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A Nonmarine Source of Variability in Adélie Penguin Demography

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A primary research objective of the Palmer Long Term Ecological Research (LTER) program has been to identify and understand the factors that regulate the demography of Adélie penguins (*Pygoscelis adeliae*). In this context, our work has been focused on variability in the marine environment on which this species depends for virtually all aspects of its life history (Ainley, 2002). As we show here, however, there are patterns evident in the population dynamics of Adélie penguins that are better explained by variability in breeding habitat quality rather than by variability in the marine system. Interactions between the geomorphology of the terrestrial environment that, in turn, affect patterns of snow deposition, drive breeding habitat quality.

Our seabird research in the Palmer LTER region has historically focused on five island rookeries (Figure 1a). At the inception of investigations in 1974, they hosted 15,202 breeding pairs of Adélie penguins (Ducklow et al., 2013, in this issue). During the 2011/2012 field season, these same rookeries hosted 2,411 breeding pairs—an 83% decrease in abundance relative to original estimates. As Figure 1b shows, changes in these populations have not been symmetrical, but instead appear to be island-specific. Most noteworthy among these changes is that, of the five original



populations, only four remain, as the Litchfield Island population went extinct in 2007. This event is remarkable, as the island's paleoecological record indicates this population has been in existence for at least 500 years (Emslie et al., 1998). It is also noteworthy that both radio and satellite telemetry data show that these five, now four, island populations have overlapping foraging ranges over the Palmer Deep Canyon during the breeding season. The canyon is a nearby (~ 15 km) bathymetric feature long thought to be important to the foraging ecology of this species (Fraser and Trivelpiece, 1996; Fraser and Hofmann, 2003; Oliver et al., 2012; Schofield et al., 2013, in this issue). Variability in the abundance and availability of marine prey cannot subsequently be regarded as

a plausible explanation for the patterns observed in Figure 1b.

Snowfall in our primary study areas on the five islands accumulates disproportionately on landscapes with a southwest exposure, where higher numbers of recently abandoned and extinct colonies also occur. These patterns are the result of wind scour during storm events, where predominant northeast winds shift snow loads from north- to south-facing landscapes (Fraser and Patterson, 1997). This pattern leads us to hypothesize that island geomorphology plays a strong role in determining breeding habitat quality (classified as optimal versus suboptimal after Patterson et al., 2003). Following this rationale, we expanded previously developed hillshade models (cf. Patterson et al., 2003) to include our

