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Population trends and reproductive success at a frequently visited penguin colony on the western Antarctic Peninsula

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Abstract Petermann Island (65°10′S, 64°10′W), one of the Antarctic Peninsula's most frequently visited locations, is at the epicenter of a rapid shift in which an Adélie penguin dominated fauna is becoming gentoo penguin dominated. Over the course of five seasons, the breeding productivity of Adélie and gentoo penguins breeding at Petermann Island were monitored to identify drivers of this rapid community change. The impact of tourist visitation on breeding success was also investigated. Consistent with larger trends in this region, the Adélie penguin population decreased by 29% and the gentoo penguin population increased by 27% between the 2003/2004 and 2007/2008 seasons. Reproductive success among Adélie penguins ranged from 1.09 to 1.32 crèched chicks/nest, which was higher than or comparable to other sites and is an unlikely explanation for the precipitous decline of Adélie penguins at Petermann Island. Whereas gentoo penguin reproductive success was lowest in colonies frequently visited by tourists, Adélie penguin colonies frequently visited by tourists had higher reproductive success than those visited only occasionally. These results are placed in the context of other studies on reproductive success and the impact of tourist visitation on breeding colonies of Adélie and gentoo penguins.

Keywords Adélie penguin · Gentoo penguin · Long-term monitoring · Breeding success · Tourism

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Introduction

Despite its small size (~1 mi long and ½ mi wide), Petermann Island (65°10′S, 64°10′W; Fig. 1) represents an important breeding area for both penguins and flying birds on the Antarctic Peninsula. Resident species include gentoo penguins (*Pygoscelis papua*), Adélie penguins (*P. adeliae*), blue-eyed shags (*Phalacrocorax atriceps*), south polar skuas (*Stercorarius maccormicki*), brown skuas (*S. antarctica*), south polar × brown skua hybrids, kelp gulls (*Larus dominicanus*), Wilson's storm petrels (*Oceanites oceanicus*), and snowy sheathbills (*Chionis alba*). Prior to the recent southward expansion of gentoo penguin breeding (Lynch et al. 2008), Petermann Island was also the southernmost documented breeding site for gentoo penguins (Croxall and Kirkwood 1979). Although no longer the southernmost gentoo colony, Petermann Island remains the fourth largest gentoo penguin colony on the western Antarctic Peninsula [after Cuverville Island (64°41′S, 62°38′W), Duroch Island (63°18′S, 57°54′W), and Gerlache Island (64°35′S, 64°16′W); H. J. Lynch, unpublished data] and probably represents an important source of migrants to new colonies further south. In addition to its biological importance, Petermann Island is also the sixth most frequently visited penguin colony on the Antarctic Peninsula (International Association of Antarctic Tour Operators 2008), and thus presents an opportunity to assess the potential impacts of tourist visitation on the breeding success and population trajectories of Antarctic penguins. For these reasons, Oceanites Inc. (a non-profit research organization monitoring breeding birds on the Antarctic Peninsula) initiated a 5-year census and reproductive study in 2003 with the goal of understanding the relative fates of the increasing gentoo population and the declining Adélie population (Lynch et al. 2008). The principal goals of the project were: (1) to obtain nest and chick census counts that conformed to the standards defined by the CCAMLR Ecosystem Monitoring Program (Scientific Committee for the Conservation of Antarctic Marine Living Resources 2004), and (2) to determine if breeding performance was related to year, colony, or the level of visitation each colony received.

Recently, Trathan et al. (2008) published the results of their research on the gentoo penguin colony at Port Lockroy, and comparing results from that study with our own presents an opportunity to compare two sites on the western Antarctic Peninsula with a mix of gentoo colonies receiving high levels of visitation and those experiencing little or no visitation. We note that although Port Lockroy receives more landed passengers than Petermann Island (16,398 vs. 11,922 in 2007/2008), both sites experience similar temporal patterns of visitation, with visitation beginning and ending within a few days of each other at the two sites. Therefore, the timing and intensity of visitation at the two sites with respect to the breeding phenology of the penguins involved is similar. Unlike the study at Port Lockroy, Petermann Island also offers the opportunity to assess the reproductive performance of Adélie penguins, a species that has been in sharp decline on the western Antarctic Peninsula (Ducklow et al. 2007; Lynch et al. 2008; McClintock et al. 2008) and which has gone locally extinct at some sites (Rejcek 2008).

Methods

The first two seasons of the Petermann Island study (2003/2004 to 2004/2005) focused on mapping the island's penguin colonies and site-wide censuses of the breeding penguins. In the austral spring of the succeeding three seasons of the study (2005/2006–2007/2008), a total of 60 Adélie nests in 12 colonies and 100 gentoo nests in 20 colonies were chosen after nest establishment but before clutch initiation for the reproductive study. (Note that we use the word “colony” to describe a contiguously nesting group of penguins. Penguin colonies, which may include more than one species, are separated by areas of unoccupied bare ground, and there are many colonies at the “site” Petermann Island.) A group of five contiguous nests were randomly selected from within the colony, and the location of each nest relative to the group was photographed and marked by a painted stone placed in the center of the group. These same five nests were then tracked throughout the remainder of the breeding season. Nests were selected equally from both small (≤25 nests) and large (>25 nests) colonies to assess the importance of colony size in population trend and reproductive success. As Adélie penguin reproductive success has been linked to proximity to colony edge (Spurr 1975; Davis and McCaffrey 1986), we also recorded whether Adélie nests were “peripheral” (i.e. at the colony edge, or one adjacent to a nest at the colony edge) or “central” (i.e. at least two nests away from the colony edge). Reproductive study nests were visited daily to assess nest contents and track the fate of reproductive effort. Observation of nest contents was passive (i.e. penguins were observed from a distance and were not manipulated in any way) and, whenever possible, observers maintained at least 5 m distance from the penguin colony to minimize unnecessary disturbance. In this way,

