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Author(s): Samanta Dodino, Tom Hart, Sabrina Harris, and Andrea Raya Rey Source: The Wilson Journal of Ornithology, 130(2):493-501. Published By: The Wilson Ornithological Society <u>https://doi.org/10.1676/17-026.1</u> URL: <u>http://www.bioone.org/doi/full/10.1676/17-026.1</u>

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Year-round colony attendance patterns for the Gentoo Penguin (*Pygoscelis papua*) at Martillo Island, Tierra del Fuego, Argentina

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ABSTRACT—Long-term monitoring of seabird breeding cycles and breeding success is essential for conservation and a valuable indicator of ecological change, but is logistically expensive and time consuming. We describe the annual cycle and year-round colony attendance patterns for Gentoo Penguins *Pygoscelis papua* at Martillo Island, Beagle Channel, by analyzing camera trap photographs. We deployed a Reconyx HC500 Hyperfire trail camera programmed in time-lapse mode to take single pictures once per hour year-round (27 Feb 2013 until 27 Feb 2014). The nonreproductive stage began 23 April 2013 when adults completed molt and ended 24 September 2013 when the first pair formation was observed. In general Gentoos Penguins performed daily trips, and the number of adults present at 1900 h ART was not significantly different at any stage except the late chick-rearing and premolt stages. Breeding success was 0.92 chicks per nest. Small variations in day length had a significant influence on penguin's trip duration during the nonreproductive stage. The method proved to be effective for monitoring this species and provided important data for management and conservation. *Received 7 July 2017. Accepted 26 December 2017.*

Key words: annual cycle, attendance patterns, breeding success, camera monitoring, Gentoo penguins, Martillo Island, reproductive biology.

Patrones de asistencia anual a la colonia en el pingüino papúa (*Pygoscelis papua*) en Isla Martillo, Tierra del Fuego, Argentina

RESUMEN (Spanish)—Monitorear a largo plazo los ciclos reproductivos y el éxito reproductivo de las aves marinas es esencial para la conservación de las especies y valioso como indicador de cambio ecológico, pero logisticamente es costoso y lleva mucho tiempo. En este estudio describimos el ciclo anual y los patrones de asistencia a la colona durante todo un año de los pingüinos papúa *Pygoscelis papua* en Isla Martillo, Canal Beagle, mediante el análisis de fotografías. Instalamos una cámara Hyperfire Reconyx HC500 programada en modo lapso de tiempo para tomar una fotografía por hora durante todo un año (27 de febrero de 2013 hasta el 27 de febrero de 2014). La etapa no reproductiva comenzó el 23 de abril de 2013 cuando los adultos completaron la muda y finalizó el 24 de septiembre de 2013, cuando se observó la formación de la primera pareja. En general, los pingüinos papúa realizaron viajes diurnos y el número de adultos presentes a las 19h00 no mostró una diferencia significativa entre las etapas, excepto para las etapas cuidado tardío de pichones y pre-muda. El éxito reproductivo fue de 0.92 pichones por nido. Pequeñas variaciones en la duración del día tuvieron una influencia significativa en la duración del viaje de los pingüinos durante la etapa no reproductiva. El método demostró ser efectivo para el monitoreo de esta especie y proporcionó datos importantes para su manejo y conservación.

Palabras clave: biología reproductiva, ciclo anual, éxito reproductivo, Isla Martillo, monitoreo con cámaras, patrones de asistencia, pingüinos papúa.

Traditional monitoring studies on seabird colonies to gather demographic, breeding, and foraging data required large investments of time and money. The benefits of automatic procedures for collecting scientific data are widely recognized (Hinkler et al. 2002, Claridge et al. 2004) and increasingly feasible with state-of-the-art technology gadgets. Recent application of timelapse cameras provides a low-cost opportunity and a noninvasive method to monitor temporal patterns of reproductive and feeding behavior of colonial seabirds (Newbery and Southwell 2009, Huffeldt and Merkel 2013, Southwell and Emmerson 2015). The benefit of this method is improved quality of long-term monitoring data that extend over full seasons, particularly when the cost to regular access sites for repeated data collection is high. Although time-lapse cameras have long been used for mammals (Carbone et al. 2001, Tobler et al. 2008, Ahumada et al. 2011) and passerine birds (Pietz and Granfors 2000, Stake and Cimprich 2003), studies on seabirds, and penguins in particular, are in their initial stages (Southwell and Emmerson 2015).

