

Previous studies finding variable distance/duration foraging trips in birds according to parental condition have been in systems where two types of habitats were distinguishable. This is in contrast with the southern Ross Sea ecosystem of our study, leading to interesting implications of the role of habitat and the environment in the shaping of foraging strategies. In situations where distinct habitat types are available at discrete distances from the colony, trip durations may be more likely to be bimodally distributed, with prey-depletion less of a factor for the farther, pelagic, habitat, and the nearer habitat exploited predominantly for provisioning young (see Ballance et al. 2009). If a single habitat is available, as in our study,
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prey-depletion factors may play an important role in determining foraging trip duration, regardless of whether adults need to regain condition.

There may be a threshold of trip duration, which if not surpassed, will hide the full suite of foraging strategies that could be employed once more desperate conditions were encountered. In Adélie penguins that threshold may be ~ 48 hours, a limit not reached in all years (Ainley et al. 1998, Clarke 2001, Watanuki et al. 2002, Ropert-Coudert et al. 2004, Clarke et al. 2006). The foraging area (Ainley et al. 2004, 2006) and volume (area x depth; Lescroël et al. in review) of the Cape Crozier colony increases during the breeding season, most likely in response to prey depletion related to interference competition. This dynamic may only be a factor in the most competitive of situations (e.g. for the largest populations; Ballance et al. 2009). In spite of wide ranging differences in adult condition, food loads, foraging trip durations and feeding frequencies among seasons, we found relatively little variation in most years of the study (see also Weimerskirch et al. 1995, 2000), and there was no clear relationship to pre-fledging chick survival (G. Ballard unpubl. data). However, under the most challenging environmental conditions brought on by giant icebergs, chick mass did suffer, as adults apparently prioritized self-maintenance. We conclude that penguins were considering their own condition, adjusting their foraging effort, and regulating their body mass and food delivered to chicks, relative to chick needs, environmental conditions and corresponding availability of prey.
Chapter IV: Working less to gain more: when breeding quality relates to foraging efficiency

PLATE 4. A parent with SPLASH tag and radio transmitter taped to its feathers returns to feed its crèched chick (photo: V. Toniolo).
4. Breeding quality and foraging efficiency

4.1 Introduction
In animal populations, a minority of individuals consistently achieves higher breeding success than others and therefore contributes the most recruits to the next generation (Clutton-Brock 1988, Newton 1989, Annett and Pierotti 1999). This kind of difference in relative fitness forms the basis for natural selection (Darwin 1859). Understanding how “high quality” breeders (i.e., individuals that reproduce better than others from the same population at the same time) outperform others is therefore of great interest to evolutionary ecologists.

A number of factors can contribute to breeding success. First, at the scale of the breeding season, it is often related to phenology, with early breeders, at least in birds, generally having the highest breeding success (e.g. Lewis et al. 2006, but see Ezard et al. 2007). Second, body size, mass or condition has been related to breeding success (Jensen et al. 2004, Robinson et al. 2005, Murphy 2007) and survival (e.g. Blums et al. 2005). Third, physiological parameters have also been investigated as potential predictors of breeding success: Blackmer et al. (2005) showed that basal metabolic rate (BMR) could influence some aspects of individual quality (hatching date, chick growth rate) in male storm-petrels but BMR did not influence lifetime hatching success. Angelier et al. (2007a) found no relationship between individual quality and corticosterone or prolactin levels among experienced breeders. However, the probability of successfully fledging a chick was negatively correlated with corticosterone levels, which corresponded to inter-individual differences in foraging behavior and success (Angelier et al. 2007b). Finally, behavior can also be an important determinant of breeding success. Mate guarding (e.g. Setchell et al. 2005), mate choice and fidelity (e.g. Ainley et al. 1983, Lewis et al. 2006) or the ability to find and secure high-quality habitat (e.g. Krüger and Lindström 2001) can significantly influence an individual’s breeding output.

Inter-individual differences in energy acquisition can affect both breeding output and survival rates (Annett and Pierotti 1999) and differences in foraging behavior can influence several of the parameters listed above. Best foragers may be able to improve condition more
4. Breeding quality and foraging efficiency

rapidly and return earlier from migration to initiate breeding activities. Or individuals that
attain higher foraging success might have lower corticosterone levels and would therefore be
less prone to abandon reproduction. The use of alternative foraging behaviors such as
kleptoparasitism (Shealer et al. 2005) or the reliance on “junk” versus “natural” food sources
(Annett and Pierotti 1999, Grémillet et al. 2008) has also been shown to impact breeding
success. More subtle adjustment of foraging parameters like trip duration (Lewis et al. 2006),
offspring feeding rates (Lewis et al. 2006, O'Dwyer et al. 2007) and foraging effort (Cam et
al. 2003, MacColl and Hatchwell 2003) can also explain inter-individual or inter-pair
differences in breeding success and offspring quality. Yet, while evidence exists that foraging
performance is an important determinant of breeding success at the population level,
evidence is scarce from longitudinal studies to show that better breeders forage differently
than poorer breeders.

This study tests the hypothesis that higher quality breeders have different foraging ability
than average or below-average individuals. For this purpose, we used a 10-year, 3 colony,
individual-based longitudinal data set on breeding success and foraging parameters (foraging
trip duration and number, food load) of a long-lived bird, the Adélie penguin *Pygoscelis
adeliae*, a species that exhibits important heterogeneity in breeding quality (Lescroël et al.
2009) and whose breeding cycle is constrained by the short duration of the Antarctic summer
(Ainley 2002a). We also assessed diving ability by investigating known-breeding quality
birds by fitting them with automatic data recorders. We made the following predictions: (1)
Better breeders (herein referred to as BB) exhibit lower overall foraging effort but more
intense diving activity than poorer breeders (herein referred to as PB); (2) BB exhibit higher
foraging success, both at the level of the trip and at the level of the dive, than PB; (3) BB are
able to dive deeper than PB, without exhibiting longer post-dive recovery intervals (hereafter
PDI); and (4) BB exhibit higher foraging efficiency and feed their chicks more often than PB.
4. Breeding quality and foraging efficiency

If differences in foraging tactics are linked to differences in individual fitness, we may wonder why the “high-quality” phenotype does not spread throughout the population. First, foraging behavior would need to be heritable. To date, two studies have shown that foraging effort (MacColl and Hatchwell 2003, in long-tailed tits) and efficiency (Missoweit et al. 2007, in scorpionflies) are repeatable within individuals and have a significant heritable component. Thus, heritability of foraging behavior is possible. We hypothesize that the strength of the relationships between breeding performance and foraging strategy is modulated by the conditions under which individuals are living and foraging. Under favorable conditions, most phenotypes succeed in raising offspring, and only under demanding conditions do the inter-phenotype differences become apparent. Adverse conditions could include harsh climate, strong competition, or the increased neediness of older offspring. We therefore formulated the following additional predictions: the strength of the relationships between breeding performance and foraging ability is stronger under (5) harsh environmental conditions; (6) higher competition levels; and (7) when offspring needs are higher.

4.2 Materials and methods

Species and study sites
The Adélie penguin is a sea-ice obligate bird that spends only 10% of its life on land, where it forms breeding colonies distributed around the Antarctic coast and high-latitude offshore islands (Ainley 2002a). Data were collected at the three Adélie penguin colonies on Ross Island, south-western Ross Sea (see Chapters 1, 3, 5 & 6 for maps of study sites): Cape Crozier (77°27’ S, 169°12’ E; 164,000 pairs), Cape Bird (77°13’ S, 166°26’ E; 43,000 pairs) and Cape Royds (78°33’ S, 166°10’ E; 2,600 pairs). These colonies span the entire breadth of colony size in this species (cf. Woehler 1993), and intra-specific competition, as a function of colony size, has been shown to be a factor that can extend trip distances, durations, and
4. Breeding quality and foraging efficiency

energy expenditure (Ainley et al. 2004, 2006, Ballance et al. 2009). Breeders arrive in late October, lay (usually two) eggs by mid-November, and feed their chicks between mid-December and early February. During the guard stage, one parent remains with the chick(s) while the other forages at sea, nest reliefs are every 1–3 d, and chicks are fed relatively small meals by the attending parent. During crèche, chick demands are too great for one parent at a time to provide, so chicks are left on their own while both parents forage simultaneously. Adélie penguins forage by diving, mostly at depths shallower than 50 m but to a maximum of ~140 m and, in the southern Ross Sea, feed almost exclusively on crystal krill (*Euphausia crystallorophias*) and Antarctic silverfish (*Pleuragramma antarcticum*; Ainley et al. 1998, Ainley 2002a, Ainley et al. 2003a). Our study period included most of chick-rearing, i.e. all of the guard stage and three-fifths of the crèche stage, mid-December to mid-January, for 10 austral summers, 1997–1998 to 2006–2007. Hereafter, we refer to austral summers as seasons, using the initial year (e.g. 1997 refers to the nesting season that began in October 1997 and ended in February 1998).

**Assessment of foraging behavior**

Instrumentation: WB and SPLASH tags. — In all three colonies and all seasons (1997 to 2006), a subcolony ranging from 90 to 259 pairs was surrounded by a plastic fence, leaving only one access point, which was filled with a weighbridge (herein referred to as WB), as described in Ballard et al. (2001). The WB consisted of an electronic scale, direction indicator, and radio-frequency identification (RFID) reader connected to a data logger (following Kerry et al. 1993; see also Beigel et al. 2004), and was installed between 10 December and 15 December - at about peak hatching in 1997-2000, and beginning 15 Nov thereafter. In each WB subcolony, 34 individuals on average (hereafter “WB birds”), that were implanted with unique RFID tags and banded on the left flipper (Dugger et al. 2006), were followed each season (mean of 39 ± 14 SD, range 25 to 59 individuals at Cape Crozier,
4. Breeding quality and foraging efficiency

33 ± 28, range 3 to 93 individuals at Cape Bird and 30 ± 25, range 16 to 74 individuals at Cape Royds, depending on season). Data were not available for Cape Bird in 1997, due to WB technical difficulties. Bird identification, date and time, direction and body mass were recorded automatically as the RFID-implanted birds crossed the WB. We used only crossings from birds that had at least one chick when they left the subcolony for foraging.

In 2005 and 2006 at Cape Crozier only, we also equipped a total of 24 (5 females and 7 males in 2005; 7 females and 5 males in 2006) banded, known-breeding history, birds (hereafter “SPLASH birds”) from a subcolony adjacent to the WB subcolony with SPLASH tags (Wildlife Computers, Redmond, WA 98052, USA) and small, streamlined cylindrical radio transmitters (46 mm long, 14 mm diameter, model A2630, Advanced Telemetry Systems, Isanti, Minnesota). SPLASH tags recorded depth, light and temperature every second; they weighed 62 g (1.6 % of a 4 kg Adélie penguin) and had a cross-sectional area of 3.2 10^-4 m² (1.0 % to 1.6 % of a bird’s cross-sectional area). One to four consecutive trips were recorded for each equipped individual (42,932 dives total). Radio transmitters were used for locating birds in the colony. For details on attachment procedures, please refer to Ballard et al. 2001.

Dive data analysis

Diving data were processed using the program divesum (v.7.5.5), written by GB. This program corrected the record baseline and computed several individual dive parameters such as maximum dive depth, post-dive interval duration (PDI, i.e., the recovery period at the water surface between consecutive dives), number of undulations, etc. According to the SPLASH tag specifications (resolution of depth sensor = ± 0.5 m) and sample rate (1 Hz), only dives ≥ 1 m deep and ≥ 3 s long were considered. Divesum classified dives into three types: F (for “foraging”), E (for “exploratory”) and O (for “others”; Chappell et al. 1993a, Schreer et al. 2001, pers. obs; (see below). Given the multimodal nature of dive parameter
4. Breeding quality and foraging efficiency

distributions, we chose to reduce variability and simplify analyses by focusing on foraging dives for all parameters except daily vertical distance, for which all dives were included.

Adélie penguins, like many other seabirds and marine mammals dive in bouts, with most dives occurring in rapid succession, with longer temporal gaps between bouts. To separate PDIs (our variable of interest) from inter-bout duration, we used a maximum likelihood approach (Luque and Guinet 2007), which allowed us to determine a bout-ending-criterion (BEC). In this study, \( \text{BEC} = 49.8 \text{ s} \); we therefore only allowed PDIs < 50 s.

Foraging dives have been called “U” dives or “Square” dives by other authors, whereas exploratory dives have commonly been called “V” dives. To categorize dives as either Foraging (F), Exploratory (E) or Other (O) we parameterized several components of each dive (Chappell et al. 1993a, Ropert-Coudert et al. 2001a, 2001b, Schreer et al. 2001, Bost et al. 2007): (1.) dive duration (s); (2.) maximum depth attained (m); (3.) depth change rate (m/s; calculated as a running average for each 5s block of the dive duration); Slow : < 1m/s; Fast > 1.5m/s; (4.) rate of ascent and descent (m/s; sustained rate of depth change in same direction from surface to bottom and from bottom to surface; bottom is any depth within 60% of the maximum depth reached on the dive); (5.) bottom time (s) – the amount of time spent within 60% of the maximum depth and with no change in depth exceeding 0.5 m/s; (6.) number of undulations. Dives for which depth change rates \( \geq 4 \text{ m/s} \) were recorded were excluded from analysis because of likely instrument error.

F and E dives both were at least 10 m. F dives had \( \geq 4 \) undulations and either had \( \geq 15 \) s bottom time, 30% of the dive duration characterized by slow depth change rate and 30% with fast depth change rate, or \( \geq 6 \) undulations and rapid (\( \geq 1 \text{ m/s} \)) ascent/descent phases. E dives had < 4 undulations or had < 15 s bottom time and fewer than 6 undulations. All other dives were categorized as O and were thought to be primarily commuting dives.
breeding quality and foraging efficiency

Attaching external devices to penguins is likely to affect the swimming performance of these streamlined animals, due to the drag that devices produce (e.g. Culik and Wilson 1991, Ropert-Coudert et al. 2007). In order to assess the effects of instrumentation (i.e., SPLASH tags and radio transmitters) on foraging behavior, we compared trip durations between SPLASH birds and WB birds, while also considering sex of individuals, year of instrumentation and study day as covariates. Instruments had no significant effect on trip duration \( (P = 0.36) \) or on the relationship between BQI and trip duration \( (P = 0.30) \). Both WB and SPLASH birds were wearing flipper bands that could also have affected foraging behavior: Dugger et al. (2006) showed that banded birds had slightly longer trip durations (8% on average) than unbanded birds but detected no difference in the amount of food brought back to the colony.

Foraging effort. Using the double-labeled water method, Ballance et al. (2009) showed that total energy expended during a foraging trip by chick-rearing Adélie penguins increases with trip duration (Chapter 5). Therefore, we used trip duration as a proxy for foraging effort in the test of our predictions. Trip durations were determined from WB data (time elapsed between the departure from and the return to the subcolony). The <5% of trips shorter than 6 h (presumably rock-carrying or other non-foraging excursions) or longer than 8 days (invariably resulting in the death of the chick) were discarded, following Ballard et al. 2001 and Chapter 3.

Daily vertical (diving) distance (i.e. \( \sum_{i=1}^{n} \frac{Maxdepth \times 2}{Tripdur} \times 0.001 \), where \( n \) = number of dives during a foraging trip, Maxdepth = maximum depth of a foraging dive in meters, Tripdur = trip duration expressed in days) calculated from SPLASH data was also used as an index of diving effort (Boyd et al. 1994).

Foraging success. — At the trip level, we used food load as an index of foraging success. Food load was calculated from WB data as the difference between individual parent’s out-

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Breeding quality and foraging efficiency

mass (departing) and their most recent in-mass (returning from sea). This is a measure of how much food a parent is able to bring back to the colony, including both food to be delivered to chicks and food to be digested by the parent itself while attending the nest. Mass was calculated using a highly accurate, year- and colony-specific algorithm because each WB installation varied slightly in physical characteristics. In all cases the scales were calibrated against known standard weights, measured mass 12.5 times \( s^{-1} \), and the bird had to be on the scale for at least 0.8 s for a valid estimate to be recorded. The scales tared themselves automatically to adjust for any weight of gravel or snow blown onto them. For analysis, we only included food loads <1300 g (Ainley et al. 2004, Ballard et al. in review 2).

At the dive level, we used number of undulations per foraging dive (i.e., number of changes in underwater swimming direction from ascent to descent > 1 m) as an index of prey catch (Ropert-Coudert et al. 2001a, Bost et al. 2007).

Foraging efficiency and feeding frequency. We calculated catch-per-unit-effort (CPUE) by dividing food load in grams by trip duration in minutes. This weight of food gathered per minute was used as an index of foraging efficiency.

The individual feeding frequency was defined by the number of foraging trips performed by a parent divided by the time (days) during which it had at least one chick.

Assessment of breeding quality

We calculated a breeding quality index (BQI) for each individual based on previous breeding success (Lescroël et al. 2009). The study birds considered here were banded as breeding adults, thus we did not know their age. The BQI reflects the relative breeding performance of an individual compared to others with the same number of years in the study (i.e., banded in the same year, and seen the same number of years) over the same time span.

Formally, the BQI was calculated as the mean per individual of the difference between the actual breeding success (0 for unsuccessful or deferred breeders, 1 for successful
4. Breeding quality and foraging efficiency

breeders; see below for definition of “successful”) and the predicted breeding success (a numeric value between 0 and 1) for every year. This led to a unique value per individual. The BQI was calculated separately for WB birds and SPLASH birds. The predicted breeding success was modeled from actual breeding success (0 or 1), using four (for WB birds) or three (for SPLASH birds) independent variables (colony, for WB birds only, breeding year, year of banding and number of years that the individual was in the study = number of years since banding minus number of years bird had not been seen) incorporated into generalized linear models with a logit link (Table 4.1). We verified that the independent variables were not correlated with each other and that the most general model fit the data. Then, an information theoretic approach and model averaging were used to derive a probability of success for each year and individual.

Breeding birds were considered “successful” when they were seen feeding a chick after the mean crèche date each year (in the first week of January). Adult banded birds seen at the colony during a given season but never with an egg or a chick were classified as “deferred breeders”. Birds seen with at least one egg or chick but whose breeding failed before mean crèche date were classified as “unsuccessful”. 
4. Breeding quality and foraging efficiency

TABLE 4.1. Models (generalized linear models with logit link, using a binomial distribution) considered for the calculation of the Breeding Quality Index for (A) WB birds and (B) SPLASH birds (see methods). For each model the following statistics related to model ranking are provided: log-likelihood (LogLik); number of estimated parameters (K); number of observations (n); second-order Akaike’s information criterion (AICc); difference between the current and the lowest AICc model (ΔAICc); Likelihood (Lik); and relative model weight (AICc weight).

A. WB birds:

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<th>n</th>
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<td>2146</td>
<td>2976.76</td>
<td>787.70</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

1^year = the breeding year treated as a factor; colony = the breeding colony; n_yrs = the number of years that the individual was in the study; bd_year = the year of banding treated as a factor.
4. Breeding quality and foraging efficiency

(Table 4.1, continued from previous page)

**B. SPLASH birds:**

<table>
<thead>
<tr>
<th>Model</th>
<th>LogLik</th>
<th>K</th>
<th>n</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Lik</th>
<th>AICc weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>year+n_yrs+bd_year</td>
<td>-385.82</td>
<td>17</td>
<td>718</td>
<td>806.52</td>
<td>0.00</td>
<td>1.00</td>
<td>0.51</td>
</tr>
<tr>
<td>year+bd_year</td>
<td>-386.91</td>
<td>16</td>
<td>718</td>
<td>806.60</td>
<td>0.09</td>
<td>0.96</td>
<td>0.49</td>
</tr>
<tr>
<td>year+n_yrs</td>
<td>-393.85</td>
<td>11</td>
<td>718</td>
<td>810.08</td>
<td>3.57</td>
<td>0.17</td>
<td>0.09</td>
</tr>
<tr>
<td>year</td>
<td>-405.65</td>
<td>10</td>
<td>718</td>
<td>831.61</td>
<td>25.09</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Intercept only</td>
<td>-477.36</td>
<td>1</td>
<td>718</td>
<td>956.73</td>
<td>150.21</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

**Foraging conditions**

Demanding environmental conditions were provided by the calving from the Ross Ice Shelf of two giant icebergs that eventually settled against Ross Island, near Cape Crozier, in January 2001 (Ainley et al. 2004). They were present until July 2006. During their presence these icebergs restricted the normal drift of pack ice, resulting in 1) higher spring/summer ice cover (ice per unit area) that induced a regional, 40% reduction in primary productivity (Arrigo et al. 2002), and 2) significantly less open water, thus reducing access, requiring more walking, for penguins on foraging trips (as reviewed in general by Ainley 2002a). Massom et al. (2006) found that short-term, anomalously heavy pack ice negatively affected Adélie penguin colony access and breeding success at a colony on the west coast of the Antarctic Peninsula. We evaluated the effect of the interaction between BQI and a binary variable corresponding to the presence/absence of the giant icebergs (no iceberg seasons, 1996 to 2000 and 2006, versus iceberg seasons, 2001 to 2005) on foraging parameters.