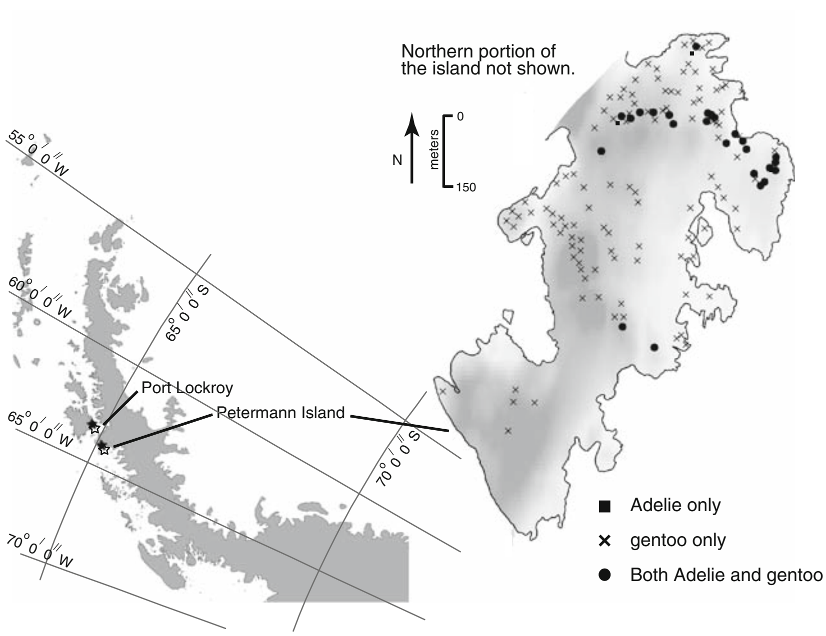

Fig. 1 Map of Petermann Island

observers determined the dates of clutch initiation and completion for each nest in the study; daily observations ensured that dates were accurate to within 1 day. Egg loss and any re-laying events were also recorded. Once each of the five nests in the group had complete clutches, the group was visited every 2 days to determine nest contents and record any egg losses or nest failures. Within a week of the peak of egg laying for each of the two species, a complete site-wide census count of nests for that species was completed for the island. In the days approaching egg hatching, nests were once again monitored daily so that the exact dates of egg hatching could be established for each of the study nests. For the remainder of the breeding season, nests were observed every other day to record any chick mortality and, eventually, the initiation of chick crèching within the colony. Within a week of the peak of chick crèching for each species, a site-wide census of chicks was completed. It is important to emphasize that the principal goal of these reproductive study nests was to establish the breeding phenology for each penguin species in each year so that site-wide nest and chick censuses could be completed at the correct times. Our analysis of population trends and colony-specific breeding productivity was derived entirely from the data collected during these site-wide censuses and are therefore less sensitive to some of the sampling issues that can arise when dealing with a sub-sample of the entire population.

To compare breeding productivity for the gentoo penguin population at Petermann Island with those at Port Lockroy, we performed the same series of parsimonious linear and linear mixed-effects models reported in Trathan et al. (2008), retaining their notation for simplicity. Occasionally, crèched chicks from neighboring colonies merged before the chick census, making it impossible to assess the breeding productivity of each colony individually, and for this reason we analyzed regions with closely spaced colonies together as a single unit. This approach differs slightly from that of Trathan et al. (2008), who considered each gentoo colony separately. Although Site Guidelines for Petermann Island detailing areas to be avoided by visitors were not adopted until 2006/2007 (Resolution 5 of the 2005 Antarctic Treaty Consultative Meeting), our experience interacting with tour visits allowed us to categorize each colony into one of three Colony Types representing Rarely Visited, Occasionally Visited, and Frequently Visited colonies on the island. Rarely Visited colonies were either expressly set aside as off-limits by the Petermann Island Site Guide or were rarely visited due to their distance from the landing site or due to difficult terrain between the landing site and the colony. On the opposite end of the spectrum, Frequently Visited sites were those that were either adjacent to the landing area or were at one of the destinations to which expedition staff would guide groups of passengers. Occasionally Visited Sites were those that were fairly easy to access by those passengers exploring the island separate from a tour group but were not areas to which groups of passengers were explicitly lead by expedition staff. We note that these categories were chosen prior to and separate from the analysis regarding the relative breeding performance of different areas of the island.

We considered nine different models for breeding productivity [y_{ij}; observation j in group (Colony, Year, Type) i], including an intercept-only model (Model 1) which pools all of the data to estimate site-wide mean productivity (β). Models 2–4 are fixed effects models with Colony (C), Year (Y), and Colony Type (T; representing the relative extent of visitation at each colony) as the fixed effects, respectively. Models 5–7 are random effects models in which Colony (C), Year (Y), and Colony Type (T) are modeled as random effects accounting for variability around the population mean (β). Model 8 includes both a fixed effects component [Colony Type (T)] and a random effects component [Colony (C)]. A ninth model was considered to evaluate the significance of colony elevation (E) in breeding productivity. Models were ranked according to their small-sample Akaike's Information Criterion (AIC_c) and model probabilities were assigned in proportion to their relative likelihood (Burnham and Anderson 2002).

Another potential factor in reproductive success and colony growth or decline is colony size. We compared the empirical relationship between colony size and reproductive success against a statistical model in which we used the proportion of nests that crèched zero, one, or two chicks from our reproductive study to simulate average productivity for all of the colonies. Repeating this simulation 1,000 times, we also assessed the extent to which variability in breeding success was due purely to expected stochastic fluctuations. Due to significant heteroskedasticity, we performed a weighted least squares regression to test for a linear relationship between productivity and colony size in which each point was weighted inverse-proportionally to its estimated variance (Fox 2002). Variance as a function of colony size is estimated by binning the data (colony size $\in$ [0,19], [20,39], [40,59], etc.) and fitting both linear and exponential models. For both Adélies and gentoos, the exponential model provided a better fit (i.e. a lower AIC) and was therefore used to weight points during the linear model fit.

Finally, to assess the potential impact of our reproductive study on breeding success, we compared the productivity of nests monitored as part of our reproductive study with the overall productivity of nests in those colonies.

Table 1 Census results from Petermann Island

	# Nests	# Chicks	Median clutch initiation date
Adélie penguins			
2003–2004	553	731	N/A
2004–2005	532	580	N/A
2005–2006	479	589	14 November 2005
2006–2007	410	458	15 November 2006
2007–2008	390	434	15 November 2007
Gentoo penguins			
2003–2004	2,145	3,260	N/A
2004–2005	2,265	2,781	7 December 2004
2005–2006	2,438	3,453	23 November 2005
2006–2007	2,293	3,343	19 November 2006
2007–2008	2,719	3,348	20 November 2007

Results

Based on our site-wide nest censuses, we found a 29% decline in the number of Adélie penguins and a 27% increase in the number of gentoo penguins between the 2003/2004 and 2007/2008 seasons (Table 1). These trends were consistent with long-term trends at Petermann Island (Fig. 2), which has a relatively long census history and has, since 1994, been one of the sites monitored by the Antarctic Site Inventory. Median clutch initiation dates were highly variable for gentoo penguins, but exhibited little year-to-year variability for the Adélies, consistent with previous analyses on breeding phenology in these two species (Lynch et al. 2009).

Overall yearly productivity (chicks crèched per nest) ranged from 1.23 to 1.52 for gentoos and 1.09 to 1.32 for Adélies. Comparing the results of the simple mean productivity model (Model 1), we found that the gentoo penguins at Petermann Island have significantly higher mean breeding productivity than those at Port Lockroy (1.39 [1.34,1.45] vs. 0.86 [0.82,0.90] where the 95% confidence intervals are shown in square brackets), despite the fact that our definition of productivity (which considers the number of chicks at the peak of chick crèching) is more conservative than that used by Trathan et al. (2008) (which considered the number of chicks when "hatching had ended") and would be expected to produce (given the same actual productivity) a measured value of productivity lower due to pre-crèche chick mortality.

We found the strongest support for Models 3 and 4 for the gentoos and Models 4 and 2 for the Adélies (Tables 2, 3). These models treat productivity as being a fixed effect of Year (Model 3), Colony Type (Model 4), and Colony (Model 2), respectively. As estimated by the model (i.e. equal weight among all the colonies), gentoos had their highest productivity (1.59) in 2003/2004 and their lowest (1.25) in 2007/2008. Adélies also had their highest productivity (1.29) in 2003/2004 but had their lowest productivity (1.06) in the following 2004/2005 season. Finally, we note that elevation (Model 9) was uncorrelated with breeding productivity for both gentoo and Adélie penguins despite the significant impact elevation has on the timing of nest completion and clutch initiation (H. J. Lynch, personal observation).

The relationship between colony size and breeding success was significantly heteroskedastic (Figs. 3, 4), with high levels of variability evident in colonies with ≤50 nests. Neither Adélie nor gentoo penguins exhibited a statistically significantly relationship between breeding productivity and colony size. Note that the variance associated with the simulated data (95th percentiles represented by the gray envelope in Fig. 4) was due entirely to stochastic fluctuations in the total number of chicks crèched in each colony, the variance of which grows rapidly as colony sizes get small. Given that only 16.6% of all the gentoo nests in our reproductive study crèched zero chicks, there was less than a 3% probability that a gentoo colony with two nests would produce zero crèched chicks, and less than a 0.5% chance that a gentoo colony with three nests would produce zero crèched chicks. Similarly, among the Adélie nests in our reproductive study, we found only 23.0% of all nests crèched zero chicks, which makes it highly improbable ($P < 0.05$) that a colony with as many as three nests would all completely fail. We found therefore, that among both gentoos and Adélies, an unexpectedly high number of colonies exhibited total colony failure (crèching zero chicks). In addition, the greater variability in average productivity at all colony sizes (relative to what would be expected by random chance alone) suggests a significant degree of autocorrelation in breeding success among nests in the same group of colonies.

Considering the role of nest location in large (>25 nests) penguin colonies, we found that Adélie eggs laid in centrally located nests had a higher probability of reaching crèche stage (54 of 63, $P = 0.86$) than eggs laid in peripherally located nests (107 of 147, $P = 0.73$), and that these differences were statistically significant (Pearson's chi-square test, $\chi^2 = 4.12$, $df = 1$, $P = 0.04$). There was an insufficient number of centrally located nests in small colonies to consider the impact of nest location in colonies with ≤25 nests.

