RESPONDING TO CLIMATE CHANGE: ADÉLIE PENGUINS CONFRONT ASTRONOMICAL AND OCEAN BOUNDARIES

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Abstract. 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. The latitudinal range of the Adélie penguin spans ~22°. 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. Previous work has suggested that Adélies require both pack ice and some ambient light at all times of year. Over a 3-yr period, which included winters of both extensive and reduced sea ice, we investigated migratory routes and characteristics and wintering locations of Adélie Penguins from two colonies of very different size on Ross Island, Ross Sea, the southernmost colonies for any penguin. We acquired data from 3-16 Geolocation Sensors affixed to penguins each year at both Cape Royds and Cape Crozier in 2003-2005. Migrations averaged 12,760 km, with the longest being 17,600 km, and were in part facilitated by pack ice movement. Trip distances varied annually, but not by colony. Penguins 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). We review how Adélie Penguin migration has likely changed since withdrawal of the West Antarctic Ice Sheet across the Ross Sea beginning 12,000 yBP. 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 than by the availability of suitable pack-ice.

Key words: Antarctica, Adélie penguin, climate change, geolocation sensor, migration, Ross Sea, sea ice, wintering ecology

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). Marine species that undertake polar-temperate long distance migrations include seabirds (e.g. Phillips et al. 2005), seals (e.g. McConnell and Fedak 1996), and whales (e.g.. 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° S 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 the species' 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 life at sea, coming ashore for a few months to breed during the short austral summer, although in the northern portion of its range the penguins visit colonies year round (Parmelee et al. 1977). Its southernmost colonies, which are occupied for only about 4 months a year, are 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 southern 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 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° S during the Last Glacial Maximum (LGM) to almost 78° S at present (Ainley 2002, Emslie et al. 2003, Emslie et al. 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), as is the situation for 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 (where extent and persistence are increasing) also but in the Southwest Atlantic Sector (extent and persistence are decreasing; Parkinson 2002, Zwally et al. 2002, Stammerjohn et al 2008, Turner et al. 2009). Investigating the migratory and wintering strategy of Adélie penguins would therefore reveal insights into how they have met the challenges of receding and otherwise changing ice sheets at various scales of climate change, from millennial to decadal periods.

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 2002, pp. 124-127).

Being a visual predator, Adélies 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 tags), 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 regard to use on penguins: 1) because they are very small they can be fastened to the leg rather than the back feathers, and hence 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. GLS tags have been used on seabirds (Phillips et al. 2004, Bost et al. 2009) and other long-distance migrants like songbirds (Stutchbury et al. 2009), tuna (Sibert et al. 2003), geese (Eichhorn et al. 2006), and turtles (Avens and Lohmann 2004). The use of GLS on penguins is of special interest because of the lack of data from the interbreeding period and the penguins' sensitivity to antenna-mounted conventional PTTs (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 potentially heightened during the winter season when food availability may be reduced (e.g. Lancraft et al. 1991), or when a penguin has to wear a PTT for long periods. Studies using feather-attached PTT's on Magellanic penguins (*Spheniscus magellanicus*; Stokes et al. 1998), king penguins (*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 carrying the apparatus.

Here we report results of the first use of GLS tags to track the year-round movements of Adélie penguins. 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). Annual survival rates at the smaller colony (Cape Royds; 2500 pairs) appear to be consistently lower than those at the larger colony (Cape Crozier; 150,000 pairs) (Dugger et al. unpublished data).

MATERIALS AND METHODS

At the end of the Adélie Penguin breeding seasons (end of January) of 2003-04, 2004-05, and 2005-06 we attached GLS tags to 10-20 penguins at each of two colonies on Ross Island: Cape Crozier and Cape Royds (98 total tags, 41 retrieved functioning; Table 1, Fig. 2; see also Table A1 in Ecological Archives). 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 nest 7-10 d later than those at Crozier and thus have a different annual phenology.

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 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 non-breeding period based on empirical results from this study. We were not attempting to define the precise area (e.g., by using kernel analysis) used by penguins. 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 100 km, 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-h 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. We report means ± SE. 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. Please see Ecological Archives for details.