The Gentoo Penguin (*Pygoscelis papua*) has one of the most extensive latitudinal ranges, breeding from the Crozet Islands (46°S) in the southern Indian Ocean (Bost and Jouventin 1990a) to Cape Tuxen (65°S) on the Antarctic Peninsula

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(Woehler 1993, Lynch et al. 2012). Despite a large range in climate and marine conditions around colonies and strong regional differentiation (Dinechin et al. 2012, Levy et al. 2016), their populations have several similar characteristics (Williamns 1995), including small-sized colonies, asynchronous laying of 2 eggs, short foraging trips near the colony, egg replacement after egg or chick loss, and year-round presence at the colony (Trivelpiece et al. 1987, Bost and Jouventin 1990a, Otley et al. 2005, Lynch 2013).

Across their geographic range, Gentoo Penguins exhibit variation in timing of breeding, foraging trip lengths during incubation and brood periods, and individual and colony-wide breeding success (Lescroël and Bost 2005, Lynch 2013). These variations have been identified as a consequence of fluctuations in prey availability around their colonies (Lescroël and Bost 2006). In Tierra del Fuego, this species has nested at Martillo Island since the mid-1980s, located within a colony of Magellanic penguins (Spheniscus magellanicus). This incipient colony is the only breeding site known for the species in South America, excluding the Falkland (Malvinas) Islands (Schiavini et al. 2005), highlighting the importance of its conservation. This colony's population has increased since 1993 (Ghys et al. 2008, Raya Rey et al. 2014), despite the rise in tourism and human population growth in the area. In 2014, the colony held 31 active nests (Raya Rey et al. 2014) and, given its small size, we determined that a trail camera could prove an effective, noninvasive method to monitor the whole colony within and outside the breeding season. We also hoped the camera would provide information to elucidate colony attendance patterns and daily, seasonal, and interannual variations known to affect population trends (Birkhead 1978, Harris et al. 1986, Cadiou 1999, Dittmann and Becker 2003).

With the exception of some reproductive parameters such as egg laying, hatching dates, and reproductive success, little is known about the species in South America (Ghys et al. 2008). The year-round colony attendance pattern is still poorly known for most of the colonies of this species in general, and for the colony of Martillo Island in particular (Lynch 2013). The main objective of this study was to describe the annual cycle and the year-round colony attendance patterns of Gentoo Penguins at Martillo Island. In particular, we aimed to (1) determine variations of colony attendance patterns according to the penguin annual cycle, (2) evaluate differences in colony attendance patterns throughout the day and between reproductive stages, and (3) examine possible relations between the "potential" foraging time at sea (i.e., difference between the hour when penguins return to the colony and sunrise) and air temperature and day length during the nonreproductive stage.

Methods

Study area

This study was conducted on Martillo Island, Tierra del Fuego, Argentina (54°54.5'S, 67°23'W). This hammer-shaped island, part of a group of small islands located in the eastern section of the shallow Argentinean waters of the Beagle Channel, is 2000 m long on its northwest-southeast axis and 750 m wide north to south.

Data collection

We deployed a Reconyx HC500 Hyperfire trail camera (Reconyx, Inc., Holmen, WI, USA) designed to operate over long periods with minimal maintenance (our 12 lithium batteries were replaced only once throughout the year, at the beginning of the breeding stage). The camera was placed inside a tree trunk roughly 20 m from the colony to observe the 31 nests (Raya Rey et al. 2014), oriented south to avoid lens glare. It was programmed in time-lapse mode to take a single picture per hour from 0900 to 1100 h and from 1400 to 2000 h ART (UTC-3), a setup chosen to maximize the use of batteries and memory card. In addition, the gap in the schedule coincides with hours when penguin attendance is fairly constant (ARR, 2012, pers. obs.). Photographs were taken from 27 February 2013 until 27 February 2014. The camera also recorded ambient temperature.

For each photo we recorded date, Julian date, time, time of sunrise and sunset, temperature, and the number of adults, nests, and chicks. Counts were made with the iTag 0.6 program (http:// sourceforge.net/projects/itagbiology/), an opensourced software that automatically counts birds and marks adults, nests, and chicks with colorcoded circles (Viquerat and van Neer 2014). Sunrise and sunset times were obtained from the US National Oceanic & Atmospheric Administration (NOAA; http://www.esrl.noaa.gov/gmd/grad/ solcalc/).