We found that productivity in our reproductive study nests (crèched chicks per nest) is not different from the colony average for gentoo penguins (mean difference = +0.07, $P = 0.53$) but was significantly higher (mean difference = +0.20, $P < 0.001$) among Adélie penguins. This was consistent with the estimates from Model 4 (the most strongly supported model for the Adélie

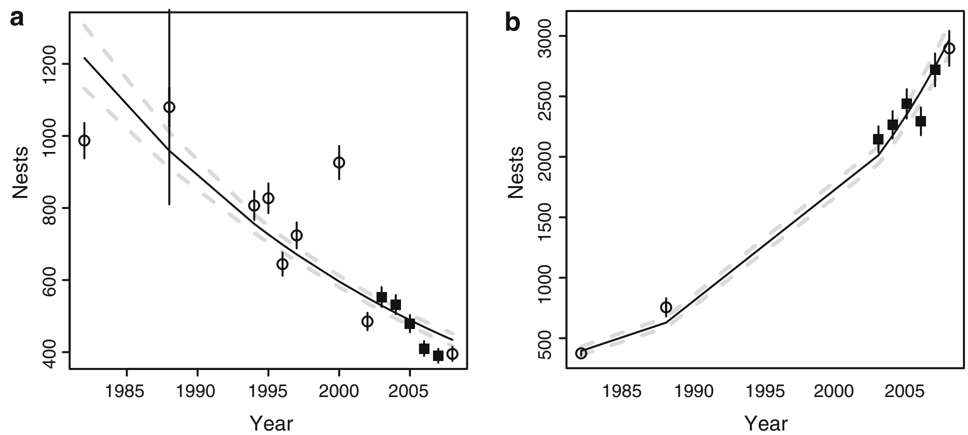

Fig. 2 Trends of Adélie (**a**) and gentoo (**b**) penguins at Petermann Island since the 1979–1980 season. Data from the 5-year study at Petermann Island are indicated by *filled squares*. The remaining data (*open circles*) come from either Oceanites' Antarctic Site Inventory project (Naveen et al. 2000; Lynch et al. 2008), Poncet and Poncet (1987), or Woehler (1993)

Table 2 Linear and linear mixed model results for gentoo penguin breeding productivity [y_{ij}; observation j in group (Colony, Year, Type) i] at Petermann Island, including an intercept-only model (Model 1) which pools all of the data to estimate site-wide mean productivity (β). Models 2–4 are fixed effects models with Colony (C), Year (Y), and Colony Type (T) as the fixed effects, respectively. Models 5–7 are random effects models in which Colony (C), Year (Y), and Colony Type (T) are modeled as random effects accounting for variability around the population mean (β). Model 8 includes both a fixed effects component [Colony Type (T)] and a random effects component [Colony (C)]. Model 9 evaluates the significance of colony elevation (E) in breeding productivity. Model fits are described by their log-likelihood (Log-lik), the number of estimated parameters (k), the small-sample AIC (AIC_c), the difference between the model AIC and the minimum AIC for the model set (Δ), and the Akaike weights representing relative model probabilities (w_i; Burnham and Anderson 2002)

Model	β/b_i	Log-lik	k	AIC_c	Δ	w_i
3: $y_{ij} = \beta_i Y_i + \varepsilon_{ij}$	[a]/–	−11.24	6	35.39		0.64
4: $y_{ij} = \beta_i T_i + \varepsilon_{ij}$	[b]/–	−14.17	4	36.76	1.37	0.32
6: $y_{ij} = \beta + b_i Y_i + \varepsilon_{ij}$	1.40 (1.28,1.51)/[c]	−19.08	2	42.28	6.89	0.02
7: $y_{ij} = \beta + b_i T_i + \varepsilon_{ij}$	1.41 (1.26,1.56)/[d]	−19.81	2	43.75	8.36	<0.01
1: $y_{ij} = \beta + \varepsilon_{ij}$	1.39 (1.34,1.45)/–	−20.39	2	44.91	9.53	<0.01
9: $y_{ij} = \beta + b_i E_i + \varepsilon_{ij}$	1.43 (1.32,1.53)/−0.003 (−0.011,0.005)	−20.06	3	46.87	11.48	<0.01
5: $y_{ij} = \beta + b_i C_i + \varepsilon_{ij}$	1.39 (1.32,1.46)/[e]	−22.19	2	48.52	13.13	<0.01
8: $y_{ij} = \beta_j T_i + b_i C_i + \varepsilon_{ij}$	[f]/[g]	−20.43	4	49.29	13.90	<0.01
2: $y_{ij} = \beta_i C_i + \varepsilon_{ij}$	[h]/–	−4.76	21	63.53	28.14	<0.01

[a] β_{2003} = 1.59 (1.47,1.71), β_{2004} = 1.30 (1.17,1.42), β_{2005} = 1.37 (1.25,1.49), β_{2006} = 1.47 (1.34,1.59), β_{2007} = 1.25 (1.12,1.37)

[b] $\beta_{Frequently}$ = 1.32 (1.22,1.41), $\beta_{Occasionally}$ = 1.35 (1.26,1.44), β_{Rarely} = 1.57 (1.46,1.68)

[c] b_{2003} = 0.155 (0.012,0.298), b_{2004} = −0.075 (−0.218,0.068), b_{2005} = −0.018 (−0.161,0.125), b_{2006} = 0.055 (−0.090,0.200), b_{2007} = −0.116 (−0.259,0.027)

[d] $b_{Frequently}$ = −0.080 (−0.237,0.077), $b_{Occasionally}$ = −0.051 (−0.208,0.106), b_{Rarely} = 0.131 (−0.030,0.292)

[e] b_i for each Colony: −0.043 (−0.193,0.108), −0.085 (−0.236,0.066), −0.058 (−0.209,0.093), −0.030 (−0.181,0.121), 0.021 (−0.130,0.172), −0.003 (−0.154,0.148), −0.002 (−0.153,0.149), −0.050 (−0.205,0.105), 0.014 (−0.137,0.165), 0.159 (0.008,0.310), 0.013 (−0.138,0.164), −0.029 (−0.180,0.122), 0.030 (−0.121,0.181), 0.023 (−0.128,0.174), −0.084 (−0.235,0.067), 0.033 (−0.118,0.183), 0.011 (−0.140,0.162), 0.042 (−0.109,0.193), −0.028 (−0.123,0.179), 0.065 (−0.086,0.216)

[f] $\beta_{Frequently}$ = 1.32 (1.22,1.41), $\beta_{Occasionally}$ = 1.35 (1.26,1.44), β_{Rarely} = 1.57 (1.46,1.68)

[g] b_i for each Colony (c.i. for all estimates are [−1.23e−5,1.23e−5]): −1.1e−10, −4.9e−10, −2.2e−10, −1.0e−10, 2.6e−10, 1.7e−10, 9.1e−11, −2.4e−10, 2.9e−10, 6.9e−10, 2.8e−10, −9.9e−11, 3.2e−10, 2.7e−10, −4.0e−10, −2.1e−10, −3.6e−10, −1.4e−10, −5.7e−12, 2.3e−11

[h] β_i for each Colony: 1.27 (1.03,1.52), 1.15 (0.91,1.40), 1.23 (0.98,1.48), 1.31 (1.06,1.56), 1.45 (1.21,1.70), 1.39 (1.14,1.63), 1.39 (1.14,1.64), 1.23 (0.95,1.51), 1.43 (1.19,1.68), 1.84 (1.60,2.09), 1.43 (1.18,1.68), 1.31 (1.06,1.56), 1.48 (1.23,1.73), 1.46 (1.21,1.71), 1.16 (0.91,1.41), 1.49 (1.24,1.73), 1.42 (1.18,1.67), 1.51 (1.26,1.76), 1.32 (1.07,1.56), 1.58 (1.33,1.83)

data), which showed that Frequently Visited sites had significantly ($P = 0.009$) higher productivity (mean 1.25) than Occasionally Visited sites (mean 1.09). (There is only a single small (≤5 nests) Adélie colony which is Rarely Visited, and it was excluded from this analysis due to low sample size.) In contrast, we found that gentoo productivity was highest in those areas that were Rarely Visited and lowest in areas that were Frequently Visited.

Table 3 Linear and linear mixed model results for Adélie penguin breeding reproduction at Petermann Island. Model parameters same as defined in Table 2

Model	β/b_i	Log-lik	k	AIC$_c$	Δ	w_i
4: $y_{ij} = \beta_i T_i + \varepsilon_{ij}$	[a]/–	14.90	3	−22.89		0.52
2: $y_{ij} = \beta_i C_i + \varepsilon_{ij}$	[b]/–	18.85	6	−22.05	0.83	0.34
1: $y_{ij} = \beta + \varepsilon_{ij}$	1.15 (1.09,1.21)/–	11.07	2	−17.70	5.19	0.04
5: $y_{ij} = \beta + b_i C_i + \varepsilon_{ij}$	1.15 (1.05,1.25)/[c]	10.89	2	−17.33	5.56	0.03
7: $y_{ij} = \beta + b_i T_i + \varepsilon_{ij}$	1.17 (1.01,1.33)/[d]	10.64	2	−16.85	6.04	0.03
9: $y_{ij} = \beta + b_i E_i + \varepsilon_{ij}$	1.15 (1.03,1.27)/−0.0002 (−0.012,0.012)	11.07	3	−15.22	7.67	0.01
3: $y_{ij} = \beta_i Y_i + \varepsilon_{ij}$	[e]/–	15.29	6	−14.94	7.95	<0.01
8: $y_{ij} = \beta_j T_i + b_i C_i + \varepsilon_{ij}$	[f]/[g]	10.91	3	−14.90	7.99	<0.01
6: $y_{ij} = \beta + b_i Y_i + \varepsilon_{ij}$	1.15 (1.07,1.23)/[h]	9.00	2	−13.56	9.33	<0.01

[a] $\beta_{\text{Frequently}} = 1.25$ (1.16,1.34), $\beta_{\text{Occasionally}} = 1.09$ (1.02,1.16)

[b] β_i for each Colony: 1.21 (1.10,1.32),1.13 (1.02,1.24),1.16 (1.05,1.27),0.97 (0.86,1.08),1.29 (1.18,1.40)

[c] b_i for each Colony: 0.044 (−0.082,0.169), −0.018 (−0.143,0.108), 0.007 (−0.119,0.132), −0.139 (−0.264,−0.014), 0.107 (−0.019,0.232)

[d] $b_{\text{Frequently}} = 0.072$ (−0.087,0.230), $b_{\text{Occasionally}} = -0.072$ (−0.230,0.087)

[e] $\beta_{2003} = 1.29$ (1.16,1.1.41), $\beta_{2004} = 1.06$ (0.93,1.19), $\beta_{2005} = 1.20$ (1.08,1.33), $\beta_{2006} = 1.09$(0.96,1.22), $\beta_{2007} = 1.12$ (0.99,1.25)

[f] $\beta_{\text{Frequently}} = 1.25$ (1.12,1.37), $\beta_{\text{Occasionally}} = 1.09$ (0.98,1.19)

[g] b_i for each Colony: −0.0244 (−0.138,0.089), 0.0250 (−0.081,0.131), 0.0441 (−0.062,0.150),−0.0691 (−0.175,0.037),0.0244 (−0.089,0.138)

[h] $b_{2003} = 0.068$ (−0.032,0.168), $b_{2004} = -0.047$ (−0.147,0.053), $b_{2005} = 0.027$ (−0.073,0.126), $b_{2006} = -0.032$ (−0.132,0.068), $b_{2007} = -0.016$ (−0.116,0.084)