RESULTS

General migration patterns

At-sea movements. The migration of most Adélie penguins from Cape Crozier roughly followed a clockwise course (Fig. 1 & Ecological Archives Figs. A1 and A2): 1) in February, birds migrated towards the NNE towards the nearest residual pack ice (eastern Ross Sea), where they began molt (Fig. A2); 2) during molt, resting on an ice floe for 3 wks, they moved northward and somewhat westward in a pattern consistent with pack ice movement (Fig. A3); 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 Antarctic Circumpolar Current (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 (Figs. 1, A1, A3); 5) by late winter they moved with the ice eastward along the ice edge; and 6) in late September and October they moved south and then west, returning to their breeding colonies. The general pattern of movement for penguins from Cape Royds was north through the various polynyas along the way, finally reaching the large scale ice edge somewhat west of most of the individuals breeding at Crozier (see below), and then movement east and south against the flow of ice in the spring (Figs. 1, A1, A3).

Overall, penguin movement speed was correlated with ice movement speed ($\beta = 5.45 \pm 1.18$ km d^{-1}, $Z = 4.60$, $P < 0.0001$; n = 11 individuals, 336 positions). We did not detect a correlation between penguin and ice movement direction ($r = 0.028$, $P = 0.76$), although the relationship with speed supports the concept that penguins were generally moving in the same direction as the ice.

Trip length. The mean trip length (including all meanders) for all years was 12,760 ± 468.9 (SE) km (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 also 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 date June 20 ± 1.7 d) and reached their maximum distance from colonies in mid

July to early August (mean July 22 ±11.9 d). Penguins traveled more rapidly while returning from their maximum wintering distance than they did while reaching this distance (31.71 ± 3.73 vs. 15.09 ± 1.99 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: $P > 0.10$). Penguins were also faster returning from their maximum distance than they were arriving to their first wintering location (10.35 ± 0.40 km/d; see Ecological Archives for precise definitions of terms). 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 ($F_{1,30} = 1.42$; $P = 0.24$).

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 6.1) 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. 2).

Arrival week to first winter location was most commonly between 11 and 17 June and varied among years (week 23 in 2003, 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 least (Figs. 1, A1). 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% or 0% ice cover (Fig. 3). 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. 3).

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 1).

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 south of 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 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, 121 km further north from this line than randomly generated points ($P < 0.0001$; Fig. 3). 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 h of daylight and 5.07 ± 0.10 h of twilight, compared with 1.41 ± 0.07 and 4.16 ± 0.11 h (respectively) for random locations.

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 (Table 1).

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° latitude (1778 km). 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 each instance (n = 3) the birds wintered near the Balleny Islands. In the latter study, all the birds were among a very small minority of birds that had molted at the colonies and thus had a relatively late start on migration, as was true of the Royds birds in our study. 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 2002).

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 full of life – including penguins, seals, whales, and their prey – though little is known about the mid- to upper-trophic level ecology of these open areas in the Antarctic ice pack (see Smith and Barber 2007).

Timing of departure at Cape Royds is delayed 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. A3; also see Jeffries and Kozlenko 2002, who report monthly averaged buoy drift up to 16 km d^{-1} in this area). In any case, the fact that they usually spend the winter 8° west of Crozier penguins means that their return to Cape Royds may more commonly be against a stronger flow of ice than what Crozier penguins encounter (Fig. A3). 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. 2004) and energy 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). It does not seem to affect breeding success or fledging mass of chicks (Ainley et al. 2004). We did not discover any other differences in wintering area characteristics between the two colonies at the scale permitted by our methods.