Annual cycle

We recorded the dates of settlement stage (pair formation and nest building), beginning and end of the incubation stage, hatching, beginning and end of chick-rearing stage, crèche formation, chick molting, chick fledging, premolt adult stage, adult molting, and beginning and end dates of the nonreproductive stage.

Evening colony attendance year-round

To evaluate the numbers of adults at the colony between the different stages (nonreproductive, pair formation and nest building, incubation, early chick-rearing stage, late chick-rearing stage, premolt stage, molting) we used the images taken at 1900 h. We chose this time for 2 reasons: (1) during winter the pictures after 1900 h were dark and difficult to count, and (2) we observed that the maximum number of adults in the daily cycle for all stages is fairly constant from 1900 h onward. We used a generalized linear model assuming a negative binomial error distribution and logit link function due to overdispersion in both Poisson and quasi-Poisson models (Crawley 2007). The response variable was the number of adults, and the explanatory variable was the different stages.

Colony attendance vs. sunrise, temperature, and day length during the nonreproductive stage

We calculated the difference between sunrise and the arrival time for the maximum number of penguins as an indicator of the potential foraging time at sea (maximum foraging time based on the span of daylight hours). We then evaluated this difference for the nonreproductive stage in relation to air temperature and day length using a generalized linear model assuming a Gaussian error distribution. The response variable was the difference between sunrise and the arrival time at the colony, and the explanatory variables were air temperature and day length. We used an information-theoretic approach to guide model selection. For each model in the candidate set, we calculated Akaike's information criterion corrected for small sample size (AICc) and Akaike weights (*wi*). Based on the entire model set, we then calculated model-averaged parameter estimates, unconditional standard errors, and 95% confidence intervals (CI) for each explanatory variable.

All statistical analyzes were performed using R software (MASS, *Intest, MuMIn, Ime4, lattice, nlme, geepack*), version 3.1.2 (R Core Team 2014). The statistical tests were considered significant at P < 0.05.

Breeding success

Breeding success was defined as the number of chicks at the end of the late chick-rearing stage divided by the number of active nests at the end of the incubation stage. Active nests were defined as any nest with a penguin incubating eggs or rearing chicks. The number of active nests was counted at the end of the incubation stage (early Nov) because Gentoo Penguins are asynchronous breeders (Bost and Jouventin 1990b). The number of chicks was counted at the end of the late chickrearing stage (early Feb) before they began to leave the colony.

Results

Annual cycle

The annual cycle of the Gentoo Penguin colony at Martillo Island (Fig. 1) indicates the nonreproductive stage began 23 April 2013, the day no more adults were observed molting. The ending date for the nonreproductive stage was 24 September 2013, and the onset of the following breeding season was registered on 25 September when we observed pair formation. The first nests were observed on 30 September, although they were abandoned within the following 5 d. On 14 October, more nests were established and the number of nests increased thereafter. Birds showing incubation postures were first noted on 16 October. Fifteen nests were established on 23 October 2013, coinciding with in situ estimates made on the island for that day (ARR, 2013, unpubl. data).

On 7 December 2013, the first chick was observed, ushering in the early chick-rearing stage that lasted until 3 January 2014. Crèche formation was observed on 4 January 2014,



Figure 1. Annual cycle of the Gentoo Penguin at Martillo Island, Argentina, from 27 Feb 2013 to 27 Feb 2014.

which we considered the onset of the late chickrearing stage. Later, on 26 January 2014, we observed the first chicks molting, which continued until 18 February 2014 when no chicks were observed at the colony, marking the beginning of the adult premolt stage. On 27 February we saw the first molting adults (start of molt stage), which ended 23 April.

Evening colony attendance year-round

We found significant differences among stages in the number of adults present at the colony at 1900 h ($\chi^2 = 134.8$, P < 0.05; Fig. 2). Between the late chick-rearing stage (1) and the premolt stage (2), the number of adults was significantly lower than the other stages: (1) late chick rearing stage (mean = 22.96 [SD 7.86] adults) vs. nonbreeding



Figure 2. Differences between stages of the annual cycle in numbers of Gentoo Penguin adults attending the Martillo Island, Argentina, colony at 1900 h, 27 Feb 2013 to 27 Feb 2014. The central rectangle spans the first to the third quartile, the intersected crossbar drawn in the boxes represents the median of the dataset, and the whiskers above and below the box indicate minimum and maximum values. Different letters indicate significant differences between these stages.