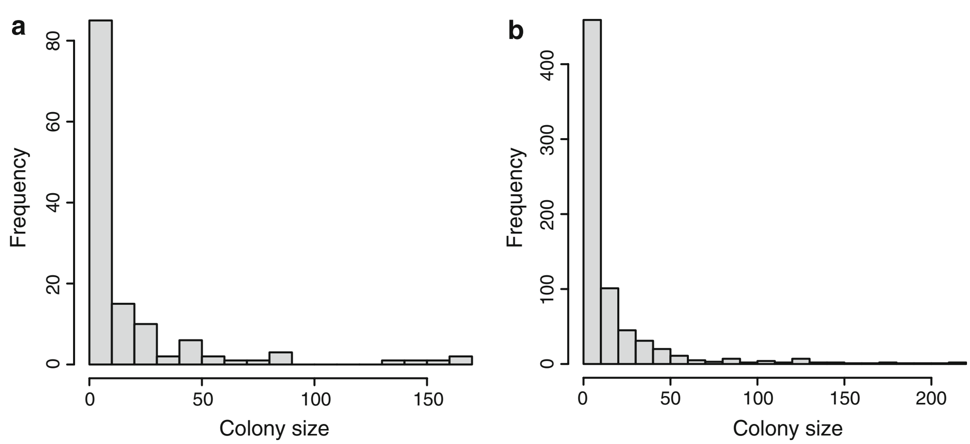

Fig. 3 Histograms of colony size for Adélies (**a**) and gentoo (**b**) penguins at Petermann Island for the 2003/2004–2007/2008 seasons. We have combined all of the years so that each colony is represented five times in the histogram, once for each year of the study. We included the sizes of all colonies in all 5 years for two reasons: (1) colony sizes change, sometimes dramatically, between years, and we wanted to include all the available information regarding the sizes of penguin colonies on Petermann Island, and (2) we wanted the information in this figure to correspond directly to that presented in Fig. 4, where each colony in each year is considered a "trial" which we could use to understand the role of colony size in breeding productivity

Discussion

The trends identified in this study closely mirror the larger trends of Adélie and gentoo penguin population dynamics along the western Antarctic Peninsula (Forcada et al. 2006; Ducklow et al. 2007; Lynch et al. 2008; McClintock et al. 2008). We found that gentoo penguin populations are increasing most quickly in the southernmost portion of their range (i.e. Petermann Island and areas to its south), and the high breeding productivity of gentoos at Petermann Island suggests that increasing gentoo populations result, at least in part, from high levels of reproduction and recruitment locally. Port Lockroy currently has both lower breeding success and a stable gentoo penguin population (Trathan et al. 2008), although a previous study on the gentoos at Port Lockroy, undertaken when the site's

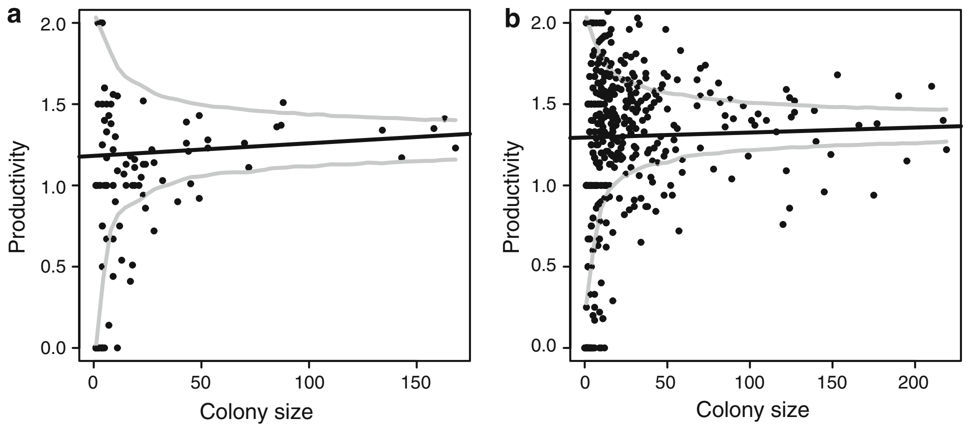

Fig. 4 Breeding productivity (chicks crèched per nest) as a function of colony size (*black dots*) for Adélie (**a**) and gentoo (**b**) penguins at Petermann Island. The linear fit produced by weighted least squares regression is shown as a *black line*; the slope of the line is non-significant for both Adélies (**a**) and gentoos (**b**). The 95th percentiles of expected productivity (*gray lines*) were constructed assuming that individual nests in each colony produced zero, one, or two crèched chicks with the same frequencies as found in the reproductive study. There are several small gentoo colonies that appear to have an average productivity that exceeds the biologically realistic value of two chicks per nest. This stems from the fact that some colonies did not finish getting established until after the nest census, and so the number of nests at the time of census does not reflect the final number of nests available to produce chicks

population was still growing, showed a comparable reproductive success rate of 1.24–1.39 chicks crèched/nest (Cobley and Shears 1999). We found further evidence for unusually high breeding success among Petermann Island's gentoo penguins by comparing to other published studies. Breeding productivity for gentoo penguins at Petermann Island (ranging from 1.23 to 1.52 crèched chicks/nest) was higher than has been reported at Bird Island, South Georgia [ranging from 0.0 to 1.20 crèched chicks/nest (Croxall and Prince 1979), 0.90 to 1.02 crèched chicks/nest (Williams 1990), and approximately 0.84 chicks fledged/nest (based on reported success of 0.44 chicks fledged/egg laid; Croxall et al. 1997)], in the South Shetland Islands [1.01–1.17 fledged chicks/nest (Trivelpiece et al. 1983 as cited by Cobley and Shears 1999)], at Possession Island [0.19–0.72 chicks fledged/pair (Bost and Jouventin 1991)], and at Macquarie Island [0.93 ± 0.45 chicks crèched/nest (Holmes et al. 2006), 0.36–1.14 chicks crèched/nest (Reilly and Kerle 1981), and 0.0–1.52 chicks crèched/nest (Robertson 1986)]. Also by comparison, 86% of all gentoo nests at Petermann Island nests hatched at least one chick, as compared to only 67% during an earlier study at King George Island (Trivelpiece et al. 1987). We might expect breeding productivity to decline with time at Petermann Island as the rapidly increasing population would be expected to include an increasing proportion of first-time breeders with relatively lower breeding success (Williams 1990), but we find no significant temporal trend in average gentoo breeding productivity. Finally, we note that although skuas do predate penguin eggs and young chicks, 2007/2008 corresponded with both the lowest breeding success for gentoo penguins and the lowest population of skuas breeding at Petermann Island (only four pairs bred on Petermann Island in 2007/2008 compared with 144 pairs in 2005/2006). Although predation pressure is only weakly related to the size of the breeding skua population (the vast majority of breeding skuas do not arrive at Petermann Island until penguin chicks have already hatched), this is inconsistent with the hypothesis that year-to-year variability in gentoo breeding success is due to variability in skua predation pressure.