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 markedly 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, but not necessarily at the edge of the consolidated pack; they appeared to be avoiding the outer area where ice extent expands and contracts weekly, 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 lower 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 this more northern extent of the pack. 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, we hypothesize that the Ross Island/southern Victoria Land penguins (0.75 million breeders) would 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 exceedingly 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, shifts the wintering area of Ross Island penguins farther north as well. This would move the penguins away from the Slope Front and closer to the ACC Southern Boundary, across which there is less food available (Tynan 1998), and perhaps also add 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 2002), 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 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 daylight. 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 population declines over the past 50 years in Adélie population 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 environmental changes. 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 (Anderson 1999). 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), and any offshore islands in the Pacific sector (of which there are very few) were almost certainly ice-covered (e.g., Balleny Islands; Anderson 1999), a Ross Sea colony most likely existed during the LGM. Ainley (2002) proposed that Cape Adare was the likely location, as the northwest corner of the Ross Sea has been glacier-free during recent glaciations, unlike the continental shelf everywhere else (which had grounded ice sheets to the shelf break; Anderson 1999), and sediment cores from the vicinity indicate a polynya there (Thatje et al. 2008). Moreover, Cape Adare has been free of land ice for ~16,000 y (Johnson et al. 2008), i.e. going back to near to the ice maximum (~19,000 yBP) and before retreat of the WAIS across the Ross Sea began. Habitats for the early colonies may now be underwater, as a result of the 120 m sea level rise since the LGM (an option in data interpretation left open by Emslie et al. 2007). At some point since the LGM, migration patterns among colonies in low-latitude Antarctica must have been formed similar to those described by Clarke et al. (2003) or Fraser and Trivelpiece (1996); which colonies were extant is unknown, as all coastal islands (e.g. South Shetlands) had an extensive ice cap (Anderson 1999). 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 sea ice edge, the Antarctic Circle, and winter daylight. On the basis of our findings, it seems unlikely that this species would colonize terrain even farther south of the current WAIS boundary, were it available, even if the species is forced to retreat from lower latitudes as sea ice disappears (Ainley et al. in press). Such an expansion seems improbable 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, but additional shortening is unlikely (Ainley 2002). 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 has often taken place on millennial or geologic temporal scales, thus giving species time to evolve the necessary behavioral and physiological adaptations to survive (e.g. Shepherd et al. 2005, 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 dramatically increased (Tans 2007). One result, a consequence of the Ozone Hole and the Southern Annular Mode having become mostly “stuck” in its “positive” phase (Stammerjohn et al. 2008, Ainley et al. in press), is that sea ice extent and persistence have been notably increasing in the Ross Sea sector but decreasing in the SW Atlantic sector (see also Parkinson 2002 and Turner et al. 2009).

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, coincident with the gradual reduction in sea ice persistence in that region (Ducklow et al. 2007). 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 (Parkinson 2002, Stammerjohn et al. 2008). Declining Adélie penguin 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 the prevalence of migratory behavior is increasing with southward receding sea ice and declining sea ice season. The current trend of diminishing winter ice is predicted to continue in that region (Ainley et al. in press), but 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, Turner et al. 2009) 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 at high latitude 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 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, following continued growth for a while, 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 life history patterns of the Adélie penguin have been in a state of flux, owing largely to adjustments in migratory behavior and routes. While the species apparently has contended with this successfully throughout its 3 million year history, as ice ages have come and gone with 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 (Ainley et al. in press) will be affected by the availability of light before the pack ice disappears entirely.

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TABLE 1. 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).

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

Figure Legends

FIGURE 1. Penguin locations and sea ice concentration and extent for February - October, 2004 (for 2003 – 2005 see Ecological Archives FIG. A1). 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; Davey 2004), 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).

FIGURE 2. Relative wintering density of penguins by colony, June – July, 2003-2005. Kernel density was calculated from geolocation sensor data for a 100 km grid using the Spatial Analyst extension for ArcGIS (ESRI 2006). Base map layers are from British Antarctic Survey (1998; land and ice shelves), Davey (2004; bathymetry), Orsi et al. (1995; Antarctic Cicumpolar Current southern boundary) and US Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneDay.php; latitude of zero winter twilight).

FIGURE 3. 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.