Regarding competition, previous studies have shown that interference or exploitative competition affects foraging effort most dramatically at the largest of the study colonies (Ainley et al. 2004, 2006). We postulated that three orders of magnitude in colony size corresponded to increasing levels of intraspecific competition. Here, we evaluated the effect of the interaction between BQI and study colony (size in descending order: Cape Crozier,
4. Breeding quality and foraging efficiency

Cape Bird, Cape Royds) on foraging parameters.

As Adélie penguins are highly synchronous breeders (Ainley 2002a), offspring needs increase consistently as the breeding season progresses, thus we considered the effect of the interaction between BQI and study day (as a continuous variable with 0 = December 20).

**Re-formulation of predictions**

With the variables of interest defined, predictions can be re-formulated as follows, BB: (1a) exhibit shorter trips but (1b) greater daily vertical distance than PB; (2a) exhibit larger food loads and (2b) a higher foraging success (undulations) per dive than PB; (3a) dive deeper than PB, (3b) without exhibiting longer post-dive recovery phases; and (4a) exhibit higher CPUE and (4b) chick feeding frequency than PB. Moreover, the strength of these relationships is stronger: (5) when the giant icebergs are present; (6) at Cape Crozier than at Cape Bird and at Cape Bird than at Cape Royds; and (7) as the season progresses.

**Statistics**

All statistics were performed using R 2.7.2 (http://www.r-project.org/) or STATA 10.1 (Stata Corp 2008), including the {lme4} package for R from Douglas Bates for fitting linear mixed models and {diveMove} package for R from Sebastián Luque for calculating BEC. Linear mixed models allowed us to take into account the heterogeneity of our data set regarding colonies, years, identity of the birds and number of trips per bird without discarding data.

As sexual differences in foraging parameters have been reported in Adélie penguins (e.g. Ballard et al. 2001), we also included “sex” as a fixed effect in the models. Sex was primarily determined using copulatory position, but we also used behavior, “tread marks” (evidence of female copulatory position), bill- and head-size differences, and body mass (Ainley et al. 1983, Kerry et al. 1992).
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Variables derived from WB data (trip duration, food load, CPUE and feeding frequency) were each used as the response variable for three (feeding frequency) or four (all others) separate linear mixed models (fitted using the method of restricted maximum likelihood REML; Patterson and Thompson 1971). These models included the following random effect terms: colony, year and identity of the bird (ID). First, we tested for the effect of sex on the response variable. If the effect of sex was significant, it was kept as a fixed effect for further modeling. Second, we tested for the (fixed) effect of the interaction of BQI and 1) the presence/absence of giant icebergs, 2) the colony (in this case, colony was removed from the random effects and included as a fixed effect), and 3) the study day (except for feeding frequency).

To begin to assess the consistency of ln(CPUE) within individuals across years, we calculated the intraclass correlation coefficient (variance of within individual residuals divided by the sum of variance of residuals of the non-random plus random components; in this case year as a main effect and individual as a random effect; Rabe-Hesketh and Skrondal 2008, Fig. 4.5)

Variables derived from SPLASH data (daily vertical distance, number of undulations, maximum depth, PDI) were each used as the response variable for two or three separate linear mixed models. These models included three random effect terms: year, ID and trip number nested within ID. As described above, we tested for the influence of sex as a fixed effect. Then, for the daily vertical distance, number of undulations and maximum depth, we tested for the (fixed) effect of the interaction of BQI and 1) the presence/absence of the icebergs, and 2) the study day. For PDI, we assessed the influence of BQI on the relationship between PDI and maximum dive depth by including the interaction of BQI and maximum dive depth as a fixed effect. The full model set is summarized in Table 4.2.
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TABLE 4.2. Fixed and random terms included in models. ID = identity of the bird; BQI = breeding quality index; PDI = post-dive interval duration.

<table>
<thead>
<tr>
<th>Model</th>
<th>Fixed term</th>
<th>Random term</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Sex</td>
<td>ID</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colony (^b)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Year</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Trip (^c)</td>
</tr>
<tr>
<td>2</td>
<td>Sex (^a)</td>
<td>ID</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colony (^b)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Iceberg</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Year (^b)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Trip (^c)</td>
</tr>
<tr>
<td>3 (^b)</td>
<td>Sex (^a)</td>
<td>ID</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Year</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colony</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI (^b) * Colony</td>
</tr>
<tr>
<td>4</td>
<td>Sex (^a)</td>
<td>ID</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colony (^b)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Study day</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Year</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI (^b) * Study day</td>
</tr>
<tr>
<td>5 (^d)</td>
<td>Sex (^a)</td>
<td>ID</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Year</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Max depth</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Trip</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI (^b) * Max depth</td>
</tr>
</tbody>
</table>

\(^a\) Sex effect was included as a fixed term only if found significant in model 1. \(^b\) Only for WB data. \(^c\) Only for SPLASH data. \(^d\) Only for PDI as response variable.

At present, p-values calculated for mixed effect models are potentially strongly anti-conservative because the number of residual degrees of freedom can not be accurately determined (Bolker et al. 2009). Therefore, we based our assessment of the significance of a fixed effect on Highest Posterior Density intervals (HPDI; Bolker et al. 2009). We considered a fixed effect significant when HPDI did not include zero. HPDI was computed from the posterior distribution of parameter estimates with Markov Chain Monte Carlo methods, using the mcmcsamp program in the [lme4] package with n = 10000 samples, assuming locally
4. Breeding quality and foraging efficiency

uniform priors for fixed effects and locally non-informative priors for random effects (Baayen et al. 2008). Means ± SE are given unless indicated otherwise.

4.3 Results

Results are summarized by prediction in Table 4.3 and described in more detail below.

**TABLE 4.3. Summary of predictions and respective outcomes for foraging parameters comparing better breeders (BB) with poorer breeders (PB). Predictions that were not explicitly evaluated are marked “NA,” otherwise, T = True and F = False.**

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1a. BB have shorter duration foraging trips than PB</td>
<td></td>
<td>T</td>
<td>F</td>
<td>F</td>
</tr>
<tr>
<td>1b. BB travel greater daily vertical distance than PB</td>
<td></td>
<td>F</td>
<td>F</td>
<td>F</td>
</tr>
<tr>
<td>2a. BB return with larger food loads than PB</td>
<td></td>
<td>T</td>
<td>T</td>
<td>F</td>
</tr>
<tr>
<td>2b. BB have higher foraging success per dive than PB</td>
<td></td>
<td>T</td>
<td>F</td>
<td>NA</td>
</tr>
<tr>
<td>3a. BB dive deeper than PB</td>
<td></td>
<td>T</td>
<td>F</td>
<td>NA</td>
</tr>
<tr>
<td>3b. BB have shorter post-dive recovery periods than PB</td>
<td></td>
<td>F</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>4a. BB have higher catch per unit effort than PB</td>
<td></td>
<td>T</td>
<td>T</td>
<td>F</td>
</tr>
<tr>
<td>4b. BB have higher chick feeding frequency than PB</td>
<td></td>
<td>F</td>
<td>F</td>
<td>F</td>
</tr>
</tbody>
</table>

**Foraging effort and diving activity**

As the season progressed, foraging trips became longer for all birds, but especially for PB (Fig. 4.1a, b; Table 4.4, model 4a). At the beginning of the season, there was no difference in trip durations between BB and PB, but later in the season BB made trips that were progressively shorter relative to PB. Females made longer trips than males (1.27 ± 0.10 days vs. 1.12 ± 0.10 days, respectively; Table 4.4, model 1a). Foraging trip duration varied as a function of colony size: longer at the largest colony (Crozier; females: 1.59 ± 0.05 days, males: 1.41 ± 0.05 days), than at the medium-sized colony (Bird; females: 1.39 ± 0.05 days, males: 1.22 ± 0.05 days), and longer at Bird than at the smallest colony (Royds; females: 0.93 ± 0.05 days, males: 0.80 ± 0.05 days; Table 4.4, model 3a). However, no significant effect on trip duration was apparent in the interaction between BQI and colony size. Foraging trips
4. Breeding quality and foraging efficiency

tended to be shorter in no-iceberg years (95% HPDI for the iceberg term: -0.51 / 0.03) but, again, the interaction between BQI and adversity, i.e. presence/absence of the icebergs, had no significant effect on trip duration.

**TABLE 4.4.** Estimates ± SE and 95% Highest Posterior Density Intervals (HPDI) for significant fixed effects in REML models fitted to the foraging behavior response variables for all individual Adélie penguins followed using the WB (n wb = 360) and SPLASH tags (n splash = 24). Trip duration and CPUE data were log transformed to meet assumptions of statistical tests. n = number of observations.

<table>
<thead>
<tr>
<th>Response</th>
<th>Model</th>
<th>Fixed term</th>
<th>Estimate</th>
<th>95% HPDI</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>log(Trip duration + 1)</td>
<td>1a</td>
<td>Sex (♂)</td>
<td>-0.07 ± 0.02</td>
<td>-0.10 / -0.04</td>
<td>5541</td>
</tr>
<tr>
<td></td>
<td>3a</td>
<td>Colony (CROZ)</td>
<td>0.08 ± 0.02</td>
<td>0.04 / 0.12</td>
<td>5541</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colony (ROYD)</td>
<td>-0.21 ± 0.02</td>
<td>-0.25 / -0.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4a</td>
<td>Sex (♂)</td>
<td>-0.07 ± 0.02</td>
<td>-0.10 / -0.05</td>
<td>5541</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Study day</td>
<td>0.01 ± 0.00</td>
<td>0.01 / 0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI * Study day</td>
<td>-0.01 ± 0.00</td>
<td>-0.01 / -0.002</td>
<td></td>
</tr>
<tr>
<td>Daily vertical distance</td>
<td>2b</td>
<td>Iceberg (no)</td>
<td>10.47 ± 3.36</td>
<td>4.71 / 16.79</td>
<td>48</td>
</tr>
<tr>
<td>Food load</td>
<td>2c</td>
<td>BQI</td>
<td>0.26 ± 0.08</td>
<td>0.12 / 0.40</td>
<td>3320</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI * Iceberg</td>
<td>-0.26 ± 0.08</td>
<td>-0.41 / -0.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4c</td>
<td>Study day</td>
<td>0.01 ± 0.00</td>
<td>0.005 / 0.008</td>
<td>3320</td>
</tr>
<tr>
<td>Number of undulations</td>
<td>4d</td>
<td>Study day</td>
<td>0.05 ± 0.01</td>
<td>0.02 / 0.07</td>
<td>18248</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI * Study day</td>
<td>0.25 ± 0.08</td>
<td>0.08 / 0.40</td>
<td></td>
</tr>
<tr>
<td>Maximum depth</td>
<td>1e</td>
<td>Sex (♂)</td>
<td>9.31 ± 3.39</td>
<td>3.59 / 14.71</td>
<td>18248</td>
</tr>
<tr>
<td></td>
<td>4e</td>
<td>Sex (♂)</td>
<td>8.46 ± 2.96</td>
<td>3.38 / 13.69</td>
<td>18248</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Study day</td>
<td>0.27 ± 0.08</td>
<td>0.13 / 0.43</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI * Study day</td>
<td>1.72 ± 0.51</td>
<td>0.81 / 2.71</td>
<td></td>
</tr>
<tr>
<td>PDI</td>
<td>5</td>
<td>Max depth</td>
<td>0.34 ± 0.01</td>
<td>0.33 / 0.35</td>
<td>15533</td>
</tr>
<tr>
<td>log(CPUE + 1)</td>
<td>1f</td>
<td>Sex (♂)</td>
<td>0.05 ± 0.01</td>
<td>0.02 / 0.07</td>
<td>3320</td>
</tr>
<tr>
<td></td>
<td>2f</td>
<td>Sex (♂)</td>
<td>0.05 ± 0.01</td>
<td>0.03 / 0.08</td>
<td>3320</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI</td>
<td>0.15 ± 0.06</td>
<td>0.04 / 0.25</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>BQI * Iceberg</td>
<td>-0.13 ± 0.06</td>
<td>-0.23 / -0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3f</td>
<td>Sex (♂)</td>
<td>0.05 ± 0.01</td>
<td>0.02 / 0.07</td>
<td>3320</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colony (CROZ)</td>
<td>-0.04 ± 0.02</td>
<td>-0.08 / -0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colony (ROYD)</td>
<td>0.11 ± 0.02</td>
<td>0.07 / 0.14</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4f</td>
<td>Sex (♂)</td>
<td>0.05 ± 0.01</td>
<td>0.02 / 0.07</td>
<td>3320</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Study day</td>
<td>0.002 ± 0.0005</td>
<td>0.0005 / 0.002</td>
<td></td>
</tr>
<tr>
<td>Feeding frequency</td>
<td>2g</td>
<td>Iceberg (no)</td>
<td>0.07 ± 0.02</td>
<td>0.02 / 0.11</td>
<td>650</td>
</tr>
<tr>
<td></td>
<td>3g</td>
<td>Colony (CROZ)</td>
<td>-0.04 ± 0.02</td>
<td>-0.07 / -0.01</td>
<td>650</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colony (ROYD)</td>
<td>0.07 ± 0.02</td>
<td>0.03 / 0.10</td>
<td></td>
</tr>
</tbody>
</table>
4. Breeding quality and foraging efficiency

Figure 4.1. Predicted effects of breeding performance and season progression on the foraging trip duration and on the maximum dive depth of (a, c) male and (b, d) female Adélie penguins. Predictions were calculated from model 4a and 4e (Table 4.4).
4. Breeding quality and foraging efficiency

We did not find any significant effect of BQI, the interaction between BQI and presence/absence of icebergs, or the interaction between BQI and the season progression on daily vertical distance. Daily vertical distance was significantly higher during the no-iceberg year (Table 4.4, model 2b), a function of there being more (135 ± 42) dives per day when icebergs were not present.

Foraging success
At the trip level, foraging success (i.e., food load) was much higher for BB than for PB when the giant icebergs were present (Table 4.4, model 2c; Fig. 4.2a). Food load also increased for all birds as the season progressed (Table 4.4, model 4c) and was not affected by the interaction between BQI and season progression. Food load was not significantly different between sexes or among colonies. We did not find any significant effect of the interaction between BQI and colony on food load.

At the dive level, foraging success (i.e., number of undulations per dive) increased as the season progressed. It was slightly higher for PB than for BB at the beginning of the season, but later became much higher for BB (Fig. 4.3; Table 4.4, model 4d). Number of undulations per dive did not differ between sexes or according to the presence/absence of giant icebergs. We did not find any significant effect on foraging success of the interaction between BQI and presence/absence of icebergs.
4. Breeding quality and foraging efficiency

Figure 4.2. Relationship between breeding performance and (a) food load, (b, c) foraging efficiency (log(CPUE+1) with CPUE in g.min\(^{-1}\)) in Adélie penguins, depending on the presence/absence of giant icebergs. Predictions were calculated from model 2c and 2f (Table 4.4). The prediction for the years when giant icebergs were present is depicted as a solid black line (with 95% HPDI as dotted black lines). The prediction for the years when giant icebergs were absent is depicted as a solid grey line (with 95% HPDI as dotted grey lines).
4. Breeding quality and foraging efficiency

(Figure 4.2, continued from previous page)

**Figure 4.3.** Predicted effects of breeding performance and season progression on the number of undulations per dive of Adélie penguins. Predictions were calculated from model 4d (Table 4.4).
4. Breeding quality and foraging efficiency

**Diving parameters**

Penguins dived deeper as the season progressed, and while there was no difference in diving depth between BB and PB initially, BB dove deeper than PB at the end of the season (Fig. 4.1c, d; Table 4.4, model 4e). Males dove deeper than females (46.9 ± 4.2 m and 37.6 ± 2.4 m, respectively) (Table 4.4, model 1e). Maximum dive depth did not differ according to the presence/absence of giant icebergs nor was it influenced by the interaction between BQI and presence/absence of icebergs.

Predictably, penguins spent more time recovering at the surface (i.e., longer PDI’s) after diving deeper (Fig. 4.4; Table 4.4, model 5). More interestingly, BB tended to exhibit shorter PDI’s than PB for shallower dives, but this difference weakened when diving deeper (Fig. 4.4; 95% HPDI for the BQI * Max depth interaction term: -0.0004 - 0.13). Despite the sex differences in diving depth, there was no significant difference in PDI between sexes.

**Figure 4.4.** Predicted effects of breeding performance and maximum dive depth on the post dive interval duration of Adélie penguins. Predictions were calculated from model 5 (Table 4.4).
4. Breeding quality and foraging efficiency

Foraging efficiency and feeding frequency

BB were more efficient foragers than PB (Table 4.4, model 2f) and the difference between BB and PB was much stronger when the giant icebergs were present (Fig. 4.2b, c). Males were more efficient than females (0.45 ± 0.05 g.min\(^{-1}\) vs. 0.38 ± 0.05 g.min\(^{-1}\), respectively; Table 4.4, model 1f). Birds that bred at the smallest Cape Royds colony gathered more food per unit of time (males: 0.58 ± 0.03 g.min\(^{-1}\), females: 0.50 ± 0.03 g.min\(^{-1}\)) than birds from medium-sized Cape Bird (males: 0.42 ± 0.03 g.min\(^{-1}\), females: 0.35 ± 0.02 g.min\(^{-1}\)); in turn the latter were more efficient foragers than birds from the biggest Cape Crozier colony (males: 0.36 ± 0.03 g.min\(^{-1}\), females: 0.29 ± 0.03 g.min\(^{-1}\); Table 4.4, model 3f). For all birds, foraging efficiency slightly increased as the season progressed (0.002 ± 0.0005 g. min\(^{-1}\).day\(^{-1}\); Table 4.4, model 4f). We did not find any significant effect of the interaction between BQI and colony, or between BQI and season progression on foraging efficiency.

Feeding frequency was not influenced by BQI, by the interaction between BQI and presence/absence of icebergs, or by the interaction between BQI and colony. Chicks were fed less often when the giant icebergs were present (0.42 ± 0.03 times per day vs. 0.49 ± 0.04 times per day; Table 4.4, model 2g). A given parent fed its chicks more often at Royds (0.52 ± 0.03 times per day), the smallest colony, than at Bird (0.46 ± 0.02 times per day), the medium-sized colony, and more often at Bird than at Crozier (0.41 ± 0.02 times per day), the largest colony (Table 4.4, model 3g). Despite sex differences in trip duration, feeding frequency was similar for males and females, meaning that males spent more time in the colony than females.

4.4 Discussion

Our results show that BB gather food more efficiently and bring back more food to the colony than PB when confronting adversity (harsh environmental conditions, higher offspring needs), therefore gaining higher net energy profit to be allocated to reproduction and survival.
4. Breeding quality and foraging efficiency

To our knowledge, this study is the first to demonstrate the importance of “extrinsic”
conditions on the relationship between foraging behavior and individual quality.

**Better breeders are more efficient foragers**

In terms of energetics, CPUE is the key parameter to look at, as ultimately it will determine
the amount of energy that can be invested in other components of life history. BB were more
efficient foragers than PB, especially when conditions were challenging. BB achieved higher
efficiency by being able to find sufficient food during shorter trips than PB when food was
becoming scarce and when food need was increasing. Indeed, both trip duration and depth of
foraging dives increased as the season progressed, therefore adding to evidence that depletion
was occurring in the vicinity of the study colonies during the breeding season (Ainley et al.
2004, Chapter 1). If food was becoming scarce, how did BB find sufficient food without
having to stay at sea as long as PB? By diving deeper and therefore exploiting a larger
foraging area (i.e., a larger volume of ocean). This might have enabled BB to make shorter
trips by reaching resources depleted or chased from shallower depths. On a daily basis, birds
of different BQI traveled similar vertical distances, thus BB overall performed smaller
numbers of deeper foraging dives while PB performed more numerous shallow dives.

Contrary to female common guillemots (*Uria aalge*; Lewis et al. 2006), Adélie penguin BB
did not take advantage of their higher foraging efficiency to increase chick feeding rates.
Rather, they spent more time attending the nest, potentially dedicating extra time to
strengthening the pair bond and defending territory and offspring (Zador and Piatt 1999,
Lewis et al. 2006). It is possible that a threshold may exist above which investing more effort
into raising chick(s) does not increase success, and therefore adults should invest more in
themselves once that level has been reached.

Thus, working harder does not improve reproductive output. Takahashi et al. (2003)
proposed two hypotheses to explain this in Adélie penguins: large inter-individual variation
4. Breeding quality and foraging efficiency

in (1) foraging efficiency (also suggested by Lewis et al. 2006) and/or (2) allocation of food between parents and offspring. Our results strongly support the first hypothesis while not ruling out the second. If Adélie penguin BB are more efficient foragers, they might also have better body condition at the beginning of the breeding season and therefore be able to afford losing mass (i.e., allocating more food to their offspring) without risking their own survival (Takahashi et al. 2003, Chapter 3, Ballard et al. in review 2).

We also highlighted sex differences in foraging efficiency. In our study, females dived shallower than males during longer trips and came back with similar food load, therefore exhibiting lower foraging efficiency. Sex-related variation in foraging efficiency has been little studied in seabirds especially in species with little size dimorphism like Adélie penguins (but see González-Solís et al. 2000, Lewis et al. 2002). In Adélie penguins, longer female trips are widely documented (e.g. Chappell et al. 1993a, Clarke et al. 1998, 2006, Ballard et al. 2001, Chapter 3) but apparently this has can have little effect on food load (Clarke et al. 1998, but see Ballard et al. in review 2, Chapter 3).

When comparing CPUE between individuals, we made the assumption that they were feeding on the same prey, or at least on prey of similar energetic content. In the southern Ross Sea, Adélie penguins feed on a mix of krill (E. crystallorophias, 4.6 ± 0.1 kcal g-1) and silverfish (P. antarcticum, 5.2 ± 0.2 kcal g-1), with diet being similar among colonies (Ainley et al. 2003a). However, proportions of fish and krill in the diet could differ between individuals, perhaps as a function of foraging depth, and the potential links between diet and individual quality remain to be assessed.

Quality matters more under difficult conditions
The relationship between BQI and foraging strategy was only, or mostly, apparent under adversity: harsh environmental conditions (when giant icebergs restricted access to foraging areas), and when offspring needs were higher (later in the season). If foraging behavior is
4. Breeding quality and foraging efficiency

heritable (MacColl and Hatchwell 2003, Missoweit et al. 2007) and a given foraging strategy is associated with higher breeding performance, this would imply that a differential in selective value among individuals only appears under particular space- and time-delimited circumstances (i.e., similar to the punctuated equilibrium hypothesis: “relatively brief episodes of rapid change that punctuate much longer periods of stasis”; Gould and Eldredge 1993, see also Grant and Grant 1993). Even a marginal benefit derived from a given foraging strategy will result in the individuals adopting this strategy doing better in the end, in terms of fitness, than those that do not. This highlights that some relationships or patterns require a sufficiently large timescale and/or heterogeneous extrinsic conditions to be detected.

Intraspecific competition (for which colony size is the proxy in our study) did not affect or reveal any relationship between BQI and foraging strategy. When considering foraging parameters only, however, colony size did matter: foraging efficiency decreased with increasing colony size, and trips were longer and feeding frequency lower at the largest colony. It would have been ideal to use actual colony size rather than static categories for this analysis, but the data are not yet available for the time period of our study. With more precision in colony size, the effect of the BQI * colony size interaction may still prove to be important. Our results show that it is probably more difficult to achieve good reproductive performance and/or to maintain good body condition in large colonies than in small ones, all other things being equal (i.e., at similar levels of food abundance). This also stresses the need to be careful when generalizing results obtained from one colony over a given timeframe to the whole species.

**Limitations of the study**
As we were not working with known-age birds, there is a possibility that the quality measure we used, the BQI, was partially confounded with age and/or experience (see further discussion on BQI in Lescroël et al. 2009). However, by looking at individuals that we were
4. Breeding quality and foraging efficiency

able to follow over time (from 1998 to 2006), we found indications that relative differences in foraging efficiency between birds of different BQI were maintained over time although the statistical correlation within individuals was relatively low (23.1%; Fig. 4.5). This subject requires further investigation, including consideration of best statistical methods to assess relative consistency in extremely variable parameters.

External devices, and in particular devices fitted with an antenna, are known to affect penguins’ at-sea energetics (see Wilson and McMahon 2006 for a review). Device size has a significant effect on diving behavior (Ropert-Coudert et al. 2007). Also, in this study, SPLASH tags had an antenna, which could have significantly increased the drag produced by the device, but the tags were also relatively small (1.0 % to 1.6 % of a bird’s cross-sectional area) and we did not detect any effect of them on foraging trip duration (i.e., on foraging effort). Further, any effect of the tags that was potentially compounded by the amount of time the tags were worn would have been controlled for in our mixed modeling approach (i.e., trip number was included as a random effect). Still, SPLASH tags could have had effects on foraging efficiency that we were not able to detect. Most of our conclusions, and particularly those regarding foraging efficiency, come from non-instrumented birds (i.e., WB birds). Nevertheless, all birds in our study were banded, which could also have affected foraging behavior (Dugger et al. 2006). As all birds were banded, we believe that our conclusions regarding the links between breeding performance and foraging strategy are valid; if anything, bands and SPLASH tags might have exaggerated differences between BB and PB (i.e., mimicking demanding conditions).
4. Breeding quality and foraging efficiency

**Figure 4.5.** Evolution over multiple breeding seasons of the mean CPUE (averaged over day 5 to day 18: December 25 to January 7) of 4 banded Adélie penguins with different breeding quality indexes (BQI: -0.10 to 0.35). Controlling for a main (categorical) effect of year, the intra-class correlation coefficient for individuals was 23.1%.

In species with biparental care, offspring survival and condition is the result of the work and coordination of both parents, not of a single individual (Lewis et al. 2006). Chick feeding rate in particular, would be more meaningful if both parents were taken into account. However, examining the behavioral determinants of quality at the level of the pair can only be done on a multi-annual basis in the case of species exhibiting high mate fidelity. Due to the shortness of the breeding season and the consequent importance of arrival and breeding cycle synchrony, mate fidelity is low in high-latitude Adélie penguins (Ainley 2002a) and we were not able to follow banded pairs through time.

**Proximate mechanisms**

In Adélie penguins, better breeders are more efficient foragers. What are the particular dynamic and/or permanent characteristics allowing some individuals to forage more
4. Breeding quality and foraging efficiency

Efficiently than others? First, these individuals could be older and/or more experienced (i.e.,
dynamic characteristics) (Pyle et al. 1991, Desrochers 1992a). However, these differences
will more likely be found between juveniles and adults than among breeders (Desrochers
1992b). Accordingly, Woo et al. (2008) did not find any relationship between age and
foraging behavior in adult Brünnich’s guillemots (Uria lomvia). Although our results also
suggest that inter-individual differences in foraging efficiency persist over time, the
relationship between age and foraging efficiency, while controlling for individual quality,
needs investigation. Second, as for permanent characteristics, BB could have higher –
genetically determined – physiological ability allowing them to repeatedly reach deeper
depths at a lower cost (in terms of time and/or energy). This hypothesis is partially supported
by our results: BB tended to have shorter recovery periods at the water surface than PB when
diving at similar deep depths but this was only true for shallow diving. Furthermore, a few
PB dived deeper than BB, and the relationship between PDI, BQI and maximum dive depth
was mainly driven by one or two data points. Thus, the potentially higher physiological
ability of BB, which could also relate to genetically affected hormone levels, needs to be
properly tested by measuring the oxygen carrying capacity of birds of varying quality.

Morphology, and body size in particular, is also an important characteristic in diving birds or
mammals as larger divers can make longer and deeper dives (Schreer et al. 2001) due to
larger capacity for O2 storage and lower rate of O2 consumption (Kooyman 1989).

At the interface of dynamic and permanent characteristics is cognitive ability, which
could be different between individuals and improve with age and experience. Little is known
about cognitive ability of seabirds in relation to foraging (but see Kitaysky et al. 2006);
testing whether BB have higher cognitive abilities than PB would require carefully controlled
experiments, which is challenging in the wild. In the field of human cognition, one
hypothesis for explaining the positive correlation between early-life cognitive ability and
longevity is that cognitive ability is an indicator of a “well-put-together system” (Deary 2008). In seabirds, BB, which can also be best survivors (Cam et al. 2002, Lescroël et al. 2009) and most efficient foragers (this study), might have the “best-wired” organism. From this perspective, it would be very interesting to investigate inter-individual differences in locomotion ability and reaction speeds. Given the relatively rapid changes in the physical environment now projected by climate models, this phenotypic plasticity in Adélie penguins will likely be tested repeatedly in the coming decades. Since some proportion of the population is capable of successful reproduction during the most demanding environmental conditions yet witnessed by humans, we predict that the capabilities of BB will become relatively more prevalent in the overall population. In fact, the consistently harsher (more competitive) conditions at the largest colonies may already serve as a facultative mechanism, encouraging wider prevalence of higher foraging performance.
Chapter V: An energetic correlate between colony size and foraging effort in seabirds

PLATE 5. Hundreds of Adélie penguins rush into the ocean off an ice floe, having waited for the right moment to avoid a possible Leopard Seal (photo: V. Toniolo).
5. An energetic constraint to colony size

5.1 Introduction
Central-place foraging seabirds deplete or reduce the availability of prey around colonies, leading to proposals that the size of such “halos” of available prey ultimately regulates population size (Storer 1952, Ashmole 1963, Birt et al. 1987). An inverse correlation is often evident between colony size and reproductive success, numbers of conspecifics at other colonies with overlapping foraging ranges, and diet quality (Furness and Birkhead 1984, Hunt et al. 1986, Lewis et al. 2001, Forero et al. 2002, Ainley et al. 2003b, 2004, Hipfner et al. 2007). In addition, interference competition for limited prey leads to higher foraging effort (longer trips both in distance and time) for individuals in larger colonies (Lewis et al. 2001, Ainley et al. 2003b, 2004) and slower colony growth (Lewis et al. 2001, Ainley et al. 2004). The proximate mechanism responsible for any of these relationships heretofore has been unknown.

In the southwestern Ross Sea, Antarctica, where about 9% of the world population of Adélie penguins *Pygoscelis adeliae* nests in four colonies, we investigated possible mechanisms involved in population regulation by directly measuring the effect of colony size on the energetic cost of foraging. The Ross Sea is the last continental shelf ecosystem on Earth yet to be altered by over-fishing, whaling, wide-spread pollution or introduction of alien invasive species (Ainley 2002a, Smith et al. 2007), and, therefore, offers an unparalleled opportunity to investigate ecological interactions free of direct anthropogenic influence (e.g. Crawford 2007, Furness 2002, Österblom et al. 2006, 2007). Three of the study colonies, all on Ross Island, have been the subject of simultaneous, extensive study (Ainley et al. 2004). Cape Crozier is one of the six largest Adélie penguin colonies in the world, with ~135,000 breeding pairs. Capes Bird and Royds are orders of magnitude smaller, supporting 47,000 and 4,000 breeding pairs, respectively. Recently, all three colonies have changed in size, but at different rates inverse to colony size, a pattern similar to seabird colonies elsewhere (e.g. Lewis et al. 2001). Size in 1997 compared to 1970 was 260% greater for Cape Royds, 160%
5. An energetic constraint to colony size

greater for Cape Bird, and 114% greater for Cape Crozier (Ainley et al. 2004). None of these colonies are space-limited but the lower growth rate at the largest colony seems to indicate approach of a ceiling, whereas the smallest colony grew quickly during the years of this study.

Ainley et al. (2003b) showed that prey quality (diet composition) is equivalent among these colonies, and surmised that prey abundance was as well, given the direction of ocean currents. Ainley et al. (2006) found that prey availability is affected for these colonies by the number of foraging whales. Herein, we report field metabolic rate (FMR) and total energy expended (TEE) for time at sea during a foraging trip, measured using doubly-labeled water (Nagy 1980), and relate these measures to colony size. We propose that colony size is limited proximately by the increasing energetic cost of obtaining food. The intercolony comparison that we were able to accomplish was based on a sample size (n = 40), that was much higher than in most other studies using this technique, the limiting factor usually being the high cost of doubly-labeled water.

5.2 Materials and methods

Study Area
We conducted research at two colonies on Ross Island (77º 30' S, 168º W) during the reproductive seasons of 1999 and 2001: Cape Crozier (137,135 breeding pairs in 1999) and Cape Bird (45,449 and 21,607 breeding pairs in 1999 and 2001, respectively; Ainley et al. 2004; the lower population size in 2001 was related to more difficult sea-ice conditions, requiring more walking, before and during the egg-laying season). We captured adults leaving the colony, apparently intending to begin a foraging trip. All study birds had at least one chick at the crèche stage.
5. An energetic constraint to colony size

**Collection of samples**
Upon capture of each bird, 1 – 3 mL of blood was collected from the jugular vein using a 3-
ml syringe and a 22-gauge, 2.5 cm needle, and 0.95 mL water labeled with 95 atom% \(^{18}\)O
and 99.9 atom% \(^{3}\)H was injected into the dorsal side of the upper thigh (\textit{gluteus maximus}
and \textit{sartorius} muscles). This muscle was chosen, rather than any swimming muscles, to avoid
were then weighed, fitted with transmitters (Ballard et al. 2001), and put into a cardboard box
with ventilation holes for a period of 3 - 4.75 h to allow for equilibration of the isotopically-
labeled water (Nagy and Obst 1992). Immediately after equilibration, a second blood sample
was drawn from the opposite jugular vein and the bird was released. Birds’ activity was
monitored in the colony by listening for transmitter signals every hour, 10 min for each bird,
around the clock. Upon return from the foraging trip, and in all but one case prior to feeding
its chick, the bird was recaptured, the transmitter removed, the bird weighed, and a third
blood sample was collected. The bird was then released whereupon, in most cases, it
proceeded to immediately feed its chick(s). All field procedures on study animals were
approved by the Committee on the Humane Use and Care of Vertebrate Animals of H.T.
Harvey and Associates.

**Sample analysis**
Isotope concentrations in blood samples were measured using mass spectroscopy at the
laboratory of Ken Nagy at the University of California, Los Angeles. To convert FMR from
\(\text{CO}_2\) production to heat production we used the following conversion factors: 25.8 kJ \text{L}^{-1}\ \text{CO}_2
for a fish diet (Nagy et al. 1984) and 26.0 kJ \text{L}^{-1}\ \text{CO}_2 for a krill diet (Davis et al. 1989). Diet
sampling indicated that during our energetic study, birds were consuming a diet of 20% fish
and 80% krill at Cape Bird during 1999, 53% fish and 47% krill at Cape Bird in 2001, and
64% fish and 36% krill at Cape Crozier in 1999 (Ainley et al. 2003a, unpublished data).
5. An energetic constraint to colony size

Accordingly, we integrated these published values to reflect the assumed diet of our study birds and used conversion factors of 25.96 and 25.86 kJ L⁻¹ CO₂ for Cape Bird penguins in 1999 and 2001, respectively, and 25.87 kJ L⁻¹ CO₂ for Cape Crozier penguins in 1999.

**Statistical analysis**

To evaluate the relationship between the energetic costs of foraging and colony size, we built and evaluated two sets of models, one for FMR and one for TEE. Both model sets included the same set of explanatory variables and combinations of these variables: breeding population size (BPS, pairs x 10⁴), colony (COL; Crozier or Bird), mass change during a foraging trip (g), and log foraging trip duration (d; Table 5.1). All 16 combinations of these variables, including the intercept-only models, were evaluated (Table 5.2). COL was included to evaluate whether BPS per se (versus some other characteristic of the colonies) was an important predictor of FMR and TEE.
5. An energetic constraint to colony size

TABLE 5.1. Mean ± SE (range) of mass, trip duration, and energetic costs of a foraging trip, as well as breeding population size of the colony for 40 Adélie penguins investigated during two years on Ross Island, Antarctica.

<table>
<thead>
<tr>
<th></th>
<th>Cape Bird</th>
<th></th>
<th>Cape Crozier</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1999</td>
<td>2001</td>
<td></td>
<td>1999</td>
</tr>
<tr>
<td>Mass at start of foraging trip (g)</td>
<td>3800 ± 82</td>
<td>3785 ± 77</td>
<td>3878 ± 89</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(3200 – 4350)</td>
<td>(3125 – 4300)</td>
<td>(3313 – 4325)</td>
<td></td>
</tr>
<tr>
<td>Mass at end of foraging trip (g)</td>
<td>4084 ± 112</td>
<td>4417 ± 146</td>
<td>4258 ± 183</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(3350 – 4750)</td>
<td>(3675 – 5500)</td>
<td>(3450 – 5150)</td>
<td></td>
</tr>
<tr>
<td>Mass change during foraging trip (g)</td>
<td>+284.4 ± 71.7</td>
<td>+632.7 ± 131.8</td>
<td>+380.4 ± 162.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-100 - +750)</td>
<td>(0 - +1550)</td>
<td>(-774 - +1275)</td>
<td></td>
</tr>
<tr>
<td>Foraging trip duration (d)</td>
<td>3.38 ± 0.30</td>
<td>1.35 ± 0.10</td>
<td>3.41 ± 0.36</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(1.90 - 6.68)</td>
<td>(0.75 - 1.88)</td>
<td>(1.79 - 5.01)</td>
<td></td>
</tr>
<tr>
<td>Field Metabolic Rate (kJ d⁻¹)</td>
<td>5248 ± 216</td>
<td>4991 ± 468</td>
<td>5761 ± 355</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(3555 - 7103)</td>
<td>(2129 - 8581)</td>
<td>(3803 - 7433)</td>
<td></td>
</tr>
<tr>
<td>Total energy expended (kJ)</td>
<td>17,768 ± 1803</td>
<td>6531 ± 573</td>
<td>20,162 ± 2772</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(10,702 - 38,063)</td>
<td>(2195 - 10,458)</td>
<td>(6800 - 37,211)</td>
<td></td>
</tr>
<tr>
<td>Breeding population size (pairs; Ainley et al. 2004)</td>
<td>45,449</td>
<td>21,607 *</td>
<td>137,135</td>
<td></td>
</tr>
</tbody>
</table>

*Barton et al. unpublished data.

The models were evaluated using generalized linear modeling in an information theoretic framework, employing the Gaussian link function for FMR and the log-link function for TEE (log-link function provided more normally distributed residuals compared to Gaussian for TEE). Each model was ranked based on its Akaike’s Information Criterion corrected for small sample size (AICc) and relative model weights were calculated (Burnham and Anderson 2002). All models contributing to 90% of the combined model weight were considered as potentially interesting and examined further to determine if 95% confidence intervals for estimated coefficients overlapped zero. Residual plots and formal statistical tests (e.g. STATA, version 10.1 sktest; Stata, College Station, Texas) indicated that residuals were independent and normally distributed, with homogeneous variances, after log-transforming foraging trip duration, which tended to be skewed towards shorter trips (cf. Ballard et al. 2001).
5. An energetic constraint to colony size

TABLE 5.2. Model selection results for effects of breeding population size (BPS), colony (COL; categorical variable), mass change during a foraging trip (MC), and trip duration (TD) on field metabolic rate (FMR) and total energy expended (TEE) during a foraging trip.*

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICwi</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>A) FMR</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BPS + MC</td>
<td>680.311</td>
<td>0.000</td>
<td>0.234</td>
<td>3</td>
</tr>
<tr>
<td>BPS + MC + COL</td>
<td>681.079</td>
<td>0.768</td>
<td>0.159</td>
<td>4</td>
</tr>
<tr>
<td>MC + COL</td>
<td>681.495</td>
<td>1.184</td>
<td>0.129</td>
<td>3</td>
</tr>
<tr>
<td>FTD + MC</td>
<td>681.809</td>
<td>1.498</td>
<td>0.111</td>
<td>3</td>
</tr>
<tr>
<td>MC</td>
<td>682.138</td>
<td>1.828</td>
<td>0.094</td>
<td>2</td>
</tr>
<tr>
<td>BPS + FTD + MC</td>
<td>682.169</td>
<td>1.858</td>
<td>0.092</td>
<td>4</td>
</tr>
<tr>
<td>FTD + MC + COL</td>
<td>682.661</td>
<td>2.350</td>
<td>0.072</td>
<td>4</td>
</tr>
<tr>
<td>BPS + FTD + MC + COL</td>
<td>683.659</td>
<td>3.348</td>
<td>0.044</td>
<td>5</td>
</tr>
<tr>
<td>BPS</td>
<td>686.258</td>
<td>5.948</td>
<td>0.012</td>
<td>2</td>
</tr>
<tr>
<td>intercept only</td>
<td>686.351</td>
<td>6.041</td>
<td>0.011</td>
<td>1</td>
</tr>
<tr>
<td>COL</td>
<td>686.524</td>
<td>5.445</td>
<td>0.015</td>
<td>2</td>
</tr>
<tr>
<td>FTD</td>
<td>687.992</td>
<td>6.913</td>
<td>0.007</td>
<td>2</td>
</tr>
<tr>
<td>BPS + COL</td>
<td>688.543</td>
<td>7.464</td>
<td>0.006</td>
<td>3</td>
</tr>
<tr>
<td>BPS + FTD</td>
<td>688.599</td>
<td>7.520</td>
<td>0.005</td>
<td>3</td>
</tr>
<tr>
<td>TD + COL</td>
<td>688.775</td>
<td>7.696</td>
<td>0.005</td>
<td>3</td>
</tr>
<tr>
<td>BPS + COL + TD</td>
<td>690.967</td>
<td>9.888</td>
<td>0.002</td>
<td>4</td>
</tr>
<tr>
<td>B) TEE</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BPS + TD + MC</td>
<td>741.446</td>
<td>0.000</td>
<td>0.404</td>
<td>4</td>
</tr>
<tr>
<td>COL + TD + MC</td>
<td>741.691</td>
<td>0.245</td>
<td>0.358</td>
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<tr>
<td>BPS + COL + TD + MC</td>
<td>743.849</td>
<td>2.403</td>
<td>0.122</td>
<td>5</td>
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<tr>
<td>TD + MC</td>
<td>743.983</td>
<td>2.537</td>
<td>0.114</td>
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<tr>
<td>COL + TD</td>
<td>753.355</td>
<td>11.909</td>
<td>0.001</td>
<td>3</td>
</tr>
<tr>
<td>BPS + TD</td>
<td>753.359</td>
<td>11.913</td>
<td>0.001</td>
<td>3</td>
</tr>
<tr>
<td>BPS + COL + TD</td>
<td>755.821</td>
<td>14.375</td>
<td>0.000</td>
<td>4</td>
</tr>
<tr>
<td>TD</td>
<td>756.880</td>
<td>15.434</td>
<td>0.000</td>
<td>2</td>
</tr>
<tr>
<td>BPS + COL + MC</td>
<td>821.557</td>
<td>80.111</td>
<td>0.000</td>
<td>4</td>
</tr>
<tr>
<td>BPS + COL</td>
<td>822.243</td>
<td>80.797</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td>BPS</td>
<td>833.659</td>
<td>92.213</td>
<td>0.000</td>
<td>2</td>
</tr>
<tr>
<td>BPS + MC</td>
<td>835.731</td>
<td>94.285</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td>COL</td>
<td>837.170</td>
<td>95.724</td>
<td>0.000</td>
<td>2</td>
</tr>
<tr>
<td>COL + MC</td>
<td>839.443</td>
<td>97.997</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td>intercept only</td>
<td>841.249</td>
<td>99.803</td>
<td>0.000</td>
<td>1</td>
</tr>
<tr>
<td>MC</td>
<td>843.372</td>
<td>101.926</td>
<td>0.000</td>
<td>2</td>
</tr>
</tbody>
</table>

* BPS reported as pairs x 10^-4, MC reported in grams, TD reported as ln (foraging trip duration) in days. Total sample size for FMR and TEE = 40 Adélie penguins studied on Ross Island, Antarctica. Models ranked according to Akaike’s Information Criterion adjusted for small sample sizes (AICc); AICc, ΔAICc, AICc weights and number of parameters (k) are given for each model.
5. An energetic constraint to colony size

5.3 Results
Foraging trip duration (FTD) and mass change during a trip varied with colony size and year (Table 5.1). Mean body mass at the start of foraging trips was similar among colonies and years, but mean mass at the end of trips varied. FMR averaged $5306 \pm 201 \text{ kJ d}^{-1}$ (range 2129 – 8581; Table 5.1), was dependent on body mass ($r^2 = 0.32, F = 17.564, P < 0.001$) and, for all but two birds, exceeded that predicted from allometric equations (Nagy et al. 1999; Fig. 5.1). FMR was a function of breeding population size (BPS, Table 5.1) and mass change during a foraging trip. The strongest explanatory model included positive effects of BPS ($\beta = 78.472; 95\% \text{ CI: } 2.201 – 154.742$) and mass change ($\beta = 1.209; 95\% \text{ CI: } 0.397 – 2.021$), and had twice as much support as the closest model that did not include BPS (Table 5.2). The second best model included BPS, mass change and COL, but the 95% CI for both BPS and COL included zero; the combined model weight for models including BPS was 0.555 compared with 0.433 for those including COL, indicating that BPS was the more influential predictor of FMR. All FMR models including mass change ranked higher than those without, and FMR was positively correlated with mass change ($r^2 = 0.15, F = 6.627, P = 0.014$), meaning that birds that worked harder per unit of time ended up gaining more mass than those with lower metabolic rates.
5. An energetic constraint to colony size

FIGURE 5.1. Field metabolic rate (FMR) as a function of body mass for 40 Adélie penguins studied on Ross Island, Antarctica ($r^2 = 0.32, F = 17.564, P < 0.001$). The predicted FMR for these same birds using allometric equations for Sphenisciformes (triangles) and all marine birds (squares) is also shown.

TEE averaged 14,774 ± 1392 kJ (range 2195 - 38,063; Table 5.1) and was a function of BPS, FTD, and mass change during that trip. The best model indicated positive effects of BPS ($\beta = 0.011; 95\% \text{ CI:} 0.001 – 0.021$), FTD ($\beta = 1.12; 95\% \text{ CI:} 1.01 – 1.24$), and mass change ($\beta = 0.0002 95\% \text{ CI:} 0.0001 – 0.0003$), with 40% of the total model weight (Table 5.2). However, the second-best model competed closely, with 36% of the total model weight, and substituted COL for BPS (and also included FTD and mass change) with confidence intervals not including zero for any term (Cape Bird 10% lower TEE than Cape Crozier; 95% CI: 1 – 19%). Overall, models including BPS performed slightly better than those including COL (53% vs. 48% of total model weights when combined). The third-strongest model was
5. An energetic constraint to colony size

the global model (BPS, COL, FTD, mass change), but estimates of effect for both BPS and COL included zero, and the model weight was only 1/3rd that of the next strongest. In this model, FTD and mass change both positively impacted TEE, but the effect of mass change was very small (FTD: $\beta = 1.11$; 95% CI: 0.96 – 1.25; mass change: $\beta = 0.0002$; 95% CI: 0.0001 – 0.0003). Not surprisingly, but in contrast to results for FMR, all models of TEE containing FTD ranked higher than models without, whereas mass change was not as consistently selected, and usually had a very weak effect. Therefore, although TEE increased with FTD ($r^2 = 0.88$, $F = 286.571$, $P < 0.001$; Fig. 5.2), compensation for longer trips in the form of increased mass gain (cf. Weimerskirch et al. 1997) was not evident.

**Figure 5.2.** Total energy expended as a function of foraging trip interval for 40 Adélie penguins studied on Ross Island, Antarctica ($r^2 = 0.88$, $F = 286.571$, $P < 0.001$). Triangles represent Cape Crozier penguins (n = 11); circles represent Cape Bird penguins (n = 29).
5. An energetic constraint to colony size

5.4 Discussion

*Intraspecific variation in FMR*

Debate exists about the importance of intraspecific differences (or lack thereof) in FMR. Some species seem to have a relatively invariant rate of energy expenditure, regardless of environmental conditions (Obst et al. 1995, Golet et al. 2000), but other species do not (Montevecchi et al. 1992). FMR is known to vary by latitude, weather, reproductive stage and/or effort, food availability, and activity mode (Ellis and Gabrielsen 2002). Perhaps the single most relevant factor affecting FMR is the allocation of time among various activities (Birt-Friesen et al. 1989, Chappell et al. 1993b). Differing rates of energy expenditure for birds engaged in travel, prey capture, or resting at sea or on a colony, can cause FMR values within the same species to vary substantially, so, ideally, intraspecific comparisons of FMR should control for activity.

FMR has been measured using doubly-labeled water for Adélie penguins at sea at the same reproductive stage in this and three other studies (Green and Gales 1990, Chappell et al. 1993b, Culik and Wilson 1992); a fourth measured birds at a slightly earlier breeding stage (Nagy and Obst 1992). Resulting values can be remarkably similar, yet the difference between the two extremes is 1641 kJ d⁻¹, roughly 30% of mean FMR for this species as a whole (Table 5.3). To our knowledge, colony size has not previously been suggested as a factor affecting FMR, but the positive relationship between the two is clear (Table 5.2, Fig. 5.3), and the one exception to this pattern (Nagy and Obst 1992) comes from a study where the authors suspected their FMR values may have been artificially elevated. In fact, the two colonies from which the highest FMR values were obtained are among the six largest colonies of this species in the world, each containing ≥120,000 breeding pairs (Esperanza and Cape Crozier; cf. Woehler 1993).
5. An energetic constraint to colony size

Table 5.3. A comparison of energetic costs of a foraging trip during chick provisioning, measured using doubly-labeled water methods, for Adélie penguins at five colonies.

<table>
<thead>
<tr>
<th>Location</th>
<th>Mean at-sea Field Metabolic Rate (kJ/day)</th>
<th>Colony Size (no. breeding pairs)</th>
<th>Mean Mass ± SE (kg)</th>
<th>Latitude (º S)</th>
<th>Reproductive Stage</th>
<th>FMR/BMR Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Torgersen Island,</td>
<td>4120</td>
<td>2,750 (in 7 colonies)</td>
<td>4.01 (SD = 0.24) b</td>
<td>64.7</td>
<td>Chicks</td>
<td>2.3 – 3.9</td>
</tr>
<tr>
<td>Antarctic Peninsula (n = 16)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Torgerson Island,</td>
<td>5605 b</td>
<td>14,170</td>
<td>Not specified d</td>
<td>64.7</td>
<td>Eggs just hatched or adults brooding</td>
<td>3.3 – 5.5 c</td>
</tr>
<tr>
<td>Antarctic Peninsula (n = 8)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cape Bird (n = 29) e</td>
<td>5133</td>
<td>35,732</td>
<td>4.01 ± 0.07 f</td>
<td>77.5</td>
<td>Chicks</td>
<td>2.9 – 4.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>45,449</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cape Crozier (n = 11) e</td>
<td>5761</td>
<td>137,135</td>
<td>4.07 ± 0.12 f</td>
<td>77.5</td>
<td>Chicks</td>
<td>3.2 – 5.3</td>
</tr>
<tr>
<td>Esperanza Bay, Antarctic Peninsula (n = 8)</td>
<td>5676</td>
<td>123,850</td>
<td>4.23 ± 0.12 f</td>
<td>63.4</td>
<td>Chicks</td>
<td>3.0 – 5.0</td>
</tr>
</tbody>
</table>

a Ranges represent Field Metabolic Rate/Basal Metabolic Rate ratios using previously published BMR values: 444 kJ kg⁻¹ d⁻¹ (Ricklefs and Matthew 1983), 313 kJ kg⁻¹ d⁻¹ (Chappell and Souza 1988), and 266.4 kJ kg⁻¹ d⁻¹ (Kooyman et al. 1976) corrected for body mass of birds in each FMR study.

b SE not published.

c Authors suggested that this value may have been elevated due to disturbance effects prior to the measurement period, or a shortage of krill swarms in the vicinity.

d Mean mass of 11 birds, including the 8 in this group, was 3.81 kg (SD = 0.27).

e This study.

We wondered whether the pattern observed in Adélie penguins was evident in other colonial seabird species. We found research results based on doubly-labeled water for the same species at multiple sites and/or multiple years for nine other species: gentoo penguin *P. papua* (Davis et al. 1989, Gales et al. 1993), little penguin *Eudyptula minor* (Costa et al. 1988, Chappell et al. 1993b, Nagy and Obst 1992, Ainley 2002b, Green and Gales 1990, Culik and Wilson 1992) and ...
5. An energetic constraint to colony size

1986, Gales and Green 1990), wandering albatross *Diomedea exulans* (Adams et al. 1986, Shaffer et al. 2001), Leach’s storm-petrel *Oceanodroma leucorhoa* (Ricklefs et al. 1986, Montevecchi et al. 1992), black-legged kittiwake *Rissa tridactyla* (Gabrielsen et al. 1987, Golet et al. 2000, Jodice et al. 2006), common murre *Uria aalge* (Cairns et al. 1990, Gabrielsen 1996), thick-billed murre *U. lomvia* (Croll 1990), black guillemot *Cepphus gryle* (Roby and Ricklefs 1986, Mehlum et al.1993), and least auklet *Aethia pusillus* (Roby and Ricklefs 1986, Obst et al. 1995). In most of these cases FMR was reported as a value that integrated all activities together, or, in one case, FMR was measured during different stages of reproduction for the same species. The often dramatic differences in rate of energy expenditure for birds engaged in flight, prey capture, or resting at sea or on a colony, can cause FMR values for individuals within the same species to vary widely. So, it is potentially misleading to compare FMR values without knowledge of the activity in which measured birds were engaged.

**Figure 5.3.** At-sea FMR as a function of colony size for Adélie penguins as measured in 5 different studies. Data and references are given in Table 5.3.
5. An energetic constraint to colony size

The following were the only three examples in which the energetics of foraging was separated from integrated measures of daily metabolic rate. Although the differences are subtle, for at least two of the three, Leach’s storm-petrel and least auklet, at-sea FMR does increase with colony size (Table 5.4). For the third, little penguin, available data on colony size are not sufficient for confirmation (Table 5.4).

Although not directly comparable to our study for the reasons just reviewed, a recent study on black-legged kittiwakes at two colonies in Prince William Sound, Alaska is instructive (Jodice et al. 2006). Breeders in a small colony (1500 pairs) were able to increase daily energy expenditure (DEE) in order to take advantage of increased prey availability during one of the study years. In contrast, breeders at the largest colony in the region, five times larger than the small colony (7500 pairs) and already foraging much farther from the colony than were birds from the smaller colony (Ainley et al. 2004), were not able to increase their energy expenditure further. By increasing DEE, breeders in the small colony increased nesting success, something which pairs in the larger colony were unable to do in spite of the increase in absolute prey abundance. This finding is consistent with the results we report here.
5. An energetic constraint to colony size

### TABLE 5.4. Intraspecific comparisons of at-sea field metabolic rate (FMR) for seabird species measured with doubly-labeled water, at multiple sites, and controlling for breeding stage.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean At-Sea (Foraging Range, km)</th>
<th>Colony Size (no. breeding pairs) × 10^2</th>
<th>Mean Mass ± SE (g)</th>
<th>Latitude of Study Site</th>
<th>Breeding Stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little penguin</td>
<td>(15-30) 1, 2, 3</td>
<td>13,000 1</td>
<td>1076 ± 3.5</td>
<td>38.5 S</td>
<td>Pre-breeding</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2030 5</td>
<td>2,015 – 19,955 6</td>
<td>1074 b</td>
<td>40.4 S</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leach’s storm petrel</td>
<td>(&gt;200) 7</td>
<td>86,000 9</td>
<td>45 b</td>
<td>44.6 N</td>
<td>Rearing Chick</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>309,313 9</td>
<td>46.6 b</td>
<td>46.9 N</td>
<td>Incubation /</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Least auklet</td>
<td>(5-56) 6</td>
<td>87,500 12</td>
<td>78.8 ± 2.0</td>
<td>60.6 N 12</td>
<td>Rearing Chicks</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>125,000 14</td>
<td>83.5 b</td>
<td>56.6 N</td>
<td>Rearing Chicks</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>265,500 12</td>
<td>78.6 ± 1.9</td>
<td>63.7 N 12</td>
<td>Rearing Chicks</td>
</tr>
</tbody>
</table>

*Colony Size is equal to the total number of breeding pairs at the study colony plus the total number breeding within the maximum reported foraging range of that colony. In some cases, colony size corresponding to the date of FMR measurements were unavailable.

b SE not published.

1 P. Dann, unpublished data.
2 Klomp and Wooler 1988
3 Weavers 1992
4 Costa et al. 1986
5 Gales and Green 1990
6 Oil Spill Response Atlas: www.thelist.tas.gov.au
7 Steele and Montevecchi 1994
8 Ricklefs et al. 1986
9 J. Chardine, pers. comm
10 Montevecchi et al. 1992
11 Obst et al. 1995
12 Sowls et al. 1978
13 Roby and Ricklefs 1986
14 Hickey and Craighead 1977

**An energetic constraint to colony size?**

We propose that the positive correlation between at-sea FMR and colony size is due to differences in prey availability (amount or access) induced by intraspecific competition — the larger the colony, the greater the alteration of prey availability, and the higher the rate of energy expenditure necessary to capture prey (Fig. 5.4). Supporting this hypothesis is, again,
5. An energetic constraint to colony size

the study of Black-legged Kittiwakes in Prince William Sound (Ainley et al. 2003b, Jodice et al. 2006), where the frequency of schools of herring *Clupea harengus* (kittiwake prey) near to the surface increases with distance from the colony, and is also higher near to smaller colonies (see also Lewis et al. 2001 who found the same for Gannet *Morus bassanus* colonies). Also in support are results from our Ross Island study in which penguins increasingly alter their foraging behavior as the breeding season progresses particularly in the case of the larger Cape Crozier colony (Ainley et al. 2004, 2006). As chicks grow and increase food demand, adults dive deeper (Chapter 1, 4, Lescroël et al. in review) and forage farther from the colony, and Cape Crozier penguins, presumably by force of numbers, exclude birds from smaller colonies (Cape Bird and nearby Beaufort Island) from their expanding foraging area (Ainley et al. 2004, 2006, Chapter 1).

How high can FMR go? The ratio of FMR to Basal Metabolic Rate (BMR), sometimes referred to as sustained metabolic scope, has been suggested to represent an energetic ceiling when FMR is time-averaged and measured for animals maintaining constant body mass whose metabolism is fueled by food intake (Peterson et al. 1990). FMR/BMR values are known to range from 1.5 to 5.0 for 37 species (5 ectothermic vertebrates, 13 birds, and 19 mammals, including human cyclists competing in the *Tour de France*; Peterson et al. 1990), and from 1.8 to 4.8 for seabirds. FMR/BMR ratios are also used to compare energetic effort for specific activities, including walking, swimming, and flying (Ellis and Gabrielsen 2002). The mean of at-sea FMR/BMR ratios for 11 species of seabirds is $3.78 \pm 1.59$ (Birt-Friesen et al. 1989).
5. An energetic constraint to colony size

**Figure 5.4.** (A) Hypothesized relationship between energetic constraint, colony size, and reproductive season. Central stars represent colonies of different sizes. Fine stippling indicates foraging area within energetic limit, but not used. Outer circles represent energetic limit to foraging distance. Shading represents time of reproductive season (darker is later). At small colony, individuals forage close to colony throughout season; a large portion of energetically available foraging area remains unused. At medium-sized colony, individuals forage close to colony early in season and farther away later in season due to depletion or alteration of prey availability, but some energetically available foraging area remains unused. At colony of maximum size, individuals forage progressively farther from colony through season, ultimately reaching energetic limit. The density of birds supported by the maximum foraging area directly determines the upper limit to colony size. (B) Study colonies and nearby Adélie penguin colonies (stars). Star size represents relative size of breeding populations (Ainley 2002b). Semi-circular areas around each colony represent hypothetical, modeled foraging ‘halos’ (maximum area utilized), based on the observed foraging ranges of penguins from these colonies (using radio and satellite telemetry; Ainley et al. 2004, 2006). Base map layers are from British Antarctic Survey (1998).
5. An energetic constraint to colony size

We calculated similar ratios using the at-sea FMR values for Adélie penguins in this and four other studies, and the three published values that we found for BMR (Table 5.3). Because FMR increases with colony size, so too does the FMR/BMR ratio. What is instructive is the absolute value of the ratio, well within the expected range if calculated using the highest BMR value (Ricklefs and Matthew 1983), but ranging as high as 5.5 and 5.0 or greater for birds from the largest two colonies if calculated using the lowest BMR value (Kooymen et al. 1976). Whether or not these values represent energetic ceilings, and whether or not Adélie penguins can sustain higher FMR/BMR effort, is debatable (see also Drent and Daan 1980). What is noteworthy is that these values are among the highest measured for seabirds at sea.

We propose that the positive relationships between colony size, presumed consequent alteration of prey availability, and FMR lead to a constraint on colony size and we believe the Cape Crozier penguins are near that limit (Fig. 5.4). By increasing FTD (a proxy for trip distance), a bird may somewhat escape the prey-depleted halo. These longer trips incur a higher TEE (as TEE increases linearly with trip duration, Figure 5.2). Most important, there is no compensation for longer trips in the form of increased mass gain nor more food fed to chicks, we believe because on the longer trips adults may begin to digest their food load during the return (Ainley et al. 1998). Unlike King Penguins Aptenodytes patagonica, which make weeks-long trips and which have mechanisms to inhibit digestion (Gauthier-Clerc et al. 2000), evidence is contrary to this in Adélie penguins (Wilson and Culik 1991). The latter can forestall digestion only until stomach contents warm to body temperature; otherwise, on long trips they bring back less food owing to increased digestion of the food load (summarized in Ainley et al. 1998). At that distance where the costs, in the form of no increase (or a decrease) in food load despite an increase in TEE, outweigh the benefits of
5. An energetic constraint to colony size

foraging outside the halo, FTD is at a maximum.

Colony size, therefore, may be directly determined by the total number of birds that can successfully rear chicks (who survive subsequent to fledging) by foraging within the radius defined by maximum trip duration (and closely correlated energetic expenditure). Greater difficulty, and related consequences, in finding food near to a colony will lead birds to breed elsewhere (Danchin et al. 1998). The degree to which the parents use up extra time that, when food is readily available, provides them with an appreciable cushion, is also involved (Zador and Piatt 1999, Enstipp et al. 2006).

Because FMR appears to increase with colony size in at least two other species of seabirds (Table 5.4), we suggest that this energetic constraint to colony size, through a density-dependent relationship, may apply to seabirds in general as well as potentially to other colonial species. Implicit in this is the assumption that in the absence of seabird colonies (and other predators), the ocean would exhibit equal prey abundance and availability everywhere. Included among the species for which the relationship is evident is a storm-petrel, which further maximizes its foraging range by having the ability to render the food captured to high energy oil. We predict that the relationship we hypothesize would be most extreme among species that carry food to their young in their bill.

For a given species, there could be regional differences in the ceiling as functions of species’ flight and food-storage capabilities (cf. very long duration trips by storm-petrels vs short ones by alcids and small penguins), as well as attributes of food abundance, which in modern times has been altered profoundly in most areas by over-fishing and other direct anthropogenic influences (e.g. Halpern et al. 2008). In fact, in the case of the Adélie penguin the few (five) colonies larger than Cape Crozier are all located in areas where cetaceans and in some cases finfish have been extirpated; in our study area abundant cetaceans and fish predators help penguins to reduce food supply and/or availability (Ainley et al. 2004, 2006,
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Ainley 2007, Ballance et al. 2006, Ainley and Blight 2009). Recently, Ainley and Hyrenbach (in press) found that in the north-central California Current, where a significant decline in productivity and zooplankton and fish biomass has been documented, the majority of seabird species that declined (four of six) are those that acquire prey by diving, i.e. the most energetically demanding mode of feeding and therefore the species most likely to reach their energetic limits with a curtailment of prey. Of further relevance, the declines involved the world’s largest colonies of two of these diving species — Pigeon Guillemot *Cepphus columba* and Cassin’s Auklet *Ptychoramphus aleuticus* — and of a third non-diving species, Western Gull *Larus occidentalis*; included as well among diving species, Sooty Shearwater *Puffinus griseus*, had been the most abundant seabird in the system. This provides something of a test of our proposal concerning colony size and energetic costs of foraging.
Chapter VI: Responding to climate change: Adélie penguins confront astronomical and ocean boundaries

PLATE 6. A pair of Adélie penguins courts at the beginning of the breeding season. The closer one has a geolocation sensor on its left leg holding the secrets of its movements since the end of the previous season (photo: V. Toniolo).
6. Migration routes, timing, and wintering areas

6.1 Introduction

Long-distance migration enables many organisms to take advantage of lucrative breeding and feeding opportunities during summer at high latitudes and then to move to lower, more temperate latitudes for the remainder of the year (cf. Cockell et al. 2000, Alerstam et al. 2003, Greenberg and Marra 2005). This is well known among terrestrial birds, exemplified by the white-crowned sparrow (Zonotrichia leucophrys), with an overall breeding range spanning ~37° latitude, but in which one subspecies (Z. l. nuttalli) remains year round where the climate is mild (California) and another (Z. l. gambelii) which winters in the nuttalli range but breeds during summer in the Arctic (Chilton et al. 1995). Although the details are usually much less known, marine species that undertake polar-temperate long distance migrations include seabirds (e.g. Storr 1968, Ainley and Manolis 1979, Phillips et al. 2005, Shaffer et al. 2006), seals (e.g. Kenyon and Wilke 1953, Stewart and DeLong 1995, McConnell and Fedak 1996), and whales (Lockyer and Brown 1981, Darling and McSweeney 1985, Clapham and Mattila 1990). Environmental changes now occurring, especially in the winter, are affecting seabird population numbers and demography (Barbraud and Weimerskirch 2003). Of particular interest is how Antarctic seabirds cope with two challenges: variability in the location of their foraging habitat (the sea ice ecosystem) and in the amount of light available to them for foraging and navigating.

The Adélie penguin (Pygoscelis adeliae) is one of the southernmost breeding bird species in the world, its overall breeding range extending ~22° latitude (56° to almost 78° S; Woehler 1993). Adélies are pack ice obligates while at sea (Ainley et al. 1983, Ainley et al. 1984, Ainley et al. 1994), previously documented as preferring areas with about 70% ice cover (Cline et al. 1969). Adélies are known to depart their southern breeding grounds in February and thus avoid a long, dark, ice-covered and extremely cold winter. However, until now its winter movements have only been investigated at the lowest-latitude portions of its range (Fraser and Trivelpiece 1996, Clarke et al. 2003). By and large this species spends most of its
6. Migration routes, timing, and wintering areas

life at sea, coming ashore for a few months to breed during the short austral summer, although in the northern portion of its range it visits colonies year round (Parmelee et al. 1977). Its southernmost colonies, which are occupied for only about 4 months, occur on Ross Island (77° 30' S), in the southern Ross Sea, which is the most productive stretch of water in the Southern Ocean (Arrigo et al. 1998, 2008). The high productivity, however, occurs entirely during summer. During the other seasons, except in several polynyas (Jacobs and Comiso 1989, Jacobs and Giulivi 1998), the Ross Sea is entirely ice-covered.

Given the short amount of time available for breeding at highest latitudes, details about non-breeding season movements for Adélie penguins are crucial but little known. This is especially true in the Pacific Sector of the Southern Ocean as the maximum extent of penguins’ journeys has been lengthening as the West Antarctic Ice Sheet (WAIS) has withdrawn southward during the Holocene, continually exposing new breeding habitat sequentially from 71° during the Last Glacial Maximum (LGM) to almost 78° S at present (Ainley 2002a, Emslie et al. 2003, 2007). This has led some penguin populations (i.e., ones that have expanded into the southern portion of the current range) in the Ross Sea from a year round existence in a food web structured by pelagic processes (at the beginning of the Holocene), which is true of most other Adélie penguin populations today, to one structured by continental shelf processes (see Smith et al. 2007). Moreover, given current rates of climate change, the seasonal schedule of sea ice advance, extent, and retreat is changing noticeably, not just in the Pacific Sector but in the Southwest Atlantic Sector as well (Parkinson 2002, Zwally et al. 2002, Stammerjohn et al. 2008). Investigating the migratory and wintering strategy of Adélie penguins would therefore reveal insights into how they have met the challenges of a receding and otherwise altering ice sheet at various scales of climate change, from millennial to decadal periods.
6. Migration routes, timing, and wintering areas

After breeding, Adélies forage intensively to gain body mass for their annual molt, which lasts about 20 days (Penney 1967). During their molt the birds must remain out of the sea or risk hypothermia and possible death as the growing feathers lack a protective waterproof layer (Erasmus et al. 1981). Except in northern areas, such as the northwestern coast of the Antarctic Peninsula where molting takes place at the colony (Parmelee et al. 1977), most Adélie penguins molt on the pack ice. Molting takes place in small groups on ice floes in the lee of hummocks and pressure ridges for wind protection (Cline et al. 1969), ideally with a supply of fresh snow for drinking water (cf. Ainley 2002a, pp. 124-127). Once molted, the birds leave immediately to feed in order to renew body condition and, in the highest latitude areas, avoid getting trapped by the rapidly freezing ocean, which would then force them to walk (rather than swim or ride moving ice floes) to the large-scale ice edge, and requires much more time and energy (Culik and Wilson 1991).

It has been suggested that Adélies, like many long-distance migrants, possess a circadian clock (cf. Cockrem 1990) and a directional sun azimuth compass sense (Emlen and Penney 1964, Penney and Emlen 1967), which enables them to navigate without the aid of fixed landmarks. The navigational ability of Adélie penguins is important because they live in a highly dynamic sea ice habitat (e.g. Parkinson 2002, Zwally et al. 2002, Stammerjohn et al. 2008). Limited studies have shown that Adélie penguins winter within the outer portions of the ice pack, the edge of which generally occurs between the Antarctic Circle (66.5° S) – the latitudinal boundary of sunrise mid-winter – and the southern boundary of the Antarctic Circumpolar Current (ACC) (Fraser and Trivelpiece 1996, Ainley 2002a, Clarke et al. 2003, Van Dam and Kooyman 2004). The region south of the ACC is one of enhanced biological production (Orsi et al. 1995, Tynan 1998, Nicol et al. 2000) compared to waters to the north. The area between this region and the Antarctic Circle has enough light and divergent ice cover for Adélie penguins to be able to forage and survive the winter (Ainley et al. 1993,
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1994). Being a visual predator, Adélie geese likely need at least a few hours of light (daylight or twilight), in order to forage with prey back-lighted against the surface (Wilson et al. 1993). See Fuiman et al. (2002) for similar hypotheses involving seals.

In the last decade, the development of small, battery powered, light-based tracking devices, called Geolocation Sensors (GLS), has enabled investigations of year-round seabird movements. Though less spatially precise, GLS tags offer two important advantages over satellite tags (Platform Terminal Transmitters, PTTs, especially with regards to use on penguins): 1) because they are very small they can be fastened to the leg rather than the back feathers so they are not lost during molt and do not create as much hydrodynamic interference (Bannasch et al. 1994) and 2) they have a longer battery life (up to 3 yrs), and can thus track a bird from its post-breeding departure in autumn until its return to the colony the following spring. They have been used on seabirds (Pütz et al. 1999, Phillips et al. 2004, Shaffer et al. 2005) and other long-distance migrants like songbirds (Stutchbury et al. 2009), tuna (Block et al. 2001, 2005, Sibert et al. 2003), geese (Eichhorn et al. 2006), and turtles (Meylan 1995, Avens and Lohmann 2004). Studies that have employed GLS tags on seabirds include albatrosses (several species; Phillips et al. 2004, Croxall et al. 2005), giant petrels (Macronectes spp; González-Solís et al. 2002), white-chinned petrels (Procellaria aequinoctialis; Phillips et al. 2006), sooty shearwaters (Puffinus griseus; Shaffer et al. 2006), and penguins (Pütz et al. 1998, Bost et al. 2009b). The use of GLS on penguins is of special interest because of the lack of data from the interbreeding period and their sensitivity to antenna mounted conventional satellite transmitters (Ropert-Coudert et al. 2007). Because they are highly streamlined seabirds, penguins are more sensitive than large flying species to back-mounted PTTs. These concerns are heightened during the winter season when food availability is reduced (e.g. Lancraft et al. 1991). Studies using feather-attached PTT’s on Magellanic penguins (Spheniscus magellanicus; Stokes et al. 1998), king penguins
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(Aptenodytes patagonica; Pütz et al. 1998, Charrassin and Bost 2001), emperor penguins (A. forsteri; Kooyman et al. 2004), and Adélie penguins (Kerry et al. 1995, Davis et al. 1996, 2001, Clarke et al. 2003) have been limited by device loss, battery failure, and the sensitivity of penguins to large, back-mounted PTTs with antennae.

Here we report results of the first use of GLS tags to track the year-round movements of Adélie penguins in relation to the sea-ice environment. We present results from two different colonies on Ross Island over a 3-yr period. We sought to document the general pattern (distance, direction, speed, location) of these movements, and we hypothesized that Adélies select wintering locations based on two criteria: (1) sea ice is present but not so consolidated as to prevent access to the ocean, and (2) there is sufficient light that they can see well enough to forage. We believe these two factors are important in the evolution of migratory patterns in this species (see Fraser and Trivelpiece 1996). We also predicted that penguins originating from two different colonies, Capes Royds and Crozier, would use different wintering locations, with potentially different arrival times, ice and light characteristics, since onset of breeding differs by as much as a week and population trends at these two colonies have followed disparate trajectories, with over-winter survival being an important determinant of population trends (Ainley et al. 1983, Trathan et al. 1996, Wilson et al. 2001, Dugger et al. in prep).

6.2 Materials and methods

Overview

At the end of the Adélie penguin breeding seasons of 2003-04, 2004-05, and 2005-06 (end of January) we attached GLS tags to 10-20 penguins at each of two colonies on Ross Island: Cape Crozier and Cape Royds (98 total, 41 retrieved functioning; Tables 6.1, 6.2, Fig. 6.1). We chose these two colonies because they are markedly different in size, which has implications for several aspects of this species’ breeding biology (Ainley et al. 2004).
Moreover, the penguins at Royds, whose colony is smaller by two orders of magnitude, nest 7-10 d later than those at Crozier and thus have a different phenology to their annual cycle.

### TABLE 6.1. GLS deployment and recovery locations, timing, and sex for Adélie penguins on Ross Island. Number retrieved functioning is listed in parentheses.

<table>
<thead>
<tr>
<th>Date</th>
<th>Location</th>
<th># Deployed</th>
<th># Retrieved (after 1 winter)</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Unknown</td>
<td>Male</td>
<td>Female</td>
<td>Unknown</td>
</tr>
<tr>
<td>Jan. 2003</td>
<td>C. Crozier</td>
<td>13</td>
<td>5</td>
<td>0</td>
<td>12 (7)</td>
<td>4 (1)</td>
<td>0</td>
</tr>
<tr>
<td>Feb. 2003</td>
<td>C. Royds</td>
<td>6</td>
<td>4</td>
<td>0</td>
<td>5 (1)</td>
<td>2 (2)</td>
<td>0</td>
</tr>
<tr>
<td>Jan. 2004</td>
<td>C. Crozier</td>
<td>7</td>
<td>9</td>
<td>4</td>
<td>3 (2)</td>
<td>6 (3)</td>
<td>4 (3)</td>
</tr>
<tr>
<td>Jan. 2004</td>
<td>C. Royds</td>
<td>7</td>
<td>14</td>
<td>0</td>
<td>5 (2)</td>
<td>7 (3)</td>
<td>0</td>
</tr>
<tr>
<td>Jan. 2004</td>
<td>C. Crozier</td>
<td>Reference tags (3)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan. 2004</td>
<td>C. Hallett</td>
<td>Reference tags (3)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan. 2005</td>
<td>C. Crozier</td>
<td>11</td>
<td>6</td>
<td>3</td>
<td>7 (5)</td>
<td>4 (3)</td>
<td>2 (2)</td>
</tr>
<tr>
<td>Jan. 2005</td>
<td>C. Royds</td>
<td>7</td>
<td>3</td>
<td>5</td>
<td>4 (4)</td>
<td>2 (2)</td>
<td>1 (1)</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>51</td>
<td>41</td>
<td>12</td>
<td>37 (16)</td>
<td>25 (13)</td>
<td>7 (4)</td>
</tr>
</tbody>
</table>

104 total deployed
68 total retrieved (41 functioning)

### TABLE 6.2. Sample sizes (individuals; positions in parentheses), mean winter locations (June – July), arrival date (week of year), hours of twilight, distance to pack ice edge (km), and pack ice concentration (%) (all ± SE).

<table>
<thead>
<tr>
<th>year</th>
<th>N</th>
<th>latitude</th>
<th>longitude</th>
<th>arrival date</th>
<th>twilight hours</th>
<th>distance to ice edge</th>
<th>ice concentration</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>11 (77)</td>
<td>-66.54 ± 0.57</td>
<td>180.43 ± 2.90</td>
<td>23.0 ± 0.0</td>
<td>6.14 ± 0.11</td>
<td>341.66 ± 24.56</td>
<td>74.12 ± 2.37</td>
</tr>
<tr>
<td>2004</td>
<td>13 (78)</td>
<td>-68.52 ± 0.41</td>
<td>177.76 ± 3.32</td>
<td>25.3 ± 0.4</td>
<td>5.20 ± 0.11</td>
<td>525.12 ± 16.26</td>
<td>81.13 ± 0.68</td>
</tr>
<tr>
<td>2005</td>
<td>17 (98)</td>
<td>-69.96 ± 0.59</td>
<td>185.44 ± 2.38</td>
<td>24.5 ± 0.3</td>
<td>4.11 ± 0.20</td>
<td>631.13 ± 22.57</td>
<td>81.56 ± 0.55</td>
</tr>
</tbody>
</table>

We calculated the potential wintering area of Adélie penguins from Ross Island by creating a polygon containing all GLS-derived penguin positions for all winters (June 1 – July 31; see detailed methods below, under “Details”) using the following boundaries: the Antarctic coastline, the eastern and western-most longitudes and the northernmost latitude in the retrieved positions. Thus, the potential wintering polygon included any place where a penguin might be found during the winter based on the fact that at least one penguin was observed to travel that far during our study. We were not attempting to define the precise area
6. Migration routes, timing, and wintering areas

(e.g., by using kernel analysis or other methods) used by penguins during our study; our interest was in estimating the area of potential use, and we do not expect that our study included the full range of possible wintering locations for these penguins. For each penguin position and for 30 random locations for each week we calculated the mean ice concentration within 100km, the distance to the large-scale ice edge (as defined by the 15% ice concentration contour), the number of hours of light (twilight and daylight), and the distance to the latitude of 24 hour darkness. The random locations were assessed so that we could compare characteristics of places that penguins utilized with ones that were available to the penguins but not necessarily occupied.

**Details**

We selected individuals from the majority of birds that were feeding large, crèched chicks and appeared in good physical condition in late January and early February. We did this to increase the probability that we would be able to find these birds the following spring, at which time we caught them again to remove the archival tags. Birds were sexed by cloacal exam (at Crozier) in 2003 and by size, behavior, and timing in all other years and locations. Encased within the epoxy block of a 9 g GLS (MK3; Afanasyev 2004) was a battery (rated for a 3-yr life), a light sensor, a clock, and a microchip for data storage. Each device was fastened to a white Darvic® plastic band, which was placed on the left leg of penguins using a Panduit® stainless steel cable tie. We chose a white band to match the color of the leg feathers because penguins are known to attempt to remove anything affixed to them that is of a color other than black or white (Wilson and Wilson 1989). This method of attachment required <5 min of handling per individual, and all possible care was taken to minimize impact to birds (no impacts were noticed at time of device attachment).

The nests were marked using a flag, with position recorded by GPS in order to facilitate tag retrieval. We searched for individuals with tags each spring by periodically scanning all birds within 5-10 m of nest markers. Birds were captured and tags were removed upon
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detection; all data pertaining to the bird’s breeding status and condition were recorded if they could be determined, and the tag’s archives were immediately downloaded. When re-captured, most birds were breeding, and had minimal feather cropping around the tag area and some callusing on the leg. Five individuals had more severe callusing, and one individual limped prior to tag removal, we think because the band was attached too loosely (the bird subsequently recovered completely). Tag attrition was a function of normal over-winter penguin mortality (estimated range 4 – 27% annual mortality for 1996 – 2002 at Cape Crozier; Dugger et al. 2006), tag loss or tag malfunction; we were able to retrieve data from 41 of 68 tags retrieved (Tables 6.1, 6.2). We retrieved 65% of the tags that we deployed within 1 year, and 68% after 2 years (data from these tags not reported in this study). We believe that some individuals were missed because GLS tags were inconspicuous, emigration rates were higher than normal (Shepherd et al. 2005) and we know that at least two were missed for one year. However, it is also possible that the tagging method increased adult mortality. Because recapture rate was as high as 89% (Crozier 2003) it seems the method can have a minimal effect. Annual variability in survival and effects of marking penguins remain under study (Dugger et al. in prep).

The GLS loggers measured visible light every 60 sec and recorded the maximum reading every 10 min. By recording light level, day length could be estimated for each day of deployment. The mid-point of a local day (light period) was taken as noon; and the mid-point of the local night (dark period) was taken as midnight. The local time of noon and midnight were compared against GMT to determine longitude; day length on a given date was used to determine latitude (Hill 1994).

Light data as collected by GLS tags were analyzed using MultiTrace software (Jensen Software Systems). Fast moving animals may cover large distances in an east/west direction during a 24 hour period. Under such scenarios, the calculated day length may be more or less
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than 24 hours and calculations of latitude must be compensated accordingly. This correction factor enables the compensation algorithm to take into account whether travel occurred mainly during the day or night. Penguins travel relatively slowly (compared with flying birds, for example), and in the absence of any evidence to suggest otherwise we applied the default correction factor of 0.5 (i.e. equally like to travel during light or dark). Given the inaccuracy of latitude estimation during equinoxes (Hill 1994), we excluded the period around the equinoxes when location estimates were clearly affected (ca. 1 wk before and 3 wk after the autumnal equinox, 3 wk before and 2 wk after the vernal equinox). Any locations derived from light curves with obvious interruptions or interference around the times of sunset or sunrise (probably as a result of diving or of changes in orientation or intermittent shading of the sensor by snow, ice or feathers) were noted during processing and subsequently excluded if obviously anomalous (Hill 1994). Data were then processed to remove any locations that required unrealistic swim speeds between estimated positions (>2.3 m s\(^{-1}\) sustained over a 12-hr period (Clark and Bemis 1979, Brown 1987). The great-circle distance between consecutive fixes was used in all velocity calculations. We were unable to obtain any positions until the time of first sunset, which in the southern Ross Sea is 20 Feb, by which time all penguins had already departed Ross Island.

To compensate for the gap in GLS data due to the absence of darkness in the first portion of each deployment, we also tracked the late summer movements of 11 individual penguins (February to early March, 2004 - 2007) using 20 - 26g satellite tags (SPOT4 and SPLASH; Wildlife Computers; note that these individuals did not also have GLS tags) affixed to the back feathers of breeders (see Wilson and Wilson 1989 and Ballard et al. 2001 for attachment methods).Tags were set to transmit every 45 seconds for the first 8 successive transmissions and then switch to once every 90 s thereafter, with up to 1440 transmissions allowed per day. Tags were programmed to turn off after being dry for 6 hours in order to conserve batteries.
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All transmissions were received and processed within the ARGOS system (CLS Corporation, Ramonville Saint-Agne, FR). Data from these tags were available until the transmitters were lost (due to molting), died (due to low battery voltage), or stopped transmitting (after being dry for >6 hrs). Satellite positions were filtered using Argos accuracy codes and adjusted for penguin swimming speed, as with GLS data, described above.

We deployed three static GLS devices to over-winter at Cape Crozier (77° S) and three at Cape Hallett (72° S) in 2004, to be used as a reference. These data were processed as above, and results compared with device locations determined precisely by GPS. Potential consistency in errors (great-circle distances) among devices and among days was examined, with midday fixes only used in the comparisons to reduce the problem of lack of serial independence. The results from the analyses of the static devices were used to help parameterize some of the inputs to MultiTrace, and to verify the importance of eliminating data near the equinoxes, as described above.

To reduce the position error, inherent in GLS data (Phillips et al. 2004), penguin positions (2/d, one at noon and one at midnight) were smoothed using a 5-day moving average weighted by location and number of neighbors. Five days was chosen because we felt that fewer days resulted in over-confidence of positions and more than five days under-utilized the detail available in the data. Weekly means of these positions for each individual were used for all analyses. For all analyses of wintering areas we used positions from 1 June to 31 July. This period corresponds to the peak of winter darkness, and the time for which we had the most consistent position data.

To assess the overall validity of the positions we report, we analyzed the known error in the data from static devices after processing these data in the same way we had processed the data from tags deployed on penguins. Thus, the position data from the Cape Hallett reference devices were evaluated to estimate mean error in penguin data using a mixed effects model.
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with tag id included as a random effect and week as a main effect. We chose to use only Cape Hallett data for this analysis because its latitude more closely approximated the average positions of the penguins in the analysis. Results of these analyses showed that weekly mean errors were lowest in June and July (33.0 ± 0.3 km) and highest in February and October (99.2 ± 0.4 km). The overall mean error was estimated to be 58.6 ± 0.8 km. Such accuracy may be surprising (cf. Philipps et al. 2004), but two factors combine to explain why this level of accuracy was achieved. First, error rates are known to be highest near the equinoxes, and these positions were removed from our data. Second, the use of a mixed-effects model would smooth estimates and further reduce error.

Mean weekly sea ice concentrations and distance to the large scale ice edge (as defined by the 15% ice concentration contour) were derived from the Special Sensor Microwave Imager (SSM/I) on board the F13 satellite of the Defense Meteorological Satellite Program (DMSP). Data were collected daily and mapped to a resolution of 25 x 25 km grid cell size (Cavalieri et al. 2006). Calculation of ice concentration was possible due to the strong contrast between microwave emissions of ice and water. Daily ice motion vector data for 2003 were obtained from the website of the Polar Remote Sensing Group of the Jet Propulsion Laboratory, California Institute of Technology (http://www-radar.jpl.nasa.gov/rgps/). We created monthly averages of daily ice flow rates and bearings to evaluate variability in these parameters in the context of penguin movements.

Weekly time of sunrise/sunset and civil twilight (sun > 6° below horizon) for each 15’ latitude were obtained from the US Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneDay.php).

We compared distance to ice edge (negative for south, positive for north), mean ice concentration values and distance to locations with at least two hours of twilight per day for actual wintering positions (n = 253; Table 6.1) with 30 randomly selected locations for each
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week (n = 630) within the potential wintering area using two-tailed t-tests. To inspect the
difference in mean ice concentrations between penguin locations and random locations we
calculated the univariate kernel density for each type of location using the Epanechnikov
kernel function (STATA: kdensity; Fig. 6.4).

After determining the mean distance from the ice edge for wintering penguins, we
calculated the minimum date that penguins reached this distance in each year (necessarily
only for penguins that did reach this distance); this was a proxy for “wintering area arrival
date.” We defined the northward migration period as winter area arrival date – Feb. 5 (=
approximate mean departure date; pers. obs.), and northward migration speed = distance from
colony on winter arrival date/northward migration period. We used ANOVA to evaluate
effects of colony and year on northward migration speed.

We calculated the maximum distance that penguins reached during winter, and the time it
took to reach that point and to return from that point (assuming an average arrival date of
Nov. 1; pers. obs) for each individual in each year. We used ANOVA to evaluate effects of
colony and year on arrival dates to maximum wintering distance, and on average speed
sustained to reach and return from maximum wintering distance. Note that sample sizes for
statistical tests vary because not all individuals had sufficient numbers of positions calculated
for the entire migration period before battery failure.

We used mixed-effects general linear models with “id” treated as a random effect to
evaluate whether latitude, longitude, twilight period, distance to ice edge, and sea-ice
concentration varied by colony and year. Twilight hours were squared and ice concentration
values were arcsine-square root transformed in order for model residuals to comply with
assumptions of normality; other terms met model assumptions without transformation. All
statistical tests were conducted using STATA (v. 10; Stata Corp 2008). Means are presented
± standard errors.
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6.3 Results

*General migration patterns*

*At sea movements.* The migration of most Adélie penguins from Cape Crozier roughly followed a clockwise course (Fig. 6.1): (1) in February, birds migrated towards the NNE to the nearest residual pack ice (eastern Ross Sea), where they begin molt (Fig. 6.2); (2) during molt, probably resting on an ice floe for 3 wks (since they have not been observed entering the water during molt, and since there is no land in the vicinity of where these penguins were during this period), they moved northward and somewhat westward, in a pattern consistent with pack ice movement (Fig. 6.3); (3) by late fall and early winter, probably as a result of ice flow, they were located in the pack-ice in the vicinity of the continental shelf break; (4) subsequently they moved farther north, occasionally visiting the Balleny Islands Polynya but otherwise remaining relatively near the large-scale ice edge, which generally occurs between the Antarctic Circle and the ACC southern boundary; once out of the Ross Sea they would become entrained in the Ross Gyre (see Figure 1 in Jacobs et al. 2002), which would prevent them from being advected much further away from Ross Island (Fig. 6.1); (5) by August they moved with the ice eastward along the ice edge; and (6) in late September and October they moved south and then west to return to their breeding colonies on Ross Island. The general pattern of movement for penguins from Cape Royds was similar, tending closer to the Victoria Land coast (though not always), finally reaching the large scale ice edge, on average somewhat west of most of the individuals breeding at Crozier (see “Wintering Areas” below), and then movement east and south against the flow of ice in the spring (Fig. 6.1, 6.3).
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**Figure 6.1.** (Next 3 pages). Penguin locations and sea ice concentration and extent for February - October, 2003-2005. Penguin locations are excluded for March and September due to inaccuracy in GLS positions near equinoxes (see text). Sea ice concentration was derived from the Special Sensor Microwave Imager on board the F13 satellite of the Defense Meteorological Satellite Program. Black is ocean, light colors represent sea ice (lighter = higher ice concentration). Orange circles are Cape Crozier penguins, blue crosses are Cape Royds penguins as determined by GLS tags. The average southern boundary of the Antarctic Circumpolar Current is shown near the top of each image, along with the Antarctic Circle (more northerly latitude line) and the latitude of zero winter twilight (72.7° S). Ross Sea shelf break is indicated with solid white line (2000 m isobath), and the average location of the Balleny Island polynya is indicated with gray oval with cross-hatching (based on combined winter sea-ice data 2003-2004). The Ross Ice Shelf is at the center of the bottom of each image. Base map layers are from British Antarctic Survey (1998). Sea ice data are from the Special Sensor Microwave Imager on board the F13 satellite of the Defense Meteorological Satellite Program, 2003-2005.
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**Figure 6.2.** Adélie penguin positions in relation to sea ice (15% or greater ice concentration indicated by cross-hashed areas) in the post-dispersal/pre-molt period, late January to late February, 2004-2007. Penguins from three colonies (Capes Royds, Crozier, and Hallett, n = 11 individuals total) in the Ross Sea were tracked using satellite transmitters (PTTs) until batteries failed or PTTs were molted off with feathers. Each color for penguin locations matches color for sea ice during February of the same season (excluding February 2007 for which we did not have sea ice data). In general, penguins traveled east-northeast or northeast, usually towards the edge of the pack ice upon leaving the colony. Base map layers are from British Antarctic Survey (1998). Sea ice data are from the Special Sensor Microwave Imager on board the F13 satellite of the Defense Meteorological Satellite Program, 2003-2005.

**Trip length.** The mean trip length (including all meanders) for all years was 12,760 ± 468.9 (SE) km per bird per year (n = 41, range 8,539 - 17,600). Trip lengths varied annually ($F_{2,27} = 29.65, P < 0.0001$) but not by colony ($F_{1,27} = 0.08, P = 0.78$). In 2003 penguins made longer trips than in 2004 and 2005 ($P < 0.0001$). Maximum great circle distance that penguins journeyed from home colonies averaged 1722 ± 66.3 km (n = 41, range 946 – 2552 km) and varied by year ($F_{2,38} = 4.96; P = 0.01$) but not by colony ($F_{1,38} = 0.55, P = 0.46$).

**Traveling speed.** Penguins reached their first wintering locations mid to late June each year (mean June 20 ± 1.7 d) and reached their maximum distance from colonies in mid July.
6. Migration routes, timing, and wintering areas

to early August (mean July 22 ±11.9 d). Penguins traveled more rapidly while returning from their maximum wintering distance than they did reaching this distance (33 ± 4 vs. 15 ± 2 km/d, respectively; \( t = -3.93, P = 0.0001 \)). Travel speeds to and from this distance did not vary by colony or year (all tests: \( P > 0.10 \)). They were also faster returning from their maximum distance than they were arriving to their first wintering location (10.35 ± 0.40 km/d). Penguins traveled northward to their first wintering locations more swiftly in 2003 than in 2004 or 2005 (12.34 ± 0.60 vs. 9.52 ± 0.41 and 9.21 ± 0.58 km/d, respectively; \( F_{2,30} = 11.22; P = 0.0003 \)) but no colony effect was evident (\( F_{1,30} = 1.42; P = 0.24 \)).

**Figure 6.3.** Monthly average ice flow vectors for March, June, and September 2003 (the last year for which data are available) obtained from the Polar Remote Sensing Group of the Jet Propulsion Laboratory. Arrow size represents speed of ice movement (larger = faster), direction represents bearing. Base map layers are from British Antarctic Survey (1998).

**Wintering Areas**

Overall mean latitude of wintering positions for Crozier penguins was 68.81° S ± 0.50 (n = 26) and for Royds penguins was 68.29° S ± 0.59 (n=15). Mean longitude for Crozier penguins at 175.29° W ± 1.87 was quite disparate from that of Royds penguins, 176.44° E ± 2.86 (note E / W difference). Latitude was significantly affected by year (\( Z = -4.59, P < 0.0001, \) Table 6.2) but not by colony \( Z = 1.31, P = 0.19 \)) whereas longitude was significantly affected by colony (\( Z = -2.76, P = 0.006 \)) but not by year (\( Z = 1.73, P = 0.08 \)). Despite the large spatial spread in wintering locations and the relatively smaller sample size from Cape
Royds, in all years Royds birds wintered west of Crozier birds (mean of 8.27° difference; Fig. 6.1, 6.4).

Arrival week to first winter location was most commonly between 11 and 17 June and varied among years (week 23 in 2003 and week 25 in 2004 and 2005; $F_{2,29} = 15.16, P < 0.0001$) but not colonies ($F_{1,26} = 2.88, P = 0.10$). Arrival date to maximum distance from colony averaged 22 July ± 11.92 d, not consistently varying among colonies or years ($F_{3,38} = 0.56, P = 0.64$).

**Characteristics of Wintering Area**

**Ice Extent and Concentration.** — Ice extent in the combined potential penguin wintering area varied annually, with 2003 having the largest extent in March - June, 2004 being intermediate and 2005 the lowest (Fig. 6.1). Maximum ice extent was reached earliest in 2003 and latest in 2005. Ice concentration at random locations in the penguin wintering area was highest in 2003 (80.9 ± 1.3 %) and lower in 2004 and 2005 (75.0 ± 1.5 % and 75.5 ± 1.5 %; $F_{2,627} = 4.87, P = 0.008$).

Ice concentrations where penguins were located were approximately the same as at random locations, 79.2 ± 0.8 % vs. 77.1 ± 0.86 % ($P = 0.16$). Penguins were not found in locations with either 100% ice cover or 0% cover (Fig. 6.5). The overall kernel density of penguin location by ice concentration implies that penguins preferred ice cover between ~75 and 85%, whereas random locations reached highest density between 80 and 90% (Fig. 6.5).

We did not detect a difference in ice concentration at wintering locations by colony ($n = 253$ positions for 41 individuals, $Z = 1.09, P = 0.28$) or by year ($Z = 1.52, P = 0.13$; Table 6.2).

**Distance to ice edge (15% ice concentration contour).** — Penguins almost never ventured north of the large-scale ice edge (4 of 253 weekly positions = 1.6%), whereas random points were more often located north of the edge (i.e., in open water, 31 of 630 positions = 4.9%). Among positions north of the ice edge, penguins averaged only 17.7 ± 6.5 km while random
points averaged 89.5 ± 11.5 km ($P = 0.03$). Taking the entire potential wintering area into account, penguins averaged 510.4 ± 14.6 km from the ice edge while random points averaged 619.5 ± 16.4 km ($P = 0.0001$).

Distance to the large-scale ice edge did not vary by colony ($Z = 0.40$, $P = 0.69$), but did vary by year ($Z = -3.96$, $P < 0.0001$; Table 6.2), with 2003 having the shortest distances and 2005 the longest.

*Distance to daylight, amount of light available.*— Winter penguin positions averaged 533.8 ± 18.0 km north of the latitude of zero twilight (this latitude was calculated separately for each week since it changes with date), 121 km further north from this line than randomly generated points ($P < 0.0001$; Fig. 6.1). They averaged 52.6 ± 18.0 km south of the latitude of zero day-length, so sunrise/sunset was not an important determinant of wintering location, while the availability of twilight was. Penguins’ positions averaged 1.27 ± 0.10 hrs of daylight and 5.07 ± 0.10 hrs of twilight, compared with 1.41 ± 0.07 and 4.16 ± 0.11 hrs (respectively) for random locations. One individual had 4 weekly positions calculated as being south of the latitude of zero twilight, another had 2 weekly positions , and two others had one week each. All of these positions were within 125km of the latitude of zero twilight, and most were within 100km. The remaining 37 individuals spent all of their time in locations with at least some twilight.

The amount of twilight available to wintering penguins varied by year ($Z = -4.72$; $P < 0.0001$) but not by colony ($Z = 1.32 P = 0.19$). Penguins experienced 0.94 and 2.03 fewer twilight hours in 2004 and 2005 than 2003, respectively (i.e., between June 1 and July 31 each year; Table 6.2).
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6. Migration routes, timing, and wintering areas

FIGURE 6.5. Characteristics of penguin wintering locations (June – July, 2003 – 2005). (A) Ice concentration for 253 penguin locations compared with 630 random locations. (B) Distance from latitude of zero twilight.

A.

B.
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6.4 Discussion

*Ocean, ice and biological boundaries*

Several factors appear to affect penguin migratory and winter movements: 1) annual sea ice motion and extent; 2) the seasonal shortening and lengthening of daylight; 3) the location of polynyas; 4) the location of the rich waters of the Antarctic Slope Front (Ainley and Jacobs 1981, Jacobs 1991); and 5) differences in timing of departure from the breeding colony. Sea ice dictates the maximum and mean latitudes where Ross Island penguins will spend midwinter. As noted by Clarke et al. (2003), and confirmed by our study, oceanic gyres, especially during molt when the birds are moving passively on an ice floe, determine much of the migration route.