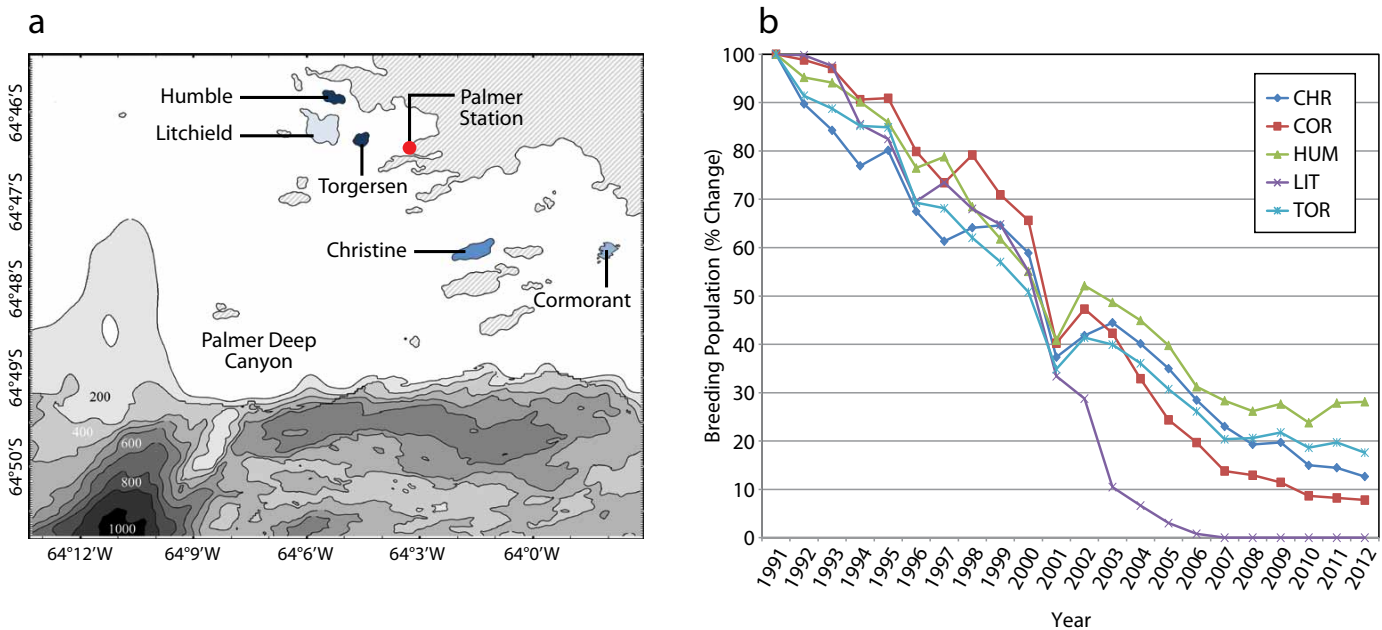


Figure 1. (a) Palmer Station, Antarctica, and vicinity showing the Palmer Deep Canyon and the five island populations of Adélie penguins. Island color shading from dark to light blue reflects an increasing percent of island-specific suboptimal penguin breeding habitat. (b) The islands' respective population trends (breeding pairs/year) since the inception of the Palmer LTER in 1991. To visually compare the trends, breeding pairs/year were standardized as (breeding pairs in year i / breeding pairs in 1991) \times 100. HUM = Humble Island. TOR = Torgersen Island. COR = Cormorant Island. CHR = Christine Island. LIT = Litchfield Island. Year denotes the austral field season, thus 1991 = 1991/1992 field season.

five primary island study sites in order to assess the relationship between island-specific breeding habitat quality and corresponding penguin population trends (changes in breeding pairs per year). Hillshade models are cartographic tools that use elevation data and an illumination source (the convention is a default direction and angle of the sun above the horizon) to produce three-dimensional shaded relief maps that highlight interactions among elevation, slope, and aspect. In this study, elevation data also informed our hillshade models, but we substituted the predominant direction of winds during storm events (north-east) for the “illumination” source. This

allowed us to highlight and thus calculate the areal proportion of suboptimal habitat (i.e., having a southwest aspect where snow is most likely to accumulate) present on each of the islands of interest.

As Table 1 shows, habitat suitability varies by island, with the proportion of suboptimal habitat being greatest for Litchfield Island (89.5%) and least for Humble Island (44.2%). Importantly, the slope of the population trend was related to the amount of suboptimal habitat (Poisson regression, interaction term = -0.31 , $P < 0.0001$); specifically, populations decrease faster as the areal extent of suboptimal habitat increases. Although variability in breeding success

(chicks crèched per pair) would seem to offer a mechanistic explanation to account for these results, this was not observed. Thus, while there is a highly significant relationship between island habitat quality and breeding success ($F = 7.7$, $df_{1,2} = 4$, 95 , $P < 0.0001$), it is only Litchfield Island that shows a significantly lower value; there were no differences in long-term breeding success among the other islands despite significant differences in their rates of population decrease.


Precipitation has been increasing for decades over the region that constitutes much of the Palmer LTER sampling grid (Turner et al., 2005), suggesting that our observations may be due at least in part to a threshold effect, that is, a change in the dynamics associated with the deposition and persistence of snow across these island landscapes. Litchfield Island exhibits the greatest amount of sub-optimal habitat, the lowest breeding success, and steepest decrease in the Adélie penguin breeding population during the

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study period. However, as previously noted, the paleoecological record indicates that Adélie penguins have occupied this island for at least 500 years (Emslie et al., 1998), implying not only that a shift has occurred in breeding habitat quality (from optimal to suboptimal as a function of increasing precipitation), but that this shift was both abrupt and relatively recent. If this is the case, we would predict that the Cormorant Island penguin population will be extinct next, as its landscape-habitat dynamics appear similarly vulnerable to a threshold effect if precipitation continues to increase. Although it has recently been proposed that variability in the biomass of Antarctic krill (*Euphausia superba*) is the dominant driver of demographic change in Adélie penguins (Trivelpiece et al., 2011), our findings suggest that models of population change based on food web processes alone may be insufficient to account for the observed variability.

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Table 1. Island-specific relationships among breeding habitat quality, Adélie penguin population (breeding pairs/year) decrease, and breeding success.

The rate of decrease is ordered from fastest to slowest.

Time series denotes number of years included in the analyses.

Island	Suboptimal Habitat (%)	Population Trend (Slope)	Slope P-Value	Rate of Decrease	Breeding Success (Mean ± SE)	Time Series (Years)
Litchfield	89.5	-0.1772	< 0.0001	1	0.80 ± 0.13 ^a	16
Cormorant	63.0	-0.1105	< 0.0001	2	1.20 ± 0.05	21
Christine	46.8	-0.0869	< 0.0001	3 ^b	1.19 ± 0.05	21
Torgersen	44.3	-0.0889	< 0.0001	3	1.20 ± 0.06	21
Humble	44.2	-0.0743	< 0.0001	4	1.32 ± 0.05	21

^a denotes a statistically significant difference (P < 0.05) when compared to the other islands.

^b the repeated value 3 for Christine and Humble Islands indicates no significant difference in the slopes (P = 0.20).

SE = Standard error.