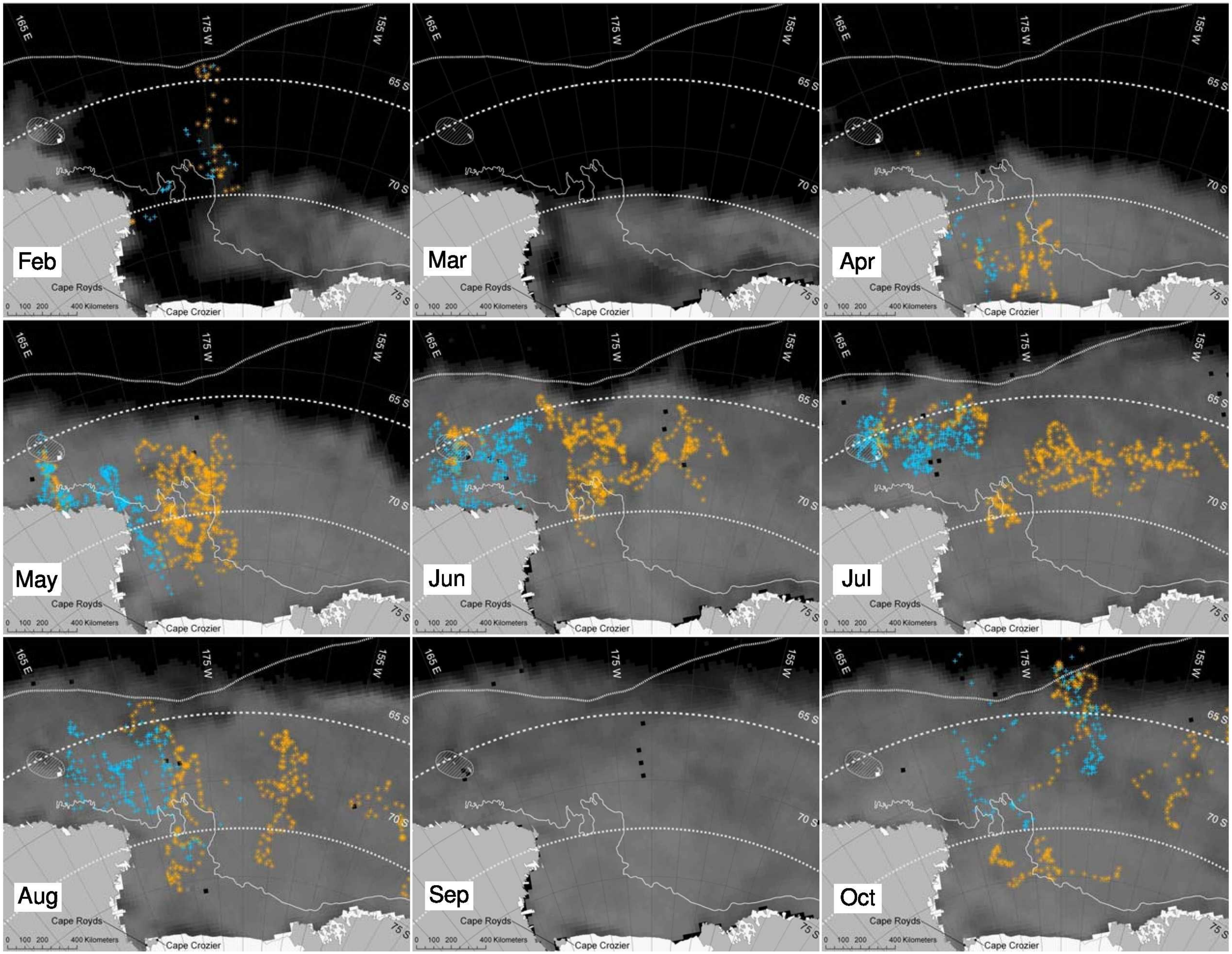