Ross Island penguins face the greatest distance of any Adélies between their breeding colony and the vicinity of the Antarctic Circle, the location where sufficient light and divergent sea ice are reliably available during mid winter, a distance of 16° (1778 km) latitude. In contrast, Adélie penguins studied at Prydz Bay, Princess Elizabeth Land (69°S; Clarke et al. 2003), Anvers and the South Shetland Islands (62-64°S; Fraser and Trivelpiece 1996) breeding close to if not north of the Antarctic Circle, would need to travel only as far as the nearest divergent sea ice. That means for Prydz Bay birds about 5° latitude north; for Anvers Island birds about 3° latitude south; and for South Shetland birds, about 10-15° longitude southeast (equivalent distance to about 4° latitude). Therefore, as currently there are no Adélie penguin colonies south of 64°S in the Weddell Sea (Woehler 1993), the Ross Island penguins make the longest migration of this species, traveling as far as 17,600 km round trip between autumn and spring.

Our results are consistent with a previous study showing that displaced penguins from Ross Island immediately headed NNE (Emlen and Penney 1964, Penney and Emlen 1967), as well as with the study by Davis et al. (1996, 2001), who tracked post-molt penguins from Cape Bird, Ross Island (77°S), and Cape Hallett, Victoria Land (72°S) and showed that in
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each instance (n = 3) the birds wintered near the Balleny Islands. In the latter study, all the
birds were among a minority of birds that had molted on land at the colonies and thus had a
relatively late start on migration. The difference in timing and direction of departure between
birds in our study (pre-molt) and in Davis et al. (1996, 2001) (post-molt) is probably due to
difference in ice conditions encountered by the two groups. The initial NE direction of the
pre-molt birds in our study might also be a way for the birds to compensate for the northwest
circulation of the Ross Sea Gyre while moving north (Penney and Emlen 1967, Ainley
2002a).

For Ross Island penguins, polynyas may provide important “stepping stones” on the way
to the outer edge of the pack ice, especially the Pennell and Ross Passage polynyas (see
Jacobs and Comiso 1989), which are located along the autumn migratory route, and the
Balleny Islands polynya, one of only a few polynyas in the Antarctic that is not along the
continental coast and lies closer to the large-scale ice edge. In the autumn and winter, these
stretches of open water are likely to be profitable feeding areas – though little is known about
the mid- to upper-trophic level ecology of these polynyas (see Smith and Barber 2007).

Timing of departure at Cape Royds is lagged by a week or more compared to birds at
Cape Crozier. Unique to Cape Royds, at such a high latitude, about one-third or more of the
population also molt at the colony (Taylor 1962). This means that departure may be delayed
by as much as a month compared to Cape Crozier. Birds that depart later are likely to
encounter more consolidated pack ice, but also a stream of relatively rapidly northward-
moving ice in the western Ross Sea (Fig. 6.3). In any case, the fact that they usually spend the
winter 8° west of Crozier penguins means that their return to Cape Royds is may more
commonly be against a stronger flow of ice than what Crozier penguins encounter (Fig. 6.3).
It also might mean that they spend their winters in the vicinity of many more penguins from
other colonies (see below), with potential consequences to food availability (Ainley et al.
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2004) and energetic expenditure (Ballance et al. 2009). However, return trip travel speeds for Royds penguins did not differ from Crozier penguins, so if they were handicapped by fighting stronger currents, they were able to compensate, potentially by expending more energy. This could help explain why Cape Royds phenology is delayed compared to Cape Crozier, and may also have negative consequences to over-winter survival (Dugger et al. in prep). We did not discover any other differences in wintering area characteristics between the two colonies, but it is possible that finer scale features important to wintering penguins were undetectable at the scale our methods permitted.

It was unexpected to find that wintering areas of Ross Island penguins were at the edge of the consolidated pack ice (and the edge of darkness), well back from the large-scale ice edge itself. This contrasts with the pattern of Adélies wintering in the northwestern Weddell Sea as reported by Ainley et al. (1993), who found that penguins were most concentrated in a belt ~100 km inside the large-scale edge where the floes are small and sea-ice cover varies weekly from sparse to consolidated, depending on wind strength and direction. Judging from the eastward gradient in longitudinal dispersion of penguins, these birds originated from colonies at the tip of the Antarctic Peninsula (Ainley et al. 1993). Assuming that Ross Sea penguins could also occupy a habitat of relatively low ice concentration, there potentially exists a wide swath with few Ross Island penguins between the 75-85% ice cover, where we found them wintering, and the 15% ice edge farther north. One factor that could help explain this pattern, and the differences from that of the Weddell Sea, is the probable unusually high density of penguins in these waters. Thirty percent of the world’s population of Adélie penguins (i.e., 1.5 million breeders, plus non-breeders) are associated with the northern Victoria Land colonies (e.g. Cape Hallett north to Cape Adare) compared to fewer penguins found over a much larger area in the western Weddell Sea (1.1 million breeders) from the South Shetlands, South Orkneys, and northern Antarctic Peninsula coast (see Woelher 1993). In other words,
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we hypothesize that the Ross Island/southern Victoria Land penguins (0.75 million breeders) might winter farther north were it not for the probable presence of huge numbers of penguins from northern Victoria Land already wintering there, since we have shown that penguins adjust their foraging areas in response to both inter- and intra-specific competition (Ainley et al. 2004, Ainley et al. 2006). However, it is also possible that the Ross Island penguins simply try to stay as close to their home colonies as possible given light and ice conditions, reducing the amount of time and energy required to return for breeding. In addition, they appear to remain as long as ice conditions allow in the vicinity of the Ross Sea continental slope and the Antarctic Slope Front, an exceeding rich area (Ainley et al. 1984). No studies on the migration of Adélie penguins in northern Victoria Land have been conducted to address these hypotheses.

In years of more extensive ice, the zone of consolidated ice shifts north (sea ice extent and sea ice concentration co-vary at the large scale; Jacobs and Comiso 1989, Stammerjohn et al. 2008), and, as we observed, shift the wintering area of Ross Island penguins farther north as well. This would move them away from the Slope Front and closer to the ACC Southern Boundary, across which there is less food available (see Introduction), and perhaps also adding to the density of the northern Victoria Land wintering penguins.

**Astronomical boundaries**

Our finding that the penguins are limited by the availability of twilight, and not necessarily daylight, is not inconsistent with the findings of Emlen and Penney (1964) and Penney and Emlen (1967), who found that Adélie penguins’ navigational ability is challenged by the lack of sunlight. As they and others have noted (summarized in Ainley 2002a), penguins remain in place where they have no geographic navigational cues and when the sun is not shining. The slow northward migration of Ross Island penguins in our study is likely the result of being advected with the ice upon which they spend most of a day, rather than swimming and actually navigating. The fact that the penguins travel much more quickly when going south
6. Migration routes, timing, and wintering areas

during the spring migration, much faster than ice motion, is consistent with movement guided by sun navigation.

However, Adélies (and all penguins) require some light in order to forage – though apparently less than is required for navigation. Wilson et al. (1993) found that Adélies made most of their foraging dives to depths where there was at least 1 lux of light available, and that foraging depth and success were much lower during the night than during the rest of the day. The range of light available at the surface during civil twilight ranges from 3.4 to 400 lux (Bond and Henderson 1963), so some shallow diving would be possible even at the darkest end of this range, and prey likely migrate closer to the surface during darker hours (Wilson et al. 1993, Fuiman et al. 2002).

**Migration and the millennial scale of sea ice variability**

Adélie penguins possess enough genetic and phenotypic plasticity to indicate that they may be able to adapt to environmental changes at a millennial (1000-yr) time scale (Shepherd et al. 2005), although rapid declines over the past 50 years in the vicinity of the Antarctic Peninsula, South Shetland Islands, and South Orkney Islands (Forcada et al. 2006, Ducklow et al. 2007, Hinke et al. 2007) show that they may not be able to adapt to more rapid changes to their environment. This adaptive capability at the longer time-scale may have evolved as a result of living in a dynamic sea ice environment, where even small climactic changes can trigger large-scale alteration of ice thickness and extent (Parkinson 2002, Stammerjohn et al. 2008).

The ability to migrate over the long distances exhibited by Ross Island Adélie penguins may be an ongoing adaptation in the evolution of this species. At the LGM (~19,000 yBP) the West Antarctic Ice Sheet (WAIS) covered most of the Ross Sea, and began to recede ~12,000 yBP (references in Ainley 2002a, Emslie et al. 2007). Given that the Ross Sea Adélie penguin has a genome that differs from members of this species in all other regions (Roeder et al. 2001), a Ross Sea colony probably existed during the LGM. Ainley (2002a) proposed that
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Cape Adare was the likely location, as its location was just north of the WAIS ice front, and sediment cores from the vicinity indicate an open sea ice environment (Thatje et al. 2008). Moreover, Cape Adare has been free of land ice for ~16,000 y (Johnson et al. 2008), i.e. before retreat of the WAIS across the Ross Sea began. Early colonies may now be underwater, as a result of sea level rise since the LGM (an option in data interpretation left open by Emslie et al. 2007). Regardless, any migration during the LGM from colonies in low-latitude Antarctica must have been similar to those of today, as described by Clarke et al. (2003) or Fraser and Trivelpiece (1996). Beginning about 12,000 yBP, the WAIS began to withdraw south, exposing new, suitable nesting habitat along the Victoria Land coast. Adélie penguins colonized the Victoria Land coastline successively southward (Emslie et al. 2007), breeding further and further from the large-scale winter ice edge, the Antarctic Circle, and winter daylight. Whether or not it would be possible for this species to colonize terrain even farther south of the current WAIS boundary, were it available, remains a question. Such a feat may be unlikely as penguins are limited by the amount of time required for breeding and migratory movement within the amount of daylight available; the penguin breeding effort at Royds is significantly shorter than at colonies farther north (Ainley 2002a). Adélies can swim fast enough to make such lengthy journeys if they are not handicapped by adverse ice conditions or a lack of sunlight by which to navigate.

*Migration and the centennial/decadal scale of sea ice variability.*

Climate change previously has generally taken place on millennial or geologic temporal scales, thus giving species time to evolve the necessary behavioral and physiological adaptations to survive (e.g. Roeder et al. 2001, Forcada et al. 2008). In recent decades, as in past instances of abrupt climate change (e.g. Mayewski et al. 2009), the rate of climate change has increased (Tans 2007). One result, a consequence of the Southern Annular Mode having become mostly “stuck” in its “positive” phase (Stammerjohn et al. 2008), is that sea
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Ice extent and persistence have been notably increasing in the Ross Sea sector but decreasing in the SW Atlantic sector.

Such drastic changes in habitat are challenging the breeding and migratory phenology of Antarctic seabirds (Barbraud and Weimerskirch 2006, Forcada et al. 2008), and potentially, as we show here, Adélie penguins as well. Before the 1980s, Adélies breeding on Anvers Island, Antarctic Peninsula (64° S), did not migrate, remaining instead in the pack ice along the coast and periodically visiting the colonies throughout the winter (Holdgate 1963, Parmelee et al. 1977). Since then their numbers have declined sharply (Ducklow et al. 2007), coincident with the gradual reduction in sea ice extent as well as persistence in that region (Stammerjohn et al. 2008). Indeed, along the NW coast of the Antarctic Peninsula sea ice is retreating 31 d earlier and advancing 54 d later than it did just a few decades ago. Declining numbers have been observed in the South Shetlands and South Orkney Islands as well (Forcada et al. 2006, Ducklow et al. 2007, Hinke et al. 2007). With the winter pack ice edge now at a higher latitude, Adélie penguins that continue to breed on Anvers Island have begun to migrate south, not north like Ross Island birds; a favored wintering area is the polynya in Marguerite Bay (66° S) (Fraser and Trivelpiece 1996), which means that migration is increasing with southward receding sea ice. If the current trend of diminishing winter ice continues, Adélie penguins will ultimately be constrained in their southward migrations by the availability of light.

In the Ross Sea sector over the past few decades, in contrast to the NW Antarctic Peninsula, sea ice extent has increased (Zwally et al. 2002) and the sea-ice season has lengthened (Parkinson 2002). Stammerjohn et al. (2008) have shown that sea ice is retreating 29 d later and advancing 31 d earlier than it did a few decades ago. At the same time, however, coastal polynyas have been increasing in extent and persistence (Parkinson 2002). Thus, on the basis of our findings, while breeding and migratory effort will be facilitated by
6. Migration routes, timing, and wintering areas

the persistence of polynyas, migration pathways likely are being altered by the earlier growth of sea ice at the time of penguin molt. The result may be that an increasing number of penguins from Ross Island will encounter heavier ice earlier on their migration, possibly increasing the occurrence of the “Royds model” of migration: later migration with its tendency to advect further west, in closer proximity to millions of Northern Victoria Land penguins and facing a longer return journey in the spring. Over the next 40 years, sea ice extent in the Ross Sea sector is predicted to decrease slightly from current levels (Ainley et al. in press), perhaps increasing penguin trophic competition as the sea ice perimeter shrinks.

In summary, the migratory behavior and routes of Adélie penguins are in a state of flux. While the species apparently has contended with this successfully throughout its 3 million year history, as ice ages have come and gone with the coincident changes in breeding and sea ice habitat, the current rate of habitat change may be unprecedented for this species. We predict that their response to the large-scale decrease in sea ice projected by climate models will be affected by the availability of light before the pack ice disappears.
Chapter VII: Conclusion

**Plate 7.** Adélie penguins make their way to and from the ocean across fast ice in front of Cape Crozier *(photo: G. Ballard).*
7. Conclusion

In this dissertation I have presented an overall context and several detailed analyses of Adélie penguin behavior and their physical and biotic environment, all related to processes influential in determining why some populations are larger than others, why some grow rapidly at times, and why others stay stable or shrink. Although Adélies are one of the best-studied wild bird species in the world, much remains to be done. In this chapter I summarize some of the key findings of my research, limitations of the studies so far, and highlight priorities for future research.

7.1 Summary of main findings

Results from analyses of the trade off between parent and offspring investment (Chapter 3) indicate that Adélies are able to regulate their condition in response to environmental and physiological factors, with consequences to the amount of food delivered to young and fledging mass. These results support “individual optimization” hypotheses framed about seabirds by Goodman (1974) and birds in general by Nur (1987). I showed that in a system where only one habitat type is available (neritic) there is no consistent pattern of bimodal trip durations, in contrast with several studies where more than one habitat was available, and confirming broader applicability (i.e., to non-flying seabirds) of hypotheses largely framed in the context of flying seabirds by Weimerskirch and others (Weimerskirch et al. 1997, Weimerskirch 1998).

I also showed that colony size positively correlated with foraging trip duration and metabolic rate and energy expenditure, that the metabolic rate while foraging may be approaching an energetic ceiling for birds at the largest colonies, and that total energy expended increases with trip duration, uncompensated by increased mass gain (Chapter 5). These patterns of energetic demands being higher at larger seabird colonies support hypotheses made for birds in general by Brown and Maurer (1987) and are substantiated by a
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few other empirical seabird studies, although there are not many who have yet investigated these correlations directly (see review in Ballance et al. 2009). A competition-induced reduction in prey availability appears to result in higher energy expenditure for birds foraging in the halo around large colonies, and to escape the halo a bird must increase its foraging distance (cf. Storer 1952, Ashmole 1963). Ultimately, the total energetic cost of a trip determines the maximum successful trip distance, as on longer trips food acquired is used more for self maintenance than for chick provisioning (cf. Ainley et al. 1998, Ballard et al. in review 2). When the net cost of foraging trips becomes too high, with chicks receiving insufficient food, chick survival suffers and subsequent colony growth is limited.

All available evidence supports the idea that (at the largest colonies) prey depletion due to competition is the primary factor determining adult condition and, ultimately, chick survival, and therefore limiting the size of the largest colonies, confirming hypotheses first framed by Malthus (1798) for animals in general, and Storer (1952) and Ashmole (1963) for seabirds more specifically. However, higher breeding quality individuals foraged more efficiently than lower quality individuals under harsh environmental conditions and when offspring needs were higher, therefore acquiring higher net energy profit to be allocated to reproduction and survival (Chapter 4). These results imply that harsh environmental conditions might select breeding individuals on the basis of their foraging ability, which is of course not a new idea (cf. Darwin 1859) but direct evidence for which is hard to acquire in many systems (but see Grant and Grant 1993, Reznick et al. 2004 for examples in birds, and fish, respectively). Adélie penguins in our studies had important phenotypic plasticity, suggesting that some portion of the population is capable of coping with large scale variability in their physical and biological environment, variability that is likely to be associated with climate change and ultimately to the species’ evolution.
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Understanding variability in non-breeding season dynamics of birds has important conservation and life-history implications, since perturbations to any component of the ecosystem considered across the entire life cycle of a species can have deleterious effects at a population or sub-population level. Further, important selective pressure can be present for some populations and not others, and diseases can spread among individuals from various populations if these populations are in contact at any part of the annual cycle (reviewed by Webster et al. 2002). Also, the timing of arrival on breeding grounds or wintering areas can impact the likelihood of an individual surviving or reproducing successfully (e.g. Marra et al. 1998). I showed that there are potentially important differences in the migration and wintering strategies of penguins from different colonies (Chapter 6), linked primarily to variation in the physical and biotic environment encountered by penguins from the different colonies. Penguins at Royds (smallest colony) wintered significantly west of penguins from the largest colony, indicating that their return to Ross Island may typically be against a stronger flow of ice than what Crozier (largest colony) penguins encounter. It also might mean that Royds penguins spend their winters in the vicinity of many more penguins from other colonies, with potential consequences to food availability, energetic expenditure, and survival. The advent of miniaturized GLS tags has enabled researchers to directly investigate variability in migration routes and rates, and location of wintering areas in a wide range of species including songbirds (Stutchbury et al. 2009), tuna (Block et al. 2001, 2005) geese (Eichhorn et al. 2006) and turtles (Avens and Lohmann 2004), but other techniques, such as the use of stable isotope analysis (Marra et al. 1998) have been employed with success for more than 10 years.

These migratory and wintering processes, in combination with the consequences to philopatry of dramatic fluctuations in the physical environment of Cape Royds during the breeding season (reviewed in Chapter 1; also see Shepherd et al. 2005) highlight the
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important role that such variability can play in constraining population size and growth, particularly in smaller populations. This is a concept that builds off of similar ones originally proposed for explaining spatial patterns in species richness of animals in general by MacArthur and Levins (1964).

Finally, because the latitudinal range of the Adélie penguin spans ~22°, a wide variety of migration strategies is to be expected within the species. Penguins from northern colonies may not migrate, but due to the high latitude of Ross Island colonies, these penguins almost certainly undertake the longest migrations for the species – the question is, how far can this migration distance be extended? Adélies rarely traveled north of the main sea ice pack, and used areas with high sea-ice concentration, ranging from 75-85%, about 500 km inward from the ice edge. They also used locations where there was some twilight (2-7 hr with sun > 6° below horizon). If sea ice extent in the Ross Sea sector decreases, as predicted by climate models, we can expect change in wintering areas, the location of which ultimately may be limited more by the availability of adequate light for visual foraging rather than the availability of suitable pack-ice (see further discussion below under “Non-breeding season”).

7.2 Limitations of the study

Inevitably there are many things that have not yet been determined, and the more that is learned, the more we can see how much we do not know. Here I identify and then elaborate on seven limitations of the work that has been accomplished to date, and place these limitations in the context of recent developments in other research programs: (1) I have no means of directly assessing prey availability in the penguin foraging area. (2) I do not yet have complete knowledge of the variation in population size among colonies and years. (3) I have not yet linked chicks to parents directly in terms of food delivery, growth, and subsequent survival. (4) I have not untangled the potentially confounding effects of age and
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experience on foraging strategy and success from our measures of adult condition and quality. (5) The methods that I have employed for measuring foraging behavior at sea (diving, foraging locations) have relied on relatively bulky devices that will undoubtedly become more and more streamlined and provide more accurate location data with less interference to the penguins. (6) Knowledge of the non-breeding season is still extremely limited (7) The ability to employ experimental manipulations in this system is limited by ethical, logistical, and financial considerations, but there are limits to the degree of inference (e.g. of causality) without conducting experiments. I show that while these are limitations to the work, they are limitations that have been faced by others researching similar topics across multiple taxa, and addressed using similar methods to the ones I have employed.

1. Prey Accessibility.

The idea that marine predator diet reflects prey availability in the environment is the basis of many of my conclusions, and at the basis of the Ecosystem Monitoring Programme of the Convention for the Conservation of Antarctic Marine Living Resources (Agnew 2004), not to mention several other studies (Furness and Birkhead 1984, Lewis et al. 2001, Suryan and Irons 2001, Ainley et al. 2003a, but see: Ainley et al. 2003b). While I assume that penguins are foraging on the prey that is most available to them, that may not be the case. For example, it may be that penguins prefer to feed their chicks krill, or that they prefer to eat fish (for themselves) at some stages of their annual cycle, potentially because of differential nutritional quality. The idea that prey depletion is importantly limiting the size of the largest colonies will not be completely verified without direct sampling, but could potentially be bolstered by experiments of prey selection by captive (possibly temporarily-captive?) Adélie penguins. At-sea sampling in the natural environment requires ship-based work, and at any latitude this is extremely expensive. At high latitudes in areas of heavy sea-ice it is even more
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expensive due to the need for ice-strengthened hulls or icebreakers (US$25K - $75K per day, pers. obs.).


In many ways, simply knowing that Cape Royds is a small colony, Cape Bird and Beaufort Island are medium-sized colonies, and Cape Crozier is a large colony provides an elegant framework by which I can evaluate the effects of colony size on various parameters of Adélie penguin life history. However, as I showed in Chapter 5 (also see Ainley et al. 2006, Ballance et al. 2009), there is important annual variability in population size within colonies which can provide more detailed information, particularly in the absence of longer term data collection (as in the case of the energetics study, where the methodology is prohibitively expensive to continue beyond 2 or 3 years). Further, the size of the colonies appears to be far more variable than previously assessed (Chapter 1) and it will be fascinating to learn if the Cape Crozier colony has reached a significantly larger size than ever previously recorded, which seems likely (pers. obs). Fortunately, the necessary data exist in the form of aerial photographs (Lyver et al. unpubl. data, Landcare Research, NZ), they just remain to be counted (an extremely tedious task). It seems possible that new computer methodologies will make counting penguins in these photographs far easier in the future (Culverhouse 2007, P. Lyver pers comm., G. Ballard unpublished), although simply counting manually, but on a computer instead of with photographic prints would be an improvement (Robertson et al. 2008).

3. Linking chicks to parents

I assume that chick growth rates for the colony overall are, on average, representative of what is happening at the individual level. This is probably true, on average, and the technique has
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been employed previously (e.g. Ainley et al. 2004). However, now that important individual heterogeneity in foraging efficiency has been demonstrated (Chapter 4), it will be very interesting to understand if the more efficient parents are able to raise larger chicks, and if those chicks are more likely to recruit into the breeding population, and to investigate whether these traits are heritable (see below). The reason this has not been done previously is because measuring chicks repeatedly causes significant disturbance, and is likely to impact their growth and subsequent survival in ways that may not be able to be controlled for. Additionally, methods of marking Adélie penguins for subsequent assessment of survival rates are prone to either high error rates (e.g. PIT tags – because individuals do not necessarily recruit to the place where a PIT tag reader can be installed) or impact to survival (e.g. flipper bands; Gauthier-Clerc et al. 2004, Dugger et al. 2006). New methods are required to repeatedly measure chicks and assess their survival. For example, a photogrammetric approach may serve well (Chiari et al. 2008)

4. Effects of age and experience

While I have good indications that there is heterogeneity in condition and quality of Adélie penguins (Chapters 3 & 4), I do not know the reasons for this variability. There are several possibilities, not the least of which are age and experience, but also including physiological factors. Age is extremely important in determining breeding success in Adélie penguins (Ainley et al. 1983), and therefore I expect that there is a link between the ability to regain condition, forage efficiently, and the age of an individual. At the same time, some individuals consistently outperform most others in terms of breeding success, implying that age is not the only factor (since it is very unlikely that these individuals were the only ones in a given age cohort and since new individuals were added each year). Further, it may be that age only has an effect in certain circumstances, such as when age brings experience with higher
7. Conclusion

competition or more challenging environmental conditions, or both. I have not previously had a known-age population with which to evaluate these ideas.

5. Instrument effects

While I have not found a direct effect of SPLASH or similar tags on foraging behavior (Chapter 4, also Ballard et al. 2001), I do expect that there could be a potentially negative effect (Bannasch et al. 1994, Ropert-Coudert et al. 2007), and I have therefore moved tags among individuals and used methods of attachment designed to minimize such effects (Wilson and Wilson 1989). Negative effects might only become apparent after repeated sampling of the same individual, or with a larger sample size (i.e., more individuals within each week of the breeding season) than I have previously collected. Also, the tags are very expensive and to achieve suitable sample sizes, moving tags among individuals is prudent. This situation can be improved when smaller and less expensive tags that collect both position and diving data are available. Meanwhile, it is likely that precise position information is less valuable in this study system, since the foraging habitat does not appear to vary substantially and I can link foraging trip duration directly to distance traveled (G. Ballard, unpublished data). In that case, dive behavior is more important, and can be collected from smaller devices (and without antennae). On the other hand, ultimately I will want to be able to match locations with diving and foraging behavior to determine if there are any physical environmental covariates determining foraging locations (cf. Bost et al. 2009a), and hopefully this will be facilitated by improvements in the resolution of remotely-sensed data for the region in addition to more precise location data from smaller tags.
6. **Non-breeding season**

The development of GLS tags has given us the ability to track animals over their entire annual cycle, because they are small enough to be attached for long-duration deployments. However, these devices provide a fairly coarse estimate of position, and (in the case of the tags available for my use so far) do not indicate diving or swimming behavior, although techniques for refinement are under continuous development by researchers investigating a wide array of taxa, from tuna to songbirds to albatrosses (Sibert et al. 2003, Phillips et al. 2004, 2005, 2006, Stutchbury et al. 2009, Bost et al. 2009b). Inclusion of depth, temperature and wet-dry sensors will allow the interpretation of activity patterns over long deployment periods, and some researchers have already been able to progress in these areas, including the use of temperature to assist with location accuracy (Bost et al. 2009b).

Additionally, GLS tags rely on some amount of twilight to calculate a position, so if penguins do spend part of the year in total darkness their positions would be unknown (although the fact that they were unknown would at least give us a minimum latitude, and positions were consistently derived for the entire deployment periods of all individuals thus far). It remains mysterious how Adélie penguins can dive to depths of complete darkness and forage there successfully, yet require at least some amount of twilight for their wintering locations, though possibly only for navigation (Penney and Emlen 1967, Wilson et al. 1993, Ballard et al. in review 1). This is in contrast with other seabirds, such as cormorants, which seem to require at least some light underwater for foraging (Grémillet et al. 2005, White et al. 2008). Without finer resolution location assessments and the ability to determine foraging behavior throughout the full annual cycle, much will remain unknown about the limitations of these animals.
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7. Observational data, experimental design, and statistical approaches
Much of traditional ecological research has relied on an expert-centered parametric analysis process. Many variations on this process have been employed, but all rely primarily on the investigator having extensive knowledge of the system of study, allowing a scientist to identify a question, formulate specific hypothetical answers, and then conduct an experiment specifically designed to establish the validity of the hypotheses. However, for many studies in ecology, reliance on this technique limits the capability to replicate the spatial variability and temporal stochasticity inherent in nature, since the efforts required to address these patterns are often logistically, financially, and/or ethically constrained (Hurlbert 1984, 2004, Hargrove and Pickering 1992).

While reliance on observational data to draw conclusions in ecology often offers limited capabilities for understanding causality, information theoretic and machine learning techniques coupled with large datasets can mitigate these limitations (Burnham and Anderson 2002, Kelling et al. in press). I have relied on a hybrid approach: extensive observational data coupled with a few opportunities to employ experimental methods (e.g. equipping parents of various quality or from colonies of greatly varying size, setting analyses in the context of whether or not a giant iceberg was present). Additionally, the use of information theory to assess various competing models enabled me to evaluate several hypothesized scenarios without relying on assumptions of ideal control and treatment tests, and the use of mixed models with robust standard errors enabled me to make the most of unbalanced longitudinal data. Ideally, I will be able to further employ rigorous experimental methods to understand (especially) the effects of age, experience, and physiology on foraging strategy, breeding investment, and natural selection in this metapopulation (see below). Further, continuous deepening of analytical techniques, such as the use of random slope mixed models (Rabe-Hesketh and Skrondal 2008, Schielzeth and Forstmeier 2009) may enable more precise
7. Conclusion

estimates of effects in such experiments (although I have not found instances where this method has improved results in my work to date).

7.3 Priorities for future research:

As noted, our findings suggest that harsh environmental conditions select breeding individuals on the basis of their foraging ability (cf. Grant and Grant 1993). Given that climate changes are affecting the physical environment of the Ross Sea in profound ways (Stammerjohn et al. 2008, Ainley et al. in press) the ability of Adélie penguins to respond to these changes will likely be tested in the future.

It is a priority to investigate the effects of climate variability on Adélie penguins at multiple levels ranging from mechanisms that allow individuals to adapt to changes, to how some individuals outcompete others causing demographic heterogeneity within a population and eventually how such factors drive colony and metapopulation trends. I have begun to explore these factors, but there are several limitations to our work so far, outlined above, some of which can be addressed with methods that are currently available. Thus, I highlight four interrelated studies that could be undertaken.

1. Determine the effect of age, experience and physiology on individual foraging efficiency.

The foraging success of a marine predator and the associated benefit to reproductive performance and ultimately, population growth, is not only influenced by prey availability but also by individual attributes (Grant 1999). In Adélie penguins, parental condition affects foraging performance, which is closely linked to breeding performance, especially in challenging conditions (Ballard et al. in review 2, Lescroël et al. in review), but it is not known how morphological/physiological properties (e.g. body mass, wing length, hematological parameters), age or experience interact with, or potentially explain individual
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differences in the penguin foraging ability. Hematological parameters are important not only for their role in oxygen storage and diving performance, but also as valuable indicators of condition and health (Potti et al. 1999, Sánchez-Guzmán et al. 2004, Suorsa et al. 2004, Mathews et al. 2006, Artacho et al. 2007).

With Amélie Lescroël (Lescroël et al. in review), we have shown previously that variation in adult survival of Adélie penguins is largely explained by heterogeneity in individual quality (i.e. individuals perform differently throughout life) independent of environmental conditions (Lescroël et al. 2009). Furthermore, some individuals can mitigate costs of reproduction even under demanding conditions (Lescroël et al. 2009, in review; Ballard et al. in review 2). A closer examination of Better Breeders’ foraging tactics revealed that they dove deeper at the end of the season when intra-species competition is high and that they are more efficient foragers (higher catch per unit effort) than Poor Breeders. These differences were exaggerated during heavy ice years when foraging conditions were demanding, suggesting “harsh” conditions might favor individuals of higher foraging ability. However, it remains to be determined whether Better Breeders are better able to maintain their own condition during breeding, whether they begin the breeding season in better condition, and under what circumstances (of physical condition) Better Breeders invest “too much” in breeding effort, thereby risking their own survival (i.e., the point in Fig. 1.10, at which survival begins to decrease).

To determine the roles of age, experience, and physiological parameters in determining foraging efficiency and breeding performance, controlled experiments could be undertaken using the known age population of penguins on Ross Island. Ideally, cross-fostering of chicks among parents of various quality, and among colonies of different sizes could be undertaken (cf. Brown and Brown 2000), although moving and keeping track of penguin chicks among colonies would be very challenging (e.g. requiring helicopter transport; there may be other
7. Conclusion

locations and species with which this work could more easily be performed). Further, a WB could be set up in an area with a high density of known-age, known history (KA) individuals, thereby allowing me to assess the roles of age and quality on penguin condition and foraging efficiency (Fig. 7.1).

![Image of subcolonies at Cape Crozier Area ‘M’.

Two easily encircled subcolonies with suitable numbers of known age penguins are outlined in blue. Satellite image courtesy of New Zealand Antarctic Program.](image)

**Figure 7.1.** Potential new weighbridge subcolonies at Cape Crozier Area ‘M’. Two easily encircled subcolonies with suitable numbers of known age penguins are outlined in blue. Satellite image courtesy of New Zealand Antarctic Program.

2. **Determine the effect of age, experience, and individual quality on breeding success and survival in varying environmental and competitive conditions at the colony level.** Our long-term banding and mark-recapture work has produced a longitudinal data set that is now invaluable, for addressing these goals. With continued development of this data set I will have access to KA individuals from what is believed to be the full range of lifespan in Adélie penguins (~20 years; Ainley et al. 1983). With the current 13-year data set, Katie Dugger and I are currently investigating age-and breeding-status related survival, breeding propensity and success, and recruitment, as well as the degree to which these rates can vary among colonies and in relation to annual environmental variation (building on previous work by Dugger et al. 2006 and Lescroël et al. 2009). With the very oldest age classes gained with 5 more years of
data collection, I can also investigate longevity, senescence, and individual contribution to colony growth (as a measure of individual fitness; Coulson et al. 2006) in relation to individual quality, environmental variation and metapopulation dynamics.

I can also further explore the quadratic relationship between breeding performance (BQI) and survival observed for breeding penguins at Crozier, where fitness components (survival and reproduction) are usually positively correlated (Fig. 1.10; Lescroël et al. 2009; see also Cam et al. 2002, Link et al. 2002). In addition, the relationships between foraging efficiency and survival, reproductive success, and individual contribution to colony growth need to be assessed in order to confirm that foraging efficiency is a phenotypic correlate of individual quality that impacts fitness parameters and provide insight into phenotypic selection (Conner and Hartl 2004). For these purposes, I have a large sample of KA birds at 3 colonies for which age and breeding histories are known (e.g. 952 individuals resighted and monitored at Cape Crozier in 2008; Table 7.1).
7. Conclusion

TABLE 7.1. Summary of known-age penguins seen at Cape Crozier in 2008-2009. Summary is for Crozier-banded individuals only.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>n Banded</th>
<th>Age</th>
<th>n Seen</th>
<th>n Nesting</th>
<th>Prop. Seen</th>
<th>Breeding</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007-2008</td>
<td>1000</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>2006-2007</td>
<td>1000</td>
<td>2</td>
<td>92</td>
<td>0</td>
<td>0.09</td>
<td>0.00</td>
</tr>
<tr>
<td>2005-2006</td>
<td>1000</td>
<td>3</td>
<td>165</td>
<td>4</td>
<td>0.17</td>
<td>0.02</td>
</tr>
<tr>
<td>2004-2005</td>
<td>1000</td>
<td>4</td>
<td>132</td>
<td>31</td>
<td>0.13</td>
<td>0.23</td>
</tr>
<tr>
<td>2003-2004</td>
<td>1000</td>
<td>5</td>
<td>95</td>
<td>48</td>
<td>0.10</td>
<td>0.51</td>
</tr>
<tr>
<td>2002-2003</td>
<td>1000</td>
<td>6</td>
<td>178</td>
<td>122</td>
<td>0.18</td>
<td>0.69</td>
</tr>
<tr>
<td>2001-2002</td>
<td>110</td>
<td>7</td>
<td>12</td>
<td>12</td>
<td>0.11</td>
<td>1.00</td>
</tr>
<tr>
<td>2000-2001</td>
<td>1000</td>
<td>8</td>
<td>92</td>
<td>67</td>
<td>0.09</td>
<td>0.73</td>
</tr>
<tr>
<td>1999-2000</td>
<td>1000</td>
<td>9</td>
<td>93</td>
<td>77</td>
<td>0.09</td>
<td>0.83</td>
</tr>
<tr>
<td>1998-1999</td>
<td>1000</td>
<td>10</td>
<td>36</td>
<td>28</td>
<td>0.04</td>
<td>0.78</td>
</tr>
<tr>
<td>1997-1998</td>
<td>1000</td>
<td>11</td>
<td>35</td>
<td>25</td>
<td>0.04</td>
<td>0.71</td>
</tr>
<tr>
<td>1996-1997</td>
<td>1000</td>
<td>12</td>
<td>21</td>
<td>15</td>
<td>0.02</td>
<td>0.71</td>
</tr>
<tr>
<td>1994-1995</td>
<td>100</td>
<td>14</td>
<td>1</td>
<td>0</td>
<td>0.01</td>
<td>0.00</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>11210</strong></td>
<td></td>
<td><strong>952</strong></td>
<td><strong>429</strong></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

3. Investigate heritability of individual quality, foraging capability, and colony size preference. Do high quality parents produce high quality young? Which traits are heritable and what are the selection pressures that are driving the plasticity and expression of individual quality in a metapopulation? Do individuals whose parents are from large colonies have a genetic predisposition to recruit to large colonies (cf. Brown and Brown 2000, Møller 2002, Serrano and Tella 2007)? Within generations, natural selection will occur if there is heterogeneity in some trait among individuals (phenotypic variation) and a consistent relationship between the trait and fitness (Grant 1999). Natural selection will have evolutionary consequences if there is descent with heritability for this trait (Futuyma 1998, Fairbairn and Reeve 2001). There is growing evidence that evolutionary responses to environmental changes can be fast enough that researchers are able to witness them both in
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the laboratory and in the wild (Grant 1999, Ferrière et al. 2004, Frankham and Kingsolver 2004, Reznick et al. 2004), and it is helpful to have access to well preserved ancient DNA for the study area (Shepherd et al. 2005). Rapid microevolution may even be the norm in populations confronting environmental change (Hendry and Kinnison 1999). The Adélie penguins of Ross Island would be a perfect system with which to investigate these ideas for many reasons, including the fact that a baseline rate of microevolution for penguins in this area has been established (Shepherd et al. 2005) and because a large population of KA individuals exists. However, such a project would be very ambitious because of the need to mark hundreds of the offspring of known age individuals and, ideally, perform cross-fostering experiments, including movement between colonies, such as has been done for at least 3 species of passerines (Brown and Brown 2000, Møller 2002, Spottiswoode 2009).

4. Develop a comprehensive population model for the Ross-Beaufort Island metapopulation incorporating all the factors investigated previously. Our work so far suggests survival rates for this species are lower and exhibit much more variation than would be expected for a species with delayed maturation and low reproductive rates (Dugger et al. 2006, in prep). It is known that flipper bands can decrease survival, but also that banded penguins can exhibit very high survival rates (Gauthier-Clerc et al. 2004, Dugger et al. 2006), so it will be important to determine whether permanent emigration away from the metapopulation (4 Ross Sea colonies) is occurring. Without additional, intensive resighting efforts at other colonies not currently studied, permanent emigration will be difficult to detect. A few Ross-Beaufort island penguins have emigrated to at least 5 other Ross Sea colonies, the farthest being ~400 km away (G. Ballard, unpubl. data). To address this question, colony-specific lambda based on estimates of survival and fecundity can be compared with rates of colony-size change as calculated from annual aerial photos (see
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above). If the rates of colony-size changes do not reflect actual patterns in breeding population size from aerial photos, I can learn something about the prevalence of movements into and out of our 4-colony metapopulation. A prospective analysis comparing the effects on lambda of a given change in a demographic trait could be conducted in the context of stochasticity in the environment (Jenouvrier et al. 2009). Links could also be made between management actions such as annual Ross Sea toothfish catch or “scientific” minke whale take and penguin population viability. The result would be a model that reflects the effects of predicted changes in habitat and management characteristics on the population growth rate of this Ross Sea Adélie penguin metapopulation. Devising robust and detailed population projections based on predicted climatological and management changes would be a fitting culmination to the study.
Return to Penguin City is a movie that I helped make during the course of my graduate studies, with Lloyd Fales, Ian Gaffney, Viola Toniolo, Katie Dugger, and David Ainley. It highlights some key findings of our work for a lay audience, especially in the context of climate change effects on Antarctica.

Photo: Viola Toniolo
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