(t = -6.86, P < 0.05), vs. pair formation (t = -5.14, P < 0.05), vs. incubation (t = -5.4, P < 0.05), vs. early chick (t = -4.28, P < 0.05), vs. premolt (t = -4.62, P < 0.05), vs. molting (t = 5.3 P < 0.05); and (2) the premolt stage (mean = 1.78 [SD 1.72] adults) vs. nonbreeding (t = -5.57, P < 0.05), vs. pair formation (t = -5.56, P < 0.05), vs. incubation (t = -5.46, P < 0.05), vs. early chick rearing (t = -5.37, P < 0.05), vs. molting (t = 5.37, P < 0.05), vs. molting (t = 5.44, P < 0.05).

Colony attendance in relation to sunrise, temperature and day length during the nonreproductive stage

Differences between sunrise and the time of arrival of birds at the colony provided estimates of trip duration or time available to forage. This difference had a quadratic relationship with day length, which meant that small variations in day length would have a significant influence on the attendance pattern, with more time to forage the longer the day (Fig. 3). By contrast, temperature did not by itself explain the attendance pattern (Tables 1 and 2).

Breeding success

We counted 26 active nests by the end of the incubation stage (4 Nov 2013) and 24 chicks at the end of the late chick-rearing stage (4 Feb 2014). Thus, breeding success was 0.92 chicks per nest at the Martillo Island colony.

Discussion

This study provides the first data of the annual cycle of the westernmost colony of Gentoo Penguins. Both latitude and longitude are important to the breeding phenology of Gentoo Penguins (Black 2016). Our study also describes the colony attendance pattern for different stages of the annual cycle and inter-stage variation in evening (1900 h) attendance, thereby adding to the growing literature on breeding and behavioral parameters obtained from time-lapse imagery (Southwell and Emmerson 2015). Further, we show that small variations in day length have a significant influence on the colony activity pattern during the nonreproductive stage while temperature by



Figure 3. Potential foraging trip duration of Gentoo Penguin adults and day length during the nonreproductive stage at Martillo Island, Argentina, 27 Feb 2013 to 27 Feb 2014.

itself does not explain the activity pattern of the colony.

With an automatic camera, we were able to record the annual cycle, important dates during the breeding period, colony attendance patterns, and breeding success of Gentoo Penguins. These parameters are all essential to the ecological knowledge base for this species and should be recorded annually to enable interannual comparisons and infer changes in environmental condi-

Table 1. Results of generalized linear models relating potential foraging time for Gentoo Penguins, Martillo Island, Argentina, during the nonreproductive period with environmental variables. K = number of estimated parameters; $\Delta AICc =$ differences in Akaike's information criterion corrected for small samples; wi = Akaike weight. All candidate models and the null model are presented, listed in descending order of wi.

Response variable	iable Model		ΔAICc	wi
Difference between sunrise and	Day length $+$ day length ²	4	0.00	0.36
the arrival of birds at the colony	Day length + day length ² + temperature ²	5	0.39	0.30
	Day length + day length ² + temperature	5	1.38	0.18
	Day length + day length ² + temperature + temperature ²	6	1.7	0.16
	Day $length^2$	3	11.93	0.001
	Day length ² + temperature ²	4	12.53	0.001
	Day $length^2 + temperatura + temperature^2$	5	13.37	0.00
	Day length ² + temperature	4	13.54	0.00
	Day length	3	27.17	0.00
	Day length $+$ temperature ²	4	27.62	0.00
	Day length + temperatura + temperature ²	5	28.42	0.00
	Day length $+$ temperature	4	28.71	0.00
	Temperature ²	3	231.51	0.00
	Temperature	3	232.29	0.00
	Temperatura $+$ temperature ²	4	233.29	0.00
	Null	2	248.49	0.00

bold.					
	Explanatory variable	Parameter likelihood	Parameter estimated (SE)	95% CI	
Response variable				Lower	Upper
	(Intercept)		13.95 (2.21)	9.57	18.32
Difference between sunrise and	Day length	1	-1.8(0.47)	-2.74	-0.86
the arrival of birds at the colony	Day length ²	1	0.14 (0.03)	0.09	0.19
	Temperature ²	0.45	0.005 (0.004)	-0.004	0.013
	Temperature	0.34	-0.14(0.05)	-0.12	0.09

Table 2. Parameter likelihoods, weighted parameter estimates with the unconditional standard error (SE), and 95% confidence intervals (CI) for explanatory variables used to describe variation in the differences between sumrise and the arrival of Gentoo Penguins at the Martillo Island, Argentina, colony. Explanatory variables with CI excluding zero are in hold.

tions (Bost and Le Maho 1993, Kitaysky et al. 2000, Davoren and Montevecchi 2003, Boersma and Rebstock 2009). In this study we observed photographs until 2000 h, but during the breeding stages the day lengths were later than that, so we suggest extending the time-lapse mode until sunset in future detailed studies on colony attendance.

Start dates of incubation and early chick-rearing stages obtained from this study were consistent with the dates of direct observations by Ghys et al. (2008). In their study, the incubation stage during the 2005-2006 and 2006-2007 seasons lasted 37 \pm 2 d and the mean hatching date was 12 December ± 4 d. In our study, we observed the first chick on 7 December 2013, which initiated the early chick-rearing stage. Moreover, these dates are similar to those known for other colonies of Gentoo Penguins in the South Atlantic region and on the Antarctic Peninsula (Bost and Clobert 1992). In particular, in one colony at Volunteer Beach, Falkland (Malvinas) Islands, Otley et al. (2005) estimated the mean hatching date as 6 December ± 4 d.

During the nonreproductive, pair formation and nest building (settlement), incubation, chickrearing, and molting stages we found similar patterns in the colony attendance at 1900 h. These similarities can be attributed to different behaviors in the various stages. During the nonreproductive stage, penguins do not have parental duties and thus returned to the colony when light was no longer available for foraging. Given that day length during winter is shorter and feeding time is consequently shorter (Wilson et al. 1989, 1993), the penguins returned near or before 1900 h. During the settlement and molting stages, a large number of adults were at the colony, which was expected because they had to build nests and pair bond or molt. Therefore, high attendance during these stages was due to limited foraging activity.

Similarities between the incubation and the early chick-rearing stages could arise from adults taking turns incubating the eggs or feeding the chick. During incubation, however, foraging trips are not constrained by the need to return to the colony to feed a chick, so potentially trips could be longer if food is scarce near the colony. During early chick rearing, adults should return regularly because chicks at this stage need more frequent meals than when they are larger (Croxall et al. 1988, Boersma et al. 1990, Walker and Boersma 2003). We therefore expected more adults at 1900 h during chick rearing compared to incubation. These numbers were similar, however, and we assume that prey availability near the colony was the same during the incubation and early chick-rearing stages.

While analyzing the late chick-rearing stage, we found that the number of adults was lower than most of the other stages, possibly because chicks during this stage are bigger, form crèches, and do not need parental care. Parents can therefore feed simultaneously, as has been found for other species (Raya Rey et al. 2007), and for a longer time. During the premolt stage the number of adults was significantly lower than during late chick-rearing stage. This finding was expected because breeders during this stage do not return to land but remain at sea to fatten before molt. The penguins observed at the colony were mainly nonbreeders or failedbreeders that had already made a premolt feeding trip and returned to molt early.

The estimated breeding success was 0.92 chicks per nest, similar to a previous direct observation estimate on similar dates (1.00 \pm 0.20 average for 4 seasons; Ghys et al. 2008). This similarity might be a consequence of ecosystem stability where penguins feed, especially because the diet of Gentoo Penguins is composed mainly of benthic prey (Clausen and Pütz 2003, Lescroël and Bost 2005). The similarity of the estimates suggests breeding success was reliably estimated from the camera data. We are aware that this estimation of breeding success may be overestimated because chicks may die off before fledging, and actual breeding success is almost impossible to assess. Nevertheless, our ongoing work is investigating whether higher frequency photographs (every 15 min), all-day recording (to capture the colony at sunset), and installing the camera closer to the colony will increase the accuracy of parameters measured at the colony.

Gentoo Penguins exhibit a high spatial and temporal variability in their diet and foraging areas during the breeding season (Clausen 2000, 2001; Pütz et al. 2001; Clausen and Pütz 2002) as well as over winter (Clausen and Pütz 2003). Consequently, a detailed study of the annual cycle and of the colony attendance of Gentoo penguins is essential to document temporal and spatial variability in the use of their breeding sites, which could reveal fluctuations in the marine ecosystem.

Acknowledgments

This study was supported by Agencia Nacional de Promoción Científica y Técnológica, PICT 2012 N° 1832, the Darwin Initiative and Wildlife Conservation Society. We thank R. Sáenz Samaniego for logistic support with the camera installation and data download. We also are grateful to Andrés and Alejandro Greco from Piratur SA for logistic support and transportation to the island.

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