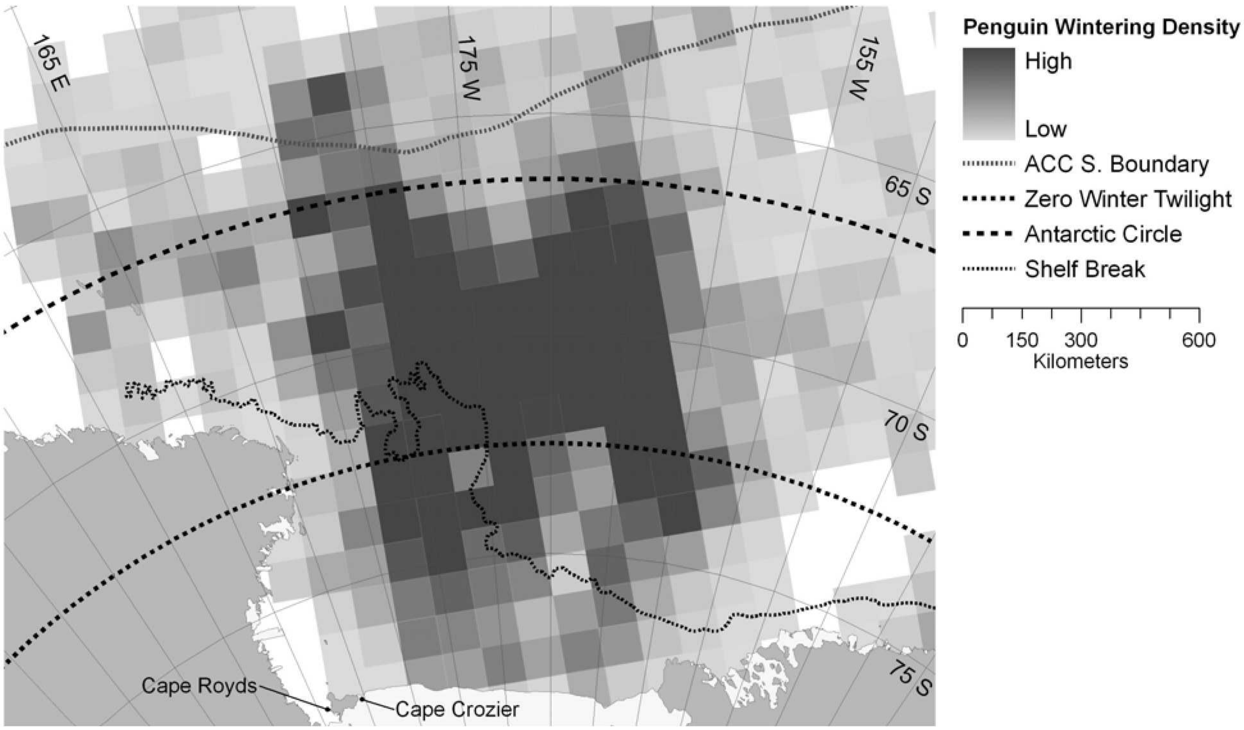

Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
165 E
175 W
155 W
65 S
70 S
75 S
Cape Royds
Cape Crozier
0 100 200 400 Kilometers

Fig. 1
2004

FIG. 2

Crozier Penguins



Royds Penguins

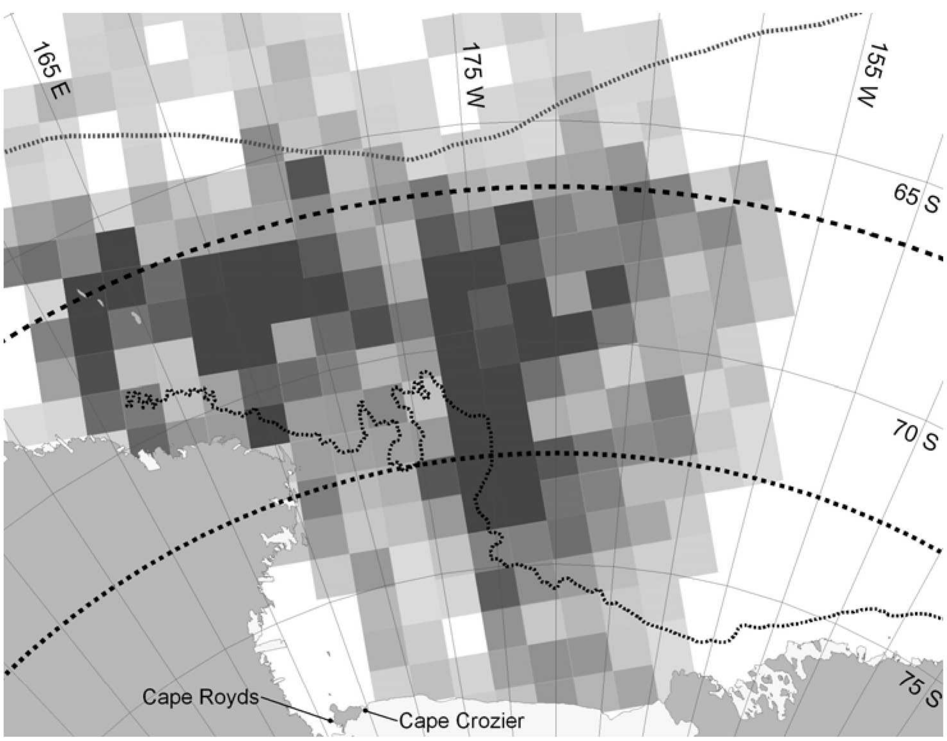
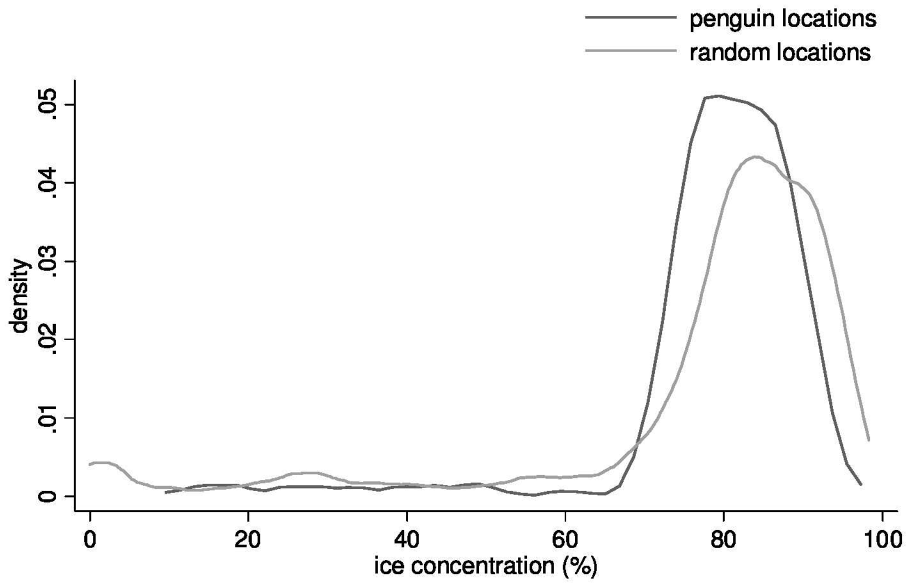


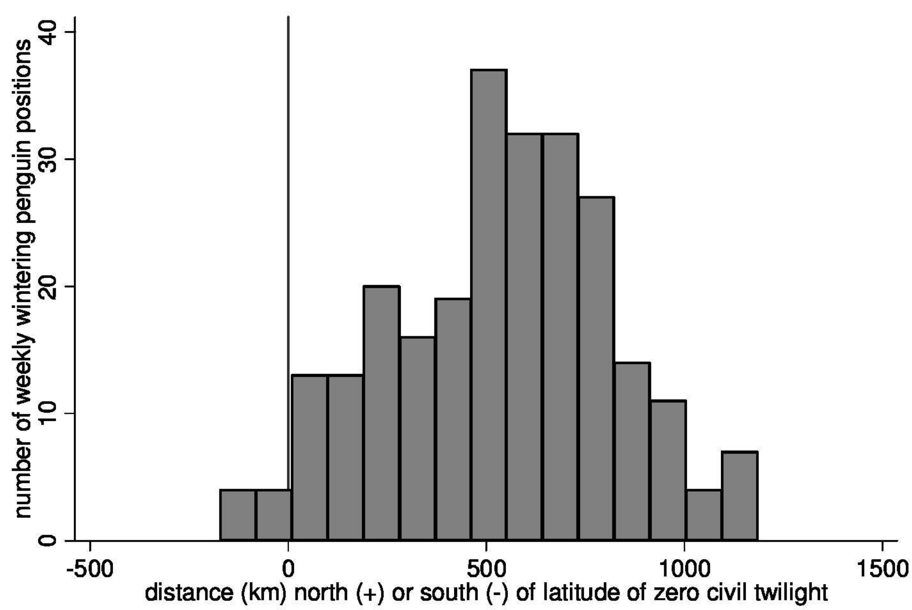
FIG. 3.

A.



penguin locations
random locations
density
0
.01
.02
.03
.04
.05
0
20
40
60
80
100
ice concentration (%)

B.



number of weekly wintering penguin positions
0
10
20
30
40
-500
0
500
1000
1500
distance (km) north (+) or south (-) of latitude of zero civil twilight