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Source: The Auk, 134(3) : 520-529

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-16-69.1

The Auk
Ornithological Advances

AmericanOrnithology.org

Volume 134, 2017, pp. 520–529
DOI: 10.1642/AUK-16-69.1

RESEARCH ARTICLE

# Peeking into the bleak midwinter: Investigating nonbreeding strategies of Gentoo Penguins using a camera network

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Submitted April 6, 2016; Accepted February 10, 2017; Published April 19, 2017

## ABSTRACT

When monitoring species with extensive ranges in harsh climates, comprehensive studies across a species' range are both logistically and technically challenging and therefore rare. Such scarcity in data collection is particularly true in the polar regions where sea ice and weather constraints prevent widespread access to sites for much of the year, specifically during winter. Penguins (Spheniscidae*)* show large variations in winter strategies with many species migrating long distances while others are distinctly sedentary, remaining at the colony year-round. However, in some species, their attendance at the breeding site during the nonbreeding winter period depends greatly on the colony location and environmental factors. Here we aim to examine fluctuations in winter attendance at the breeding site in Gentoo Penguins (*Pygoscelis papua*) along a latitudinal gradient of 7 sites, ranging from Martillo Island, a colony in Argentina, to Petermann Island, a colony located toward the southern edge of the species' range on the Western Antarctic Peninsula. We use an established network of cameras to observe winter populations of penguins across a large latitudinal gradient. This study provides the first evidence of across-year variation in Gentoo Penguin nonbreeding attendance at the breeding site. We found that both temporal and spatial factors drive winter attendance in this species with distinct patterns between years and colony locations, particularly at the edges of its range. Additionally, environmental and temporal factors, including sea ice extent directly offshore and photoperiod, appear to dictate Gentoo Penguin winter attendance across their range. As Gentoo Penguins are neither sedentary nor migratory during the nonbreeding period, understanding patterns in winter site occupation across time and space provides insight into half of the species' annual cycle and has important implications in the face of changes in climate, direct human disturbance, and fisheries activities.

*Keywords:* Antarctic, Gentoo Penguin, phenology, polar biology, *Pygoscelis papua*

### Coup d'œil au milieu d'un hiver rude – examiner les stratégies non reproductives chez *Pygoscelis papua* à l'aide d'un réseau de caméras

## RÉSUMÉ

Lors du suivi d'espèces comportant des aires de répartition vastes dans des climats rigoureux, les études approfondies sur toute l'aire de répartition de l'espèce représentent un défi logistique et technique, et sont par conséquent rares. Une telle rareté de collecte de données est particulièrement vraie dans les régions polaires, où la glace de mer et les contraintes météorologiques empêchent d'accéder aisément aux sites une bonne partie de l'année, particulièrement en hiver. Les manchots (Spheniscidae*)* présentent une grande variation dans les stratégies hivernales, plusieurs espèces migrant sur de longues distances alors que d'autres sont distinctement sédentaires et restent dans la colonie toute l'année. Toutefois, chez certaines espèces, la fréquentation du site de reproduction au cours de la période hivernale non reproductive dépend beaucoup de l'emplacement de la colonie et de facteurs environnementaux. Notre étude vise à examiner les fluctuations de la fréquentation hivernale au site de reproduction de *Pygoscelis papua* le long d'un gradient latitudinal de sept sites, allant de l'île Martillo, une colonie en Argentine, à l'île Petermann, une colonie située près de la limite sud de l'aire de répartition de l'espèce, sur la péninsule antarctique occidentale. Nous utilisons un réseau de caméras déjà en place pour observer les populations hivernales de manchots le long d'un important gradient latitudinal. Cette étude fournit les premières preuves d'une variation interannuelle de la fréquentation du site de reproduction par cette espèce en dehors de la période de reproduction. Nous avons trouvé que des facteurs temporels et spatiaux gouvernent la fréquentation hivernale chez cette espèce avec des patrons distincts entre les années et l'emplacement des colonies, particulièrement aux confins de leur aire de répartition. De plus, les facteurs environnementaux et temporels, dont l'étendue de la glace de mer côtière et la photopériode, semblent dicter sa fréquentation hivernale à travers l'aire de répartition. Puisque *P. papua* n'est ni sédentaire ni migrateur en dehors de la période de reproduction, la compréhension des patrons d'occupation hivernale du site dans le temps et l'espace donne un aperçu de la moitié du cycle annuel de l'espèce et a d'importantes implications face aux changements climatiques, au dérangement humain direct et aux activités de pêche.

*Mots-clés: Pygoscelis papua,* biologie polaire, Antarctique, phénologie

## INTRODUCTION

When monitoring species with extensive ranges in harsh climates, comprehensive studies across a species' range are both logistically and technically challenging and therefore rare. Such scarcity in data collection is particularly true in the polar regions where sea ice and weather constraints prevent widespread access to sites for much of the year, specifically during winter. However, year-round studies across a species' complete range are especially relevant in polar environments because animals present during the summer breeding months may migrate, remain close to summer breeding sites, or adopt partial migration strategies during the nonbreeding period, which is poorly understood (Black 2016). Examining the mechanisms that govern these strategies is important in the face of climate change, changing fishing pressure, and increasing human visitation (Chown et al. 2015).

Penguins (Spheniscidae*)* show large variations in winter strategies with many species migrating long distances (e.g., Chinstrap Penguin [*Pygoscelis antarctica*], Magellanic Penguin [*Spheniscus magellanicus*]), while others are distinctly sedentary, remaining at the colony year-round (e.g., African Penguin [*S. demersus*], Yellow-eyed Penguin [*Megadyptes antipodes*]) (Croxall and Davis 1999, Biuw et al. 2009). However, in some species (e.g., Adélie Penguin [*P. adeliae*], Gentoo Penguin [*P. papua*]), attendance at the breeding site during the nonbreeding winter period depends greatly on the colony location (Bost and Jouventin 1990, Wilson et al. 1998, Erdmann et al. 2011). In addition, environmental factors, particularly sea ice extent, photoperiod, and food availability, influence winter migration both temporally and spatially (e.g., Clarke et al. 2003, Pütz et al. 2007, Ballard et al. 2010) and winter whereabouts can impact reproductive success, as individuals must build condition during the nonbreeding period to successfully breed the subsequent summer (e.g., Irvine et al. 2000, Clarke et al. 2002).

Gentoo Penguins inhabit a large range in the Southern Ocean and Antarctic Peninsula and can therefore be used as an exemplar study species when examining behavioral changes along a latitudinal gradient. Gentoo Penguins are currently of interest in studies observing environmental change, as their populations are increasing at their southern limit along the Western Antarctic Peninsula (WAP), while competitor populations (Adélie and Chinstrap penguins) are declining (Lynch et al 2012). Few studies have been conducted of nonbreeding behavior, examining either winter diet (LaCock et al. 1984, Williams 1991, Clausen and Pütz 2002) or winter locations using GPS or temperature loggers (Hindell 1989, Williams et al. 1992, Wilson et al. 1998, Tanton et al. 2004, Hinke and Trivelpiece 2011). Gentoo Penguins are known to remain present at breeding sites over winter in the sub-Antarctic islands of South Georgia (Williams et al. 1992), the South Shetlands (Wilson et al. 1998, Hinke and Trivelpiece 2011), and Crozet Islands (see Bost and Jouventin 1990 and references therein), but there are large spatial gaps in our knowledge of their winter behavior beyond these locations, particularly comparisons between behavior at sub-Antarctic islands and the southern edge of their range on the WAP.

Here we aim to examine fluctuations in winter attendance at the breeding site in Gentoo Penguins along a latitudinal gradient of 7 sites, ranging from Martillo Island, a colony in Argentina, to Petermann Island, a colony located toward their southern edge of range on the WAP. Using time-lapse cameras, this study aims to determine inter-site and interannual variation in colony occupation during the nonbreeding period. In particular, we aim to answer the following a priori hypotheses: (1) attendance will increase as latitude decreases; colonies located farther north will increasingly remain sedentary at the breeding site; (2) winter attendance on land will increase as the number of daylight hours decreases and will peak at the winter equinox, when minimal time is available to visually forage offshore; (3) winter attendance will increase with the presence of open water conditions directly offshore, when foraging conditions are optimal for this near-shore habitat–linked species (Fraser et al. 1992, Wilson et al. 1998, Clausen and Pütz 2003, Tanton et al. 2004); and (4) if attendance is closely associated with photoperiod, no significant interannual variation in colony occupation numbers will occur; however, if attendance is instead linked primarily with sea ice extent, interannual variation in attendance will occur.

## METHODS

### Study Sites

We deployed cameras at 7 sites to study winter attendance in Gentoo Penguins along a latitudinal gradient: (1) Martillo Island (54.895°S, 67.401°W) in the Tierra del Fuego region of Argentina, (2) Maiviken (54.505°S, 36.595°W) on South Georgia, and (3) Cuverville Island (64.688°S, 62.622°W), (4) Danco Island (64.734°S, 62.594°W), (5) Neko Harbor (64.838°S, 62.532°W), (6) Port Lockroy (64.823°S, 63.484°W), and (7) Petermann Island (65.172°S, 64.142°W) along the WAP (Figure 1).

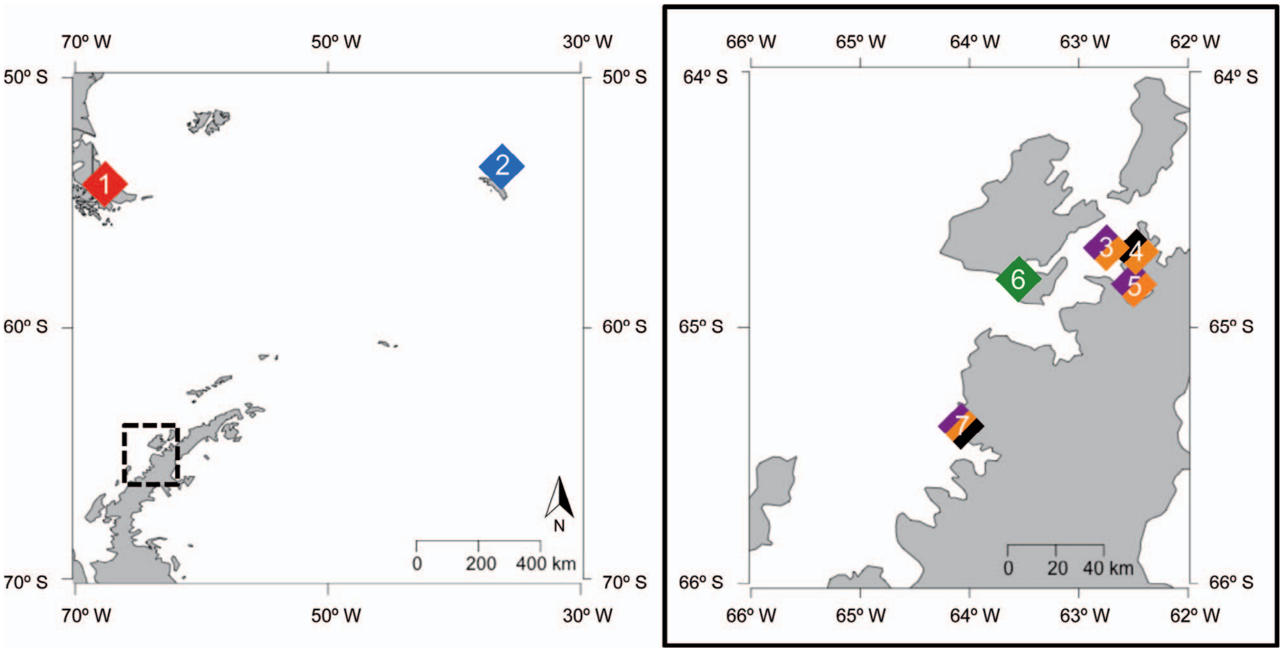

**FIGURE 1.** Map of 7 study sites, including (1) Martillo Island, Argentina; (2) Maiviken, South Georgia; (3) Cuverville Island; (4) Danco Island; (5) Neko Harbor; (6) Port Lockroy: and (7) Petermann Island on the Western Antarctic Peninsula. Similar colors indicate sites that are *not* significantly different in their counts of nonbreeding attendance when examining their orthogonal contrasts. The dashed box designates the region of study sites 3–7.

## Camera System

Seven cameras were deployed, one at each of our 7 study sites; each camera was installed roughly 10 m from a nesting sub-colony (Appendix Figure 3). The cameras were installed using techniques similar to those described in Newbery and Southwell (2009) and Southwell and Emmerson (2015), with minor adjustments to the camera system. At each site, a Reconyx HC500 Hyperfire trail camera (Reconyx, Holmen, Wisconsin, USA) was mounted to a scaffold pole and anchored using a rock basket. The cameras were programmed in time-lapse mode to take between 8 and 14 photographs daily, beginning at 0700 hours and ending at 2000 hours (GMT–2), depending on the camera, and each camera captured images of 21–100 nests. To avoid bias due to low daylight hours during winter and therefore a lower volume of visible counts around the winter equinox and to keep our data consistent with the techniques described in Southwell and Emmerson (2015), we used only those images taken at 1400 hours local time. Date, time of day, and temperature data were recorded by each camera in each image and extracted from the image metadata.

We must note that it is highly possible that individuals were present at the colony site during winter outside of the camera's range of view, which serves as a major limitation of this study. However, the camera was installed at the best possible location and angle to observe a large proportion of the colony (Appendix Figure 3). Attendance during both the nonbreeding and breeding phases has been noted (Figure 2, Table 1) to allow for comparisons between the 2 periods in what was observed by the cameras.

## Data Extraction

Counts of individuals were extracted from each image using either a Zooniverse interface (www.penguinwatch.org), developed by our team for this specific purpose, or iTag, an open-sourced software for counting individual objects within images (Viquerat and van Neer 2015). In both programs, in each image, a point was centered over each visible individual to avoid counting individuals twice (Appendix Figure 3). The number of points in each image was then extracted to determine counts. This process was used for counting adults at each site in each image and all individuals at the edge of the image frame were included in our analysis. One individual (CB) performed all counts. We analyzed nonbreeding data from each of our 7 study sites beginning at the end of adult molt (last adult seen molting) and ending one month prior to an initial peak in attendance during the breeding season (see Table 1 for dates).

The Danco Island, Neko Harbor, Port Lockroy, and Petermann Island cameras overlooked the nearby marine environment enabling the extent and type of near-shore sea ice to be determined. Sea ice extent was extracted from the

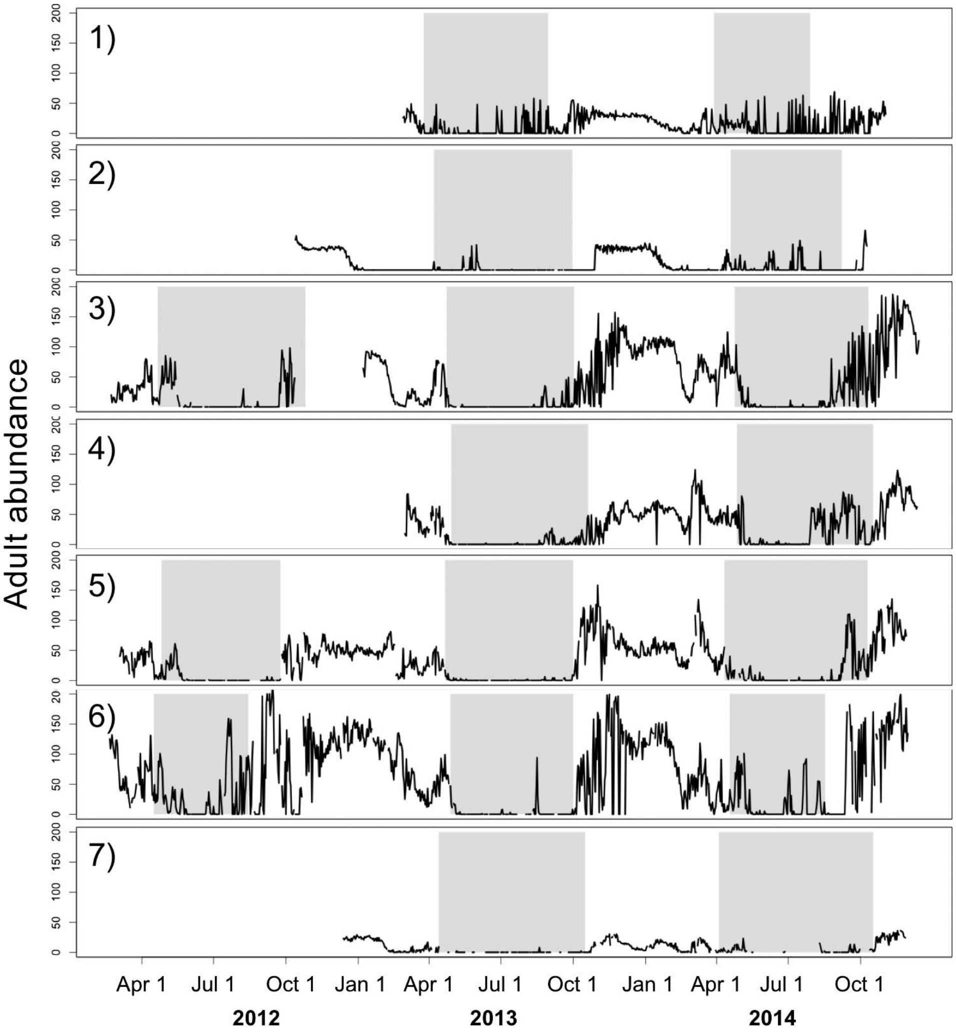

**FIGURE 2.** Time series of adult attendance from 2012 to 2014 at each of 7 study sites, including (1) Martillo Island, (2) Maiviken, (3) Cuverville Island, (4) Danco Island, (5) Neko Harbor, (6) Port Lockroy, and (7) Petermann Island. Shaded areas indicate nonbreeding period (see Table 1 for dates).

images using the guidelines described in Smith (2000); sea ice in each image from these 4 sites was ranked from 1 to 10 and categorized as either open water, pack, or compact (also known as fast) ice based on photographs provided in Smith (2000*).* For the 2 sub-Antarctic colonies where sea ice is not present during the winter offshore (Martillo Island and Maiviken), the sea ice type was categorized as open water throughout the nonbreeding period.

Date, time of day, and temperature data were extracted from the image metadata. Daylight hours were extracted using the suncalc function in the RAtmosphere package of R (R Core Development Team 2013, Biavati 2014).

### Statistical Analysis

All analyses were conducted in R (v. 3.1.3) language for statistical computing using the stats package (R Core Development Team 2013). Variability in the rate of the Poisson process among individual birds was expected and, as anticipated, we found overdispersion in both Poisson and quasi-Poisson generalized linear models (GLMs). Variability among otherwise identical individuals is usually well accounted for by a gamma distribution across the Poisson rate parameter and we therefore opted for fitting negative binomial GLMs (glm.nb function, MASS package; Venables and Ripley 2002) to understand relationships between each of our coefficients and the nonbreeding counts at all 7 study sites (Table 2). Our final model included the year, sea ice type, Julian date, and interactions between site location and both temperature and photoperiod as explanatory variables (Table 2). Interactions between sea ice type and both year and location were fitted but ultimately omitted during model

**TABLE 1.** Summary of data at each study site, including the total number of images, nonbreeding (N-B) dates, and both breeding (B) and nonbreeding attendance means and ranges for 2012–2014. NAs indicate data is not available.

| | | Year | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2012 | | | | | 2013 | | | | | 2014 | | |
| Site | Total # of images | N-B dates | N-B mean | N-B range | B mean | B range | N-B dates | N-B mean | N-B range | B mean | B range | N-B dates | N-B mean | N-B range |
| Martillo | 614 | NA | NA | NA | NA | NA | Mar 25–Aug 30 | 5.67 | 0–58 | 19.60 | 0–55 | Mar 29–Jul 29 | 10.76 | 0–63 |
| Maiviken | 778 | NA | NA | NA | 14.70 | 0–57 | Apr 7–Sep 30 | 1.16 | 0–42 | 15.83 | 0–45 | Apr 19–Sep 7 | 3.89 | 0–49 |
| Cuverville | 1027 | Apr 21–Sep 6 | 9.64 | 0–85 | 35.63 | 0–98 | Apr 23–Oct 2 | 2.41 | 0–49 | 73.56 | 0–157 | Apr 24–Oct 11 | 16.38 | 0–134 |
| Danco | 729 | NA | NA | NA | NA | NA | Apr 29–Oct 20 | 2.45 | 0–43 | 48.75 | 0–124 | Apr 27–Oct 17 | 19.05 | 0–87 |
| Neko | 1000 | Apr 26–Sep 24 | 5.39 | 0–61 | 40.84 | 0–81 | Apr 21–Oct 1 | 0.52 | 0–11 | 57.10 | 0–158 | Apr 11–Oct 10 | 11.38 | 0–110 |
| Lockroy | 1015 | Apr 16–Aug 14 | 27.12 | 0–159 | 87.31 | 0–213 | Apr 28–Oct 1 | 2.31 | 0–94 | 78.53 | 0–199 | Apr 18–Aug 17 | 16.62 | 0–101 |
| Petermann | 717 | NA | NA | NA | 12.04 | 0–29 | Apr 13–Oct 16 | 0.10 | 0–8 | 11.06 | 0–30 | Apr 4–Oct 17 | 3.05 | 0–23 |

simplification (ANOVA, $P = 0.413$ and $P = 0.862$, respectively).

To account for the differences between the angle and view within each camera frame, we counted the total number of nests at peak breeding in 2013 at each study site and used these nest counts as an offset term (–log(x)) in each of our models (offset function, stats package). All models were first fitted with and without the inclusion of an autocorrelation structure; both autoregressive (AR) and autoregressive moving average (ARMA) models were used. There was no evidence of any temporal autocorrelation in any of our models and therefore our final models did not include such structures. The final model resulted in a goodness-of-fit statistics with a $p$ value of 1; there was no evidence in favor of rejection of the model's fit.

## RESULTS

Analyses revealed relationships between year, sea ice type (compact, pack, or open water), time of year (Julian day), colony location, photoperiod (number of daylight hours daily), and temperature and nonbreeding counts across 7 study sites (Table 2). Our data, examining attendance only at 1400 hours local time, may underestimate the number of individuals at the breeding site because, as found in past studies (Williams 1991, Williams et al. 1992, Tanton et al. 2004), Gentoo Penguins are diurnal foragers, usually taking one trip daily, and may be foraging at the time the image was captured.

When examining temporal variation, we discovered significant differences between the 3 years across sites; penguin nonbreeding attendance in 2014 ($\mathrm{SE} = 3.79$, $P < 0.001$) was significantly greater than in 2013 ($\mathrm{SE} = 1.90$, $P < 0.001$) and 2012 ($\mathrm{SE} = 22.93$, $P < 0.001$) and attendance was also significantly greater in 2013 than in 2012 (Table 2, Figure 2).

We found that Gentoo Penguins were present at the breeding site in significantly higher numbers when either open water ($\mathrm{SE} = 22.9$, $P < 0.001$) or pack ice ($\mathrm{SE} = 23.0$, $P < 0.001$) was present, whereas they were less present when compact (fast) ice was located directly offshore during winter ($\mathrm{SE} = 0.498$, $P < 0.001$).

When examining variation in the timing of site occupation during the nonbreeding period, we found a significant negative relationship between Julian date and counts ($\mathrm{SE} = 0.002$, $P < 0.001$). In other words, Gentoo Penguins occupied the breeding site in larger numbers earlier in the nonbreeding season (Table 2, Figure 2).

We also discovered a relationship between location and photoperiod and Gentoo Penguin attendance. At our 5 WAP sites, the penguins increased in nonbreeding counts as daylight hours increased (Table 2). However, at the 2 sub-Antarctic sites (Martillo Island and Maiviken), the

**TABLE 2.** Coefficients resulting from a negative binomial generalized linear models (GLM) on Gentoo Penguin nonbreeding attendance: year, sea ice type, Julian date, photoperiod, and temperature at 7 study sites related to adult nonbreeding attendance. Offsets of the –log(nest counts) were used in both models to account for differences in the camera angle and view between sites; therefore, all estimates reflect the relationship between each coefficient and adult nonbreeding attendance per nest unit. Significance is indicated as *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

| Coefficient | Estimate | SE | $Z$ | $P$ |
|---|---|---|---|---|
| Year | | | | |
| 2012 (intercept) | 8.08 | 0.733 | 11.03 | <0.001*** |
| 2013 | −2.61 | 0.236 | −11.08 | <0.001*** |
| 2014 | −0.833 | 0.228 | −3.66 | <0.001*** |
| Sea Ice Type | | | | |
| Open Water (intercept) | 8.08 | 0.733 | 11.03 | <0.001*** |
| Compact | −3.73 | 0.539 | −6.92 | <0.001*** |
| Pack | 0.100 | 0.295 | 0.34 | 0.735 |
| Julian Date | −0.011 | 0.002 | −5.88 | <0.001*** |
| Location | | | | |
| Martillo Island | 4.73 | 1.05 | 4.49 | <0.001*** |
| Maiviken | 7.95 | 1.50 | 5.28 | <0.001*** |
| Cuverville Island | −4.98 | 0.819 | −6.07 | <0.001*** |
| Danco Island | −3.67 | 0.762 | −4.82 | <0.001*** |
| Neko Harbor | −5.63 | 0.823 | −6.84 | <0.001*** |
| Port Lockroy (intercept) | 8.08 | 0.733 | 11.03 | <0.001*** |
| Petermann Island | −4.69 | 1.08 | −4.34 | <0.001*** |
| Location: Photoperiod | | | | |
| Martillo Island: Photoperiod | −0.728 | 0.127 | −5.73 | <0.001*** |
| Maiviken: Photoperiod | −1.43 | 0.198 | −7.19 | <0.001*** |
| Cuverville Island: Photoperiod | 0.355 | 0.120 | 2.95 | 0.003 ** |
| Danco Island: Photoperiod | 0.279 | 0.114 | 2.45 | 0.014 * |
| Neko Harbor: Photoperiod | 0.181 | 0.120 | 1.51 | 0.131 |
| Port Lockroy: Photoperiod | 0.386 | 0.104 | 3.72 | <0.001*** |
| Petermann Island: Photoperiod | 0.020 | 0.141 | 0.14 | 0.887 |
| Location: Temperature | | | | |
| Martillo Island: Temperature | −0.034 | 0.074 | −0.46 | 0.643 |
| Maiviken: Temperature | −0.034 | 0.063 | −0.53 | 0.594 |
| Cuverville Island: Temperature | −0.001 | 0.055 | −0.03 | 0.979 |
| Danco Island: Temperature | −0.142 | 0.046 | −3.09 | 0.002 ** |
| Neko Harbor: Temperature | −0.022 | 0.057 | −0.39 | 0.697 |
| Port Lockroy: Temperature | 0.142 | 0.046 | 3.09 | 0.002 |
| Petermann Island: Temperature | −0.112 | 0.072 | −1.55 | 0.120 |

opposite relationship was found: Gentoo Penguins increased in winter attendance as daylight hours decreased.

We also found that temperature influenced Gentoo Penguin nonbreeding counts, but only at one site, Danco Island, located on the WAP (SE $= 0.046$, $P = 0.002$); as temperature increased, the Danco Island colony winter counts decreased.

Lastly, we found distinct patterns in Gentoo Penguin occupation at the breeding site during the nonbreeding period dependent on site location (Figure 1). Re-leveling our model revealed the following contrasts where letters indicate that sites are *not* significantly different in their overall winter counts: (1) Martillo Island (A), (2) Maiviken (B), (3) Cuverville Island (C, F), (4) Danco Island (D, F), (5) Neko Harbor (C, F), (6) Port Lockroy (E), and (7) Petermann Island (C, D, F) (Figure 1). In other words, the colonies located at Maiviken (South Georgia), Martillo Island (Argentina), and Port Lockroy (WAP) occupied the breeding site during winter in significantly higher numbers than did the colonies at the other 4 WAP sites: Cuverville Island, Danco Island, Neko Harbor, and Petermann Island.

We cannot conclude that these relationships are due to site fidelity as individuals could not be discerned and were not marked in this study. However, Gentoo Penguins on South Georgia and the Antarctic Peninsula were often seen sitting directly on the nest areas during the winter and even building or maintaining nests year-round, providing evidence that it is likely that many of the same individuals were present during both the breeding and nonbreeding periods.

## DISCUSSION

By using a time-lapse camera system, we have, for the first time, been able to show the pattern of attendance at

Gentoo Penguin breeding sites throughout the nonbreeding period. This study provides the first evidence of across-year variation in Gentoo Penguin nonbreeding attendance at the breeding site. We found that both temporal and spatial factors drive winter attendance in this species with distinct patterns between years and colony locations, particularly at the edges of its range. Additionally, environmental and temporal factors, including sea ice extent directly offshore, photoperiod, and temperature, appear to dictate Gentoo Penguin winter attendance across their range. As Gentoo Penguins are neither sedentary nor migratory during the nonbreeding period, understanding patterns in winter site occupation across time and space provides insight into half of the species' annual cycle and has important implications in the face of changes in climate, direct human disturbance, and fisheries activities (Chown et al. 2015).

The distinct patterns we found in Gentoo Penguin winter attendance across the 7 study sites separate site attendance into 3 spatial groups: the Falkland Islands, South Georgia, and the WAP. Gentoo Penguins inhabiting the sub-Antarctic sites (Martillo Island, Argentina, and Maiviken, South Georgia) demonstrated consistently higher site occupation over the years studied when compared to the 5 WAP sites, representing Gentoo Penguin behavior at their northernmost edge of range (Figure 1). Past studies have provided evidence that birds in colonies located farther south are absent from the breeding site for longer periods over winter, often for over 2 months (see Bost and Jouventin 1990 and references therein), consistent with winter attendance studied here. However, we also found fine-scale spatial variation across our 5 WAP sites with one site, Port Lockroy, emerging as statistically distinct from the other 4 sites (Figure 1, Table 2). These spatial patterns provide evidence that, although edge of range effects play a role in winter behavior in this species, local environmental factors also dictate nonbreeding attendance.

We found the same patterns in the relationship between photoperiod and winter counts as we did spatially across sites, separating the colonies into the same 2 distinct groups: the sub-Antarctic Islands and WAP colonies. Past studies have also found evidence that winter behavior is dictated by photoperiod in other penguin species (Wilson et al. 1989, Fraser and Trivelpiece 1996, Ainley 2002, Forcada and Trathan 2009) and Gentoo Penguins (Tanton et al. 2004), linking decreased daylight hours with reduced foraging ability as penguins are visual foragers and therefore need daylight to adequately navigate and feed (Emlen and Penney 1964, Penney and Emlen 1967, Wilson 1993). In addition, Hinke and Trivelpiece (2011) found that Gentoo Penguins at the South Shetland Islands forage daily, are absent from the colony between 0900 hours and 1500 hours (local time) throughout the winter, and lengthen their foraging trip duration as daily daylight hours also increase. However, this study is the first to show discrete differences in a response to photoperiod depending on the colony location. Sub-Antarctic Gentoo Penguin winter occupation increased as daylight hours diminished, while the opposite held true with our WAP colonies. The 2 spatial groups peak in winter attendance at opposite times in the nonbreeding season, governed by a relationship with photoperiod, although other environmental factors, particularly sea ice in the WAP, which is not present to the same extent at the 2 sub-Antarctic sites, likely play a large role in winter attendance. In particular, individuals at the WAP colony sites may maximize foraging during shorter days by staying nearer to more optimal foraging areas, whether at other colony sites or on sea ice floes, when the colony sites studied are not at their optimal sea ice level for these near-shore foragers.

When examining the role of sea ice in winter attendance using the time-lapse cameras, we found a clear relationship with open water and pack ice compared to compact ice conditions. Gentoo Penguins were significantly more abundant during the nonbreeding period when open water or pack ice was present and significantly less abundant when compact ice appeared directly offshore. Past studies have indicated that Gentoo Penguins are restricted to inshore foraging during the winter months to the same extent that they are during the breeding season (Williams et al. 1992, Tanton et al. 2004) and have similar prey compositions during these periods (Williams 1991, Clausen and Pütz 2002). We provide evidence that Gentoo Penguins on the WAP overwinter at breeding sites during periods when sea ice conditions are optimal for foraging directly inshore, using the breeding site as a resting area between foraging periods.

Lastly, we found considerable temporal variation in the counts of Gentoo Penguins wintering at the breeding site; both year and the date within year influenced the extent of Gentoo Penguin site occupation during the nonbreeding period. Across the study sites, Gentoo Penguins were more abundant in winter in 2014 than in 2013 or 2012 and in 2013 than in 2012. We also found that at all sites penguins were significantly more abundant earlier in the nonbreeding season. To our knowledge, we are the first to examine differences in Gentoo Penguin winter attendance between years across multiple sites, which provide critical insight into the plasticity of this behavior.

The restraints associated with feeding and raising chicks are no longer present during the winter months, which may allow for greater flexibility in foraging extent and the timing when Gentoo Penguins are found onshore. However, foraging is limited by the number of daylight hours (Tanton et al. 2004) and Gentoo Penguins must rest ashore or on ice during the night, at the very least, to conserve energy (Bevan et al. 1995). Resting on land may allow Gentoo Penguins to discover or maintain nest location, avoid predation at sea, or even aid in the exchange of information on prey quality and location (Ward and Zahavi 1973). Ultimately, we provide evidence that Gentoo Penguins are found at the breeding site over winter depending on the number of daylight hours daily and when sea ice conditions are ideal for foraging, although these relationships are highly dependent on the colony location. Gentoo Penguins are neither sedentary nor migratory during the nonbreeding period, reflecting their large behavioral plasticity and ability to adapt to changing environmental conditions, which may have positive effects in the face of increasing threats, putting them at competitive advantage to other penguin species inhabiting the same range. Gentoo Penguin winter attendance at colony sites also has large implications for fisheries management, particularly in the allocation of catch limits near breeding aggregations year round. Understanding winter behavior provides critical information on local ecosystem effects, interspecies and intraspecies competition for resources, and best management practices in the face of increasing threats to polar species.

## ACKNOWLEDGMENTS

We gratefully acknowledge the anonymous reviewers for their valuable input on earlier manuscript drafts. We gratefully acknowledge the support of Quark Expeditions Ltd, Exodus Travel, Yusuf Aytar, Piratour SA, Andrew Zisserman, Gemma Clucas, Chris Perrins, the Zooniverse community, and CONICET. Fieldwork was carried out under permits from the UK Foreign and Commonwealth Office, the Government of South Georgia and the South Sandwich Islands, and Dirección de Areas Protegidas, Secretaria de Desarrollo Sustentable y Ambiente Argentina. Work on South Georgia was permitted by the Government of South Georgia and the South Sandwich Islands (GSGSSI). Permits for Antarctica were issued by the UK Foreign and Commonwealth Office under the Antarctic Treaty system.

**Funding statement:** This project was supported by a Darwin Initiative Challenge Fund and a Darwin Plus grant and by public donations on board Quark Expeditions Ltd.

**Ethics statement:** Each of these permits was issued following independent ethical review of the sampling and the study received ethical approval from the University of Oxford and the Zoological Society of London.

**Author contributions:** C.B., A.R., T.H. designed the project and developed the methods. T.H. and A.R. contributed substantial materials and resources. C.B. wrote the paper and collected and analyzed the data.

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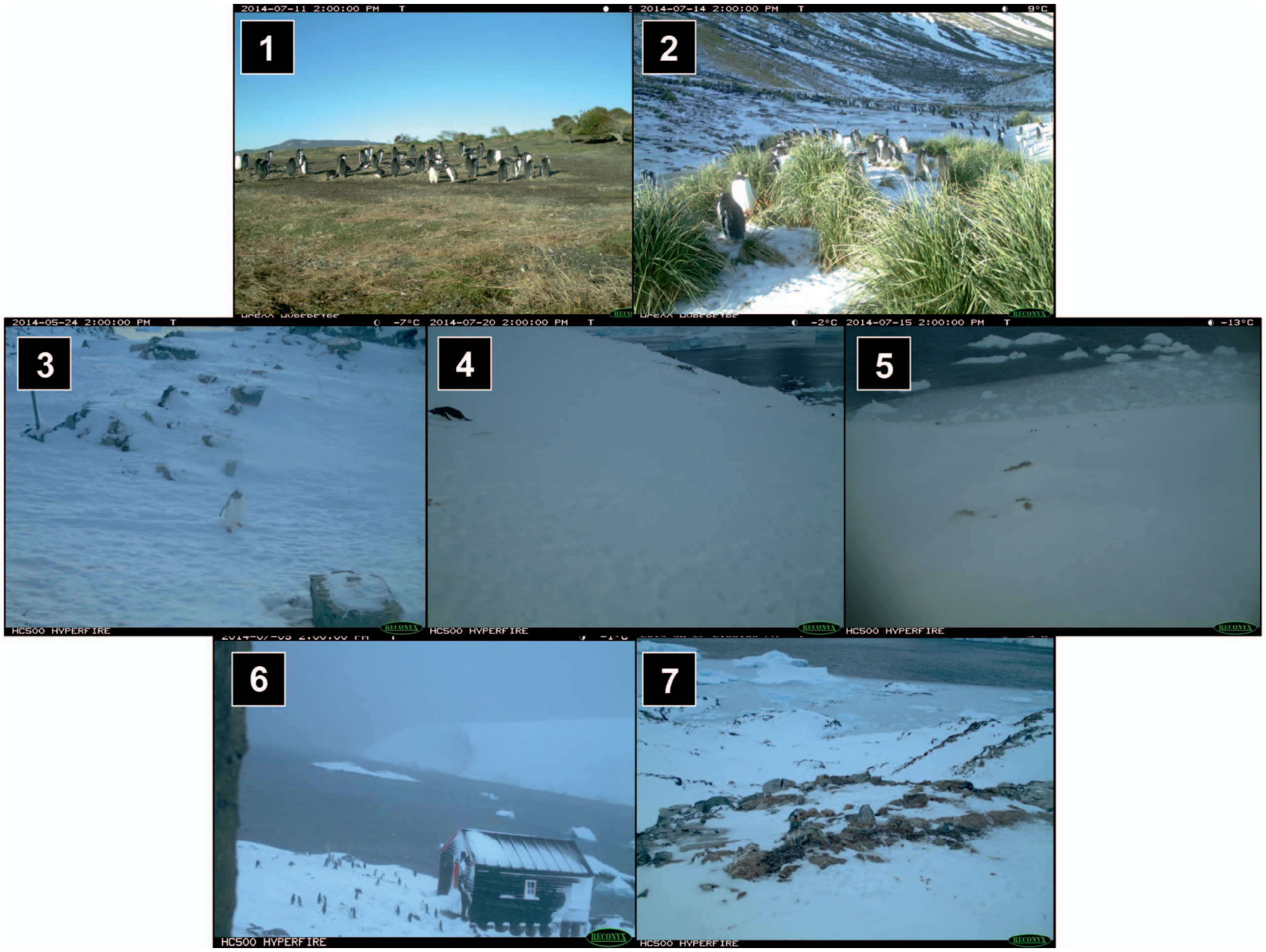

**APPENDIX FIGURE 3.** Example images taken during the nonbreeding period of 2014 at (1) Martillo Island, (2) Maiviken, (3) Cuverville Island, (4) Danco Island, (5) Neko Harbor, (6) Port Lockroy, and (7) Petermann Island.