It is difficult to assess why the Adélie penguin population at Petermann Island (or elsewhere) is declining, as over-winter mortality rates of Adélies in this region are poorly known. It is therefore difficult to discern whether the observed Adélie decline is principally related to unusually low breeding success (relative to a colony with stable population numbers) or unusually high overwinter mortality. Average productivity among Adélie penguins at Petermann Island (1.09–1.32 crèched chicks/nest) was either higher than or comparable to a host of other studies that have measured Adélie breeding success [0.92–1.40 chicks fledged/nest at Cape Royds (Taylor 1962; Yeates 1968), 0.89–1.37 chicks crèched/nest at Cape Hallett (Reid 1968), 0.68–1.23 chicks fledged/nest at Cape Bird (Spurr 1975), 0.98 chicks crèched/nest at King George Island (Trivelpiece 1981 as cited by Lishman 1985), 0.15–1.27 chicks fledged/nest at Signy Island (Lishman 1985), 0.67 chicks fledged/nest at Cape Bird (Davis and McCaffrey 1986), and 0.42–1.58 at Hope Bay, Antarctic Peninsula (Carlini et al. 2007)], despite an outbreak of ticks in 2006/2007 and 2007/2008 that led to several known cases of nest abandonment (Appendix). Only Ainley (2002) reports Adélie breeding success significantly higher than was found at Petermann Island (1.6 ± 0.1 crèched chicks/nest). We also note that mean Adélie breeding success on Petermann Island was consistent with average productivity of Adélies on the Peninsula during that period (H. J. Lynch et al., unpublished data).

One possible explanation would be that disturbance to the colony lowers recruitment to the colony, and that first time and returning breeders are less likely to establish nests at a site frequented by tourists (even if reproductive success at the disturbed site is unaffected). Woehler et al. (1994) suggested that pre-breeders "prospecting" a site may be discouraged from establishing nests at a frequently disturbed colony, and found a shift in the spatial distribution of breeding Adélies away from Casey station and disturbance from station personnel. [A similar explanation for the redistribution of gentoo penguins in response to tourism was offered by Trathan et al. (2008).] Under this scenario, we would expect that Adélie populations would be stable or increasing at neighboring but less visited sites which would, in theory, benefit from the additional recruitment of Adélies from Petermann. However, this is not the case, and Adélie populations are declining rapidly throughout the entire region (Lynch et al. 2008). A more likely explanation is provided by other studies (Croxall et al. 2002; Hinke et al. 2007) suggesting that over-winter mortality, particularly among juveniles, may play a key role in the relative trajectories of sympatrically breeding penguins on the Peninsula. Therefore, we conclude that the rapid decline of Adélie penguins at Petermann Island is not due to insufficient breeding productivity or discouraged pre-breeders but is likely due to factors (such as juvenile recruitment or adult survival) occurring outside of the breeding season. We hope that the results presented here can be compared against future studies to clarify this issue.

As to the detailed linear and linear mixed model analysis presented in Tables 2 and 3, our results are inconsistent with the results from Port Lockroy. Whereas Trathan et al. (2008) found greatest support for Models 5 and 8 (which both include colony as a random effect), we found strong support for Models 3 and 4 which include the fixed effects of Year and Visitation Type (respectively). The importance of year on the breeding success of gentoo penguins is not surprising, as gentoos are known to be highly adaptive in their breeding phenology (Croxall and Prince 1980; Bost and Jouventin 1990; Lynch et al. 2009) and to demonstrate high inter-annual variability in reproductive performance (Bost and Jouventin 1991; Trathan et al. 2007) and the number of breeding pairs and eggs laid (Trathan et al. 2008). However, the relatively greater support for year over colony as determinants of gentoo breeding productivity in our study may also stem in part from the different number of colonies considered and the length of time over which reproductive success was studied. In our study, we studied 20 gentoo colonies (strictly speaking, colony groups) over a 5-year period, whereas Trathan et al. (2008) studied 10 gentoo colonies over a 12-year period. Finally, we note that although identifying specific drivers of annual population fluctuations was not our principal goal, we did find a statistically significant negative correlation between breeding productivity in both gentoo ($P = 0.02$) and Adélie ($P = 0.03$) penguins and total December precipitation (sum of melted plus solid; precipitation data from Baker 2008). This is consistent with our own personal observations that heavy rain or snow in the austral spring can result in nest flooding or abandonment, an issue of increasing importance as precipitation has increased on the Peninsula (Boersma 2008; Turner et al. 2005).

Previous studies on the impact of human disturbance on penguins have been inconsistent, in large part due to difference in methods and metrics [i.e. whether impact is measured as a physiological/behavioral response (e.g., Nimon et al. 1995; Walker et al. 2005, 2006; Wilson et al. 1991), a change in breeding success/productivity (e.g., Cobley and Shears 1999; Giese 1996; Trathan et al. 2008), or a change in long-term population trends (e.g., Woehler et al. 1994)]. It is also widely acknowledged that impacts are likely to be species-specific (Holmes 2007; Trathan et al. 2008). Here we restrict our discussion only to those prior studies which have considered the impact of tourism (as opposed to visitation by or close proximity to research station personnel) on gentoo and Adélie penguin breeding success, as these were the specific metrics we investigated. With respect to the impact of visitation on gentoo breeding success, our findings closely mirror those from Port Lockroy (Trathan et al. 2008) and show that Frequent Visitation is associated with a significant decrease in breeding productivity relative to those colonies which are only Occasionally or Rarely Visited. Note that our results are more statistically significant that those of Trathan et al. (2008), although their findings of reduced productivity in visited colonies is consistent with their more statistically significant finding that visited colonies had a negative population trend relative to unvisited 'control' colonies. Both of these studies contradict an earlier study of gentoo penguins breeding at Port Lockroy (Cobley and Shears 1999) and a study at a research station on Macquarie Island (Holmes et al. 2006), in which no statistically significant differences were found between gentoos living in visited and unvisited colonies. However, both of these earlier studies were comprised of only a single season and it may be that, as suggested by Cobley and Shears (1999), gentoos in disturbed colonies are not disadvantaged during particularly successful breeding seasons. Longer term studies are crucial for understanding the potential interaction between overall breeding success (reflective of environmental conditions and prey availability) and the impacts of visitation.

While other studies have shown either significant decreases in breeding success among Adélie penguins receiving visitation (Giese 1996) or no effect (Carlini et al. 2007), we found that Frequently Visited sites actually had higher productivity than Occasionally Visited sites. We did not have a sufficient sample size of Rarely Visited Adélie colonies to include in our study, and so we do not know whether Occasionally or Frequently Visited colonies have higher or lower productivity than Rarely Visited colonies.

We note that there is no relationship between years of relatively high and low reproductive success among the gentoos at Petermann Island and those at Port Lockroy, despite the fact that they are only about 30 mi apart. As gentoo penguins feed in inshore areas close to their breeding colonies (Croxall and Prince 1980), it is not surprising that the breeding success of gentoos at Port Lockroy and those at Petermann Island reflect local conditions which are not shared across large regions. As the Antarctic Site Inventory project continues to collect nest and chick census data at each of their Inventory sites (>130), it should be possible to determine the spatial scale over which gentoo penguin reproductive success is correlated and, by extension, the spatial scale over which the main drivers of breeding success operate.

To improve future studies on the reproductive success of pygoscelid penguins, we would like to understand why the Adélie penguin nests that we monitored had significantly higher breeding success than the site average. One possibility is an unintentional bias in the selection of nests for our reproductive study. Another possibility is that our presence frightens off penguin predators such as skuas (Holmes et al. 2006), although this seems an unlikely explanation since the colonies are, on average, quite small and our presence at the colony is likely to affect all the nests in the colony and not just those we happen to be monitoring. It is therefore important that, in future, such reproductive studies establish a mechanism for choosing nests in advance so that inadvertent biases do not affect the study results.

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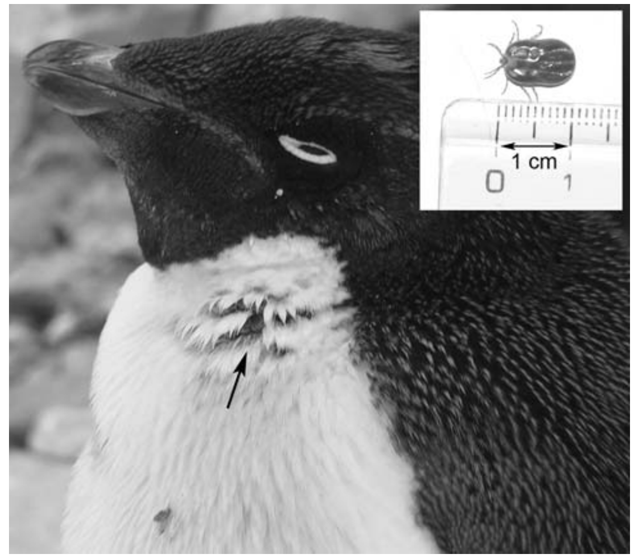

Fig. 5 Adélie penguin with *I. uriae* attached near the neck (*arrow*). *Inset* close-up of *I. uriae*. Photos by Steve Forrest

Appendix

Although not a component of our original study, we discovered an infestation of ticks (*Ixodes uriae*) among the penguins at Petermann Island in 2006/2007 and, to a lesser extent, in 2007/2008. Although *I. uriae* is a common seabird tick endemic to the region (Kerry et al. 1999; Rick Lee, personal communication) and is known to infest penguins at other sites (Murray and Vestjens 1967; Bergström et al. 1999; Gauthier-Clerc et al. 1999, 2003; Frenot et al. 2001), this was the first time that we had noted a tick infestation at Petermann Island since we first started doing census work in 1994. Tick infestation appeared completely restricted to Adélie penguins, even in mixed Adélie/gentoo colonies. Ticks attached themselves at high densities to the neck area where penguins were unable to preen, and tick infestations were characterized by swelling and severe, bloody infections of the neck and chest (Fig. 5). Affected penguins showed a number of unusual behaviors, including in several documented cases nest abandonment. Tick infestations were seen to spread among penguins at a colony. We do not know why *I. uriae* infestation was evident in these two seasons but not in any others, or whether climate change on the Peninsula may be related to improved conditions for *I. uriae* or other seabird parasites. However, we note that such an infestation may provide an additional mechanism contributing to Adélie decline, particularly for colonies in which a historically low number of breeding Adélies may be coping with a stable or increasing number of parasites at a particular location.

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