

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

Samanta Dodino^{A,C}, Sabrina Harris^A, Tom Hart^B and Andrea Raya Rey^A

^ACentro Austral de Investigaciones Científicas (CADIC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Bernardo Houssay #200, Ushuaia 9410, Argentina.

^BDepartment of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.

^CCorresponding author. Email: sami.dodino@gmail.com

Abstract. Seabirds are an important component of the marine ecosystem and they may also be valuable indicators of ecological changes. Thus, it is essential to monitor their colonies to know their reproductive and feeding behaviour in each particular location, and also its inter-annual variation. The objective of this study was to describe the annual cycle and year-round colony attendance patterns for Gentoo penguins at Martillo Island. We deployed a Reconyx HC500 Hyperfire trail camera programmed in time-lapse mode to take single pictures once per hour year-round (February 27 2013 until February 27 2014). Thus, we could record the annual cycle, important dates during the breeding period, colony attendance patterns and breeding success. All these parameters are essential to enrich the knowledge of the ecology of this species and to evidence temporal and spatial variability within and between their breeding sites which could reveal fluctuations in the marine ecosystem.

Key words: Gentoo penguins, trail camera, Martillo Island, year-round cycle, breeding success, reproductive biology, attendance patterns

Introduction

Seabirds have been distinguished as indicators of climate change and the health of marine systems (Piatt et al. 2007, Einöder 2009, Mallory et al. 2010), presuming that we can measure the reproductive and feeding characteristics of a species in each location and inter-annual variation in these parameters. Traditional monitoring of seabird colonies for demographic and foraging data requires a large investment of time and money. However, the recent application of time-lapse cameras provides a low-cost opportunity to monitor reproductive and feeding parameters as well as to obtain data on the daily, seasonal and annual trends for colonial seabirds (Newbery and Southwell 2009, Huffeldt and Merkel 2013, Southwell and Emmerson 2015).

The Gentoo penguin *Pygoscelis papua* has one of the most extensive latitudinal ranges of any penguin species, breeding from the Crozet Islands (46°S) in the southern Indian Ocean to Cape Tuxen (65°S) on the

Antarctic Peninsula (Woehler 1993). Despite a large range in climate and marine conditions around colonies and strong regional differentiation, their populations show several similar characteristics (Williams 1995). Those features included small sized colonies, asynchronous laying of two eggs, short foraging trips near the colony, new egg laying (in case of losing eggs or chicks) and year-round presence at the colony (Trivelpiece et al. 1987, Bost and Jouventin 1990, Otley et al. 2005, Lynch et al. 2013). In contrast to other penguin species, Gentoos exhibit high plasticity (Lescro  l et al. 2009, Lynch et al. 2009) which can confer numerous advantages confronting environmental and climatic changes (Forcada & Trathan 2009).

Across its geographic range, the Gentoo Penguin exhibits variation in timing of breeding, foraging trip lengths during incubation and brood periods, and individual and colony-wide breeding success (Otley et al. 2005). As this species forages close to its breeding grounds (Lescro  l and Bost 2005), different population trends among colonies might be explained by variation in local prey availability (Lescro  l and Bost 2006). This feature and the fact that they remain feeding nearby the colony outside the breeding season make the Gentoo penguin a potentially sensitive indicator of ecological changes in marine ecosystems (Williams 1990, Williams & Rothery 1990, Williams et al. 1992).

In Tierra del Fuego, this species has been reported nesting at Martillo Island since the mid-1980s and its nests are located within a colony of Magellanic penguins (*Spheniscus magellanicus*). This colony is the only breeding site known for this species in South America, excluding the Falkland (Malvinas) Islands (Schiavini et al. 2005), which highlights the importance of its conservation. This population has increased in numbers since 1993 (Ghys et al. 2008, Raya Rey et al. 2014) in spite of the increase in tourism in the area and human population growths.

Except for the knowledge of some reproductive parameters such as eggs laying and hatching date and reproductive success, little is known about the species within 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 et al. 2013).

The main objective of this study was to describe the annual cycle and the year-round colony attendance patterns for Gentoo penguins at Martillo Island. In particular, we aim to answer the following hypotheses:

- 1) Does the colony attendance at a fixed time point vary between the different stages?
- 2) Are there differences in colony attendance over the day and between reproductive stage?
- 3) Does the “potential” foraging time at sea (i.e. difference between the hour in which penguins return to the colony and sunrise) relate to air temperature and day length during the non-reproductive stage?

Materials and methods

Study Area

This study was conducted at the colony of Gentoo penguins on Martillo Island, Beagle Channel, Tierra del Fuego, Argentina (54° 54.5 'S, 67° 23'W). This hammer-shaped island is part of a group of small islands located in the eastern section of the shallow Argentinean waters of the Beagle Channel. It is 2000m long on its NW-SE axis and 750m long N-S. The colony of Gentoo penguins has increased since the 1980's and holds 31 active nests to date (Raya Rey et al. 2014).

Data Collection

We deployed a Reconyx HC500 Hyperfire trail camera (Reconyx, Inc., Holmen, WI, USA) designed to operate over long periods with minimal maintenance. The camera was placed inside a tree trunk and oriented South to avoid lens glare. It was programmed in time-lapse mode to take a single picture per hour from 9am to 11am and from 2 pm to 8 pm. Photographs were taken from 27 February 2013 until 27 February 2014. The camera also records environmental temperature and it was installed roughly 20 meters from the colony in order to observe the 31 nests (Raya Rey et al. 2014).

For each photo, we recorded in a database: the date, the Julian date, the hour, the temperature, the number of adults, nests and chicks, and the sunrise and sunset. We did the counts using iTag 0.6 program (<http://sourceforge.net/projects/itagbiology/>), an open-sourced software that allows marking adults, nests and chicks with circles with different colors and get an automatic count of them (Viquerat 2015).

The record of the sunrise and sunset were obtained from the site of the National Oceanic & Atmospheric Administration of the United States <http://www.esrl.noaa.gov/gmd/grad/solcalc/> Annual cycle

We recorded the dates of pair formation and nest building, beginning and end of the incubation stage, hatching, beginning and end of chick-rearing stage, crèche formation, chicks molting, chicks fledging, pre-molt stage, adults molting. Beginning and end of the non-reproductive stage were also recorded.

Year-round colony attendance at 19 pm

To evaluate the numbers of adults at the colony between the different stages (non-reproductive, formation and nest building, incubation, early chick-rearing stage, late chick-rearing stage, pre-molt stage, molting) we used the images taken at 1900 hours. This time of the day was chosen for two reasons; firstly, during winter the pictures after 1900 time were dark and difficult to count. Secondly, we observed that in the daily cycle for all stages, the maximum number of adults is fairly constant from 1900 onwards. 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 numbers of adults and the explanatory variable was the different stages.

Colony attendance throughout the day within each stage.

To evaluate the number of adults at the colony throughout the day we used generalized linear mixed model with the method of penalized quasi-likelihood (PQL) with Poisson errors distribution and log link function for each stage, given the over-dispersion data (Bolker et al. 2009). The response variable was the number of adults per hour in each stage and the random variable was the Julian date to account for repeated measures within the same day (Pinheiro & Bates 2000, Bolker et al. 2009).

Relationship between the difference in the hour that the penguins return to the colony and the hour of sunrise, as a function of air temperature and day length during the non-reproductive stage.

We calculated the difference between the arrival time for the maximum number of penguins and the hour of sunrise as an indicator of the potential foraging time at sea. We then evaluated, for the non-reproductive stage, this difference in relation with air-temperature and day length using Akaike information criteria.

All statistical analyzes were performed using the statistical program R 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 maximum number of chicks at the beginning of the late chick-rearing stage divided by the maximum 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 maximum number of active nests was counted by the end of the incubation stage (early November) because Gentoo penguins are asynchronous. The maximum number of chicks was counted at the beginning of the late chick-rearing stage (early January) before they begin to leave the colony.

Results

Annual cycle

The annual cycle of the colony of Gentoo penguins at Martillo Island is shown in Figure 1. The beginning of the non-reproductive stage was recorded on April 23, 2013, which corresponded to the day that no more adults were observed molting. Non reproductive stage ending date was recorded on September 24, 2013 as the onset of the following breeding season was registered on the 25 when we observed pair formation. On the first nests were observed on September 30, although they were abandoned within the following 5 days. On October 14 the nests were established and the numbers increased since then, showing the first incubation

postures on October 16. 15 nests were established on October 23 2013 which coincided with estimates made *in situ* on the island for the same day (Raya Rey pers. comm.).

On December 7, 2013 the first chick was observed, which ushered the early chick-rearing stage and lasted until January 3, 2014. *Crèche* formation was observed on December 4 and was the onset of the late chick-rearing stage.

Later, on January 26, 2014, the first chicks molting were observed, until February 18, 2014 when no more chicks were observed at the colony which marked the beginning of the pre-molt stage. Finally, on January 27 we visualized the first adults molting (molt stage).

Evening colony attendance year-round

When analyzing the colony attendance at 1900 hours for differences between stages we found no significant difference in the number of adults present between the non-reproductive stage, the pair formation and nest building stage, the incubation stage, the early chick-rearing stage and the molting stage. The number of adults was only lower during the late chick-rearing stage and the pre-molt stage compared with the rest of the stages, and we also found significant differences between both, being the numbers of adults lower during the pre-molt stage (Table 1, Fig. 2).

Colony attendance throughout the day within each stage.

Number of adults increased throughout the day (from 0900 to 1100, and from 1400 to 2000) for all stages except the pre-molt stage (Fig.3. a, b, c, d, e, g). During pre-molt period numbers remain constant and low throughout the day (Fig.3. f).

Colony attendance to the colony versus sunrise, temperature and day length during the non-reproductive stage.

Differences between the arrival time at the colony and hour of sunrise give estimates of trip duration or time available to forage. This difference presented a quadratic relationship with day length (Fig IX.), this means that small variations in day length would have a significant influence on the attendance pattern with penguins having more time to forage the longer the day. In contrast, temperature does not explain by itself the attendance pattern (Table 2).

Breeding success

Twenty-six active nests were counted by the end of the incubation stage (November 4, 2013) and a total of 27 chicks at the beginning of the late chick-rearing stage (January 5, 2014). Thus, breeding success was 1.04 chicks per nest at the Martillo Island colony.

Discussion

This study provides the first data of the annual cycle of the furthest West colony of Gentoo penguins at Martillo Island, relevant as both latitude and longitude have been demonstrated to be important to Gentoo breeding phenology. It also describes the colony attendance pattern throughout the day within each stage and establishes the differences between each stage at a fixed time (1900 hours) and adds to the growing literature on extracting breeding and behavioral parameters from timelapse imagery. Finally, it shows that small variations in day length have a significant influence on the colony activity pattern during the non-reproductive stage, while temperature does not, by itself, explain the activity pattern of the colony.

We found that the dates of start of incubation and early chick-rearing stages in this study are consistent with the dates found *in situ* by Ghys et al. (2008). In that study, the incubation stage during the 2005/2006 and 2006/2007 seasons lasted 37 ± 2 d and the mean hatching date was 12 December ± 4 d. In our study, we observed the first chick on December 7, 2013, which ushered the early chick-rearing. Moreover, these dates are similar to those known for other colonies of Gentoos in the South Atlantic region and the Antarctic Peninsula (Bost & Clobert 1992). In particular, in one colony at Volunteer Beach, Falkland (Malvinas) Islands, Otley et al. (2005) estimated the mean hatching date on December 6 ± 4 days.

During the non-reproductive stage, *pair formation and nest building* stage, the *incubation*, *early chick-rearing* and *molting stage*, similar patterns were found in the colony attendance at 1900h. These similarities can be attributed to different factors according to the stage. During the non-reproductive stage, penguins do not have parental duties and thus they returned to the colony when light is no longer available for foraging. Given day length during winter is shorter and consequently they have less daylight hours to feed (Wilson et al. 1989, 1993) they return near or before 1900h. During *pair formation and nest building*, and *molting* stages we found a large number of adults at the colony, which was expected because they have to build nests, pair bond and molt. We therefore see high attendance numbers due to limited foraging activity during these stages.

Similarities between the incubation and the early chick-rearing stages could arise through adults needing to take turns incubating the eggs or feeding the chick. However, incubation 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 chick rearing, adults should return more regularly as chicks at this stage need more frequent meals (Boersma et al 1990, Walker and Boersma 2003). We would therefore expect there will be more adults at 1900h during chick rearing compared to incubation. Given the similarities in numbers in this study we assume that prey availability near the colony was alike during incubation and early chick-rearing stages. Although we did not find differences, we cannot say there were none, during those stages day lengths are longer and we only observed the pictures until 2000h but there is a possibility that the difference could be evident if we extended the time lapse mode until sunset.

While analyzing late chick-rearing stage we found that the number of adults was lower compared to most of the other stages. This could be explained by the fact that during this stage chicks are bigger and they have already entered *crèche* (both parents are away feeding) so they do not require adults care and food frequently as has been found in other species (Raya Rey et al. 2007). Thus, both parents can go feeding for a long time. During the pre-molt stage number of adults was also low but significantly lower than during late chick-rearing stage. This was expected as during this stage breeding adults do not return to land while feeding and preparing for molting. The penguins observed at the colony were mainly non-breeders or failed-breeders that had already made the feeding trip and returned early to molt.

The colony attendance pattern throughout the day within each stage showed that in all stages the number of individuals increased except for the pre-molt stage. However, this increase was most notable during the non-reproductive stage, as adults do not have parental duties and all could stay all day feeding at sea. During pair formation and nest building, and molting stages though a constant number of individuals throughout the day were expected, the observed differences might be explained by the movement of penguins to the beach (outside the camera range). Future work might include the installation of another trail camera at the beach or at the sea-access area.

The potential foraging time at sea showed a clear relationship with the day length but no relationship with the temperature by itself. Moreover, past studies have indicated that penguins are visual predators that depend on ambient light to locate prey (Wilson et al. 1989, 1993), that they dive shallower at night than during the day, and that even when successful at catching prey, their foraging success at night is reduced (Wilson et al. 1993, Jansen et al. 1998). Therefore, this study provides evidence of the importance of the ambient light for feeding during the non-reproductive stage.

The breeding success was 1.04 chicks per nest, which was similar to the previously estimated *in situ* (1.00 ± 0.20 average for four seasons, Ghys et al. 2008). This similarity in the value among different seasons might be consequence of the stability of the ecosystem where penguins feed, especially because Gentoo's diet is comprised mainly of benthic prey (Clausen & Pütz 2003, Lescroël & Bost 2005). The estimation of this parameter allowed us to confirm the effectiveness of the methodology in contrast with an *in situ* study. Nevertheless, current work is investigating whether higher frequency of photographs (every 15 minutes) and all day recording (to capture the colony at sunset) and installing the camera closer to the colony will increase the accuracy of parameters.

With an automatic camera, we were able to record the annual cycle, important dates during the breeding period, colony attendance patterns and breeding success. All these parameters are essential to enrich the knowledge of the ecology of this species and should be recorded annually to ensure inter-annual comparisons that would allow us to infer changes in environmental conditions related to natural or anthropic factors (Bost & Le Maho 1993, Kitaysky et al 2000, Davoren & Montevecchi 2003, Boersma & Rebstock 2009). 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 & Pütz 2003). Consequently, the detailed study of the annual cycle and the colony attendance of Gentoo penguins are essential to evidence temporal and spatial variability in the use of their breeding sites which could reveal fluctuations in the marine ecosystem.

Acknowledgements

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

Tables and figures

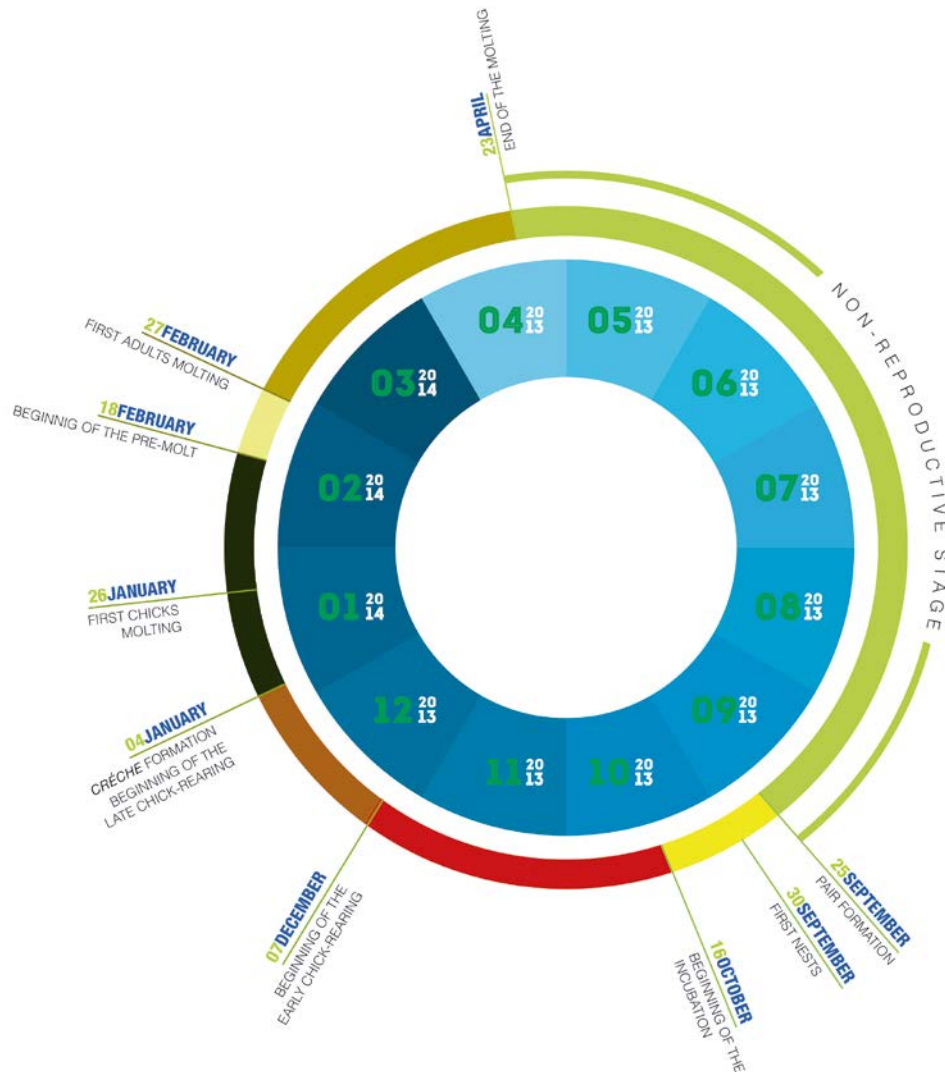


Fig. 1. Annual cycle of the Gentoo penguin at Martillo Island between April 9, 2013 and April 9, 2014.

Table 1. Differences between stages in the number of adults at 19hs by a generalized lineal model, estimated value, test of significance and the probability. Significant probabilities are indicated in bold.

Stages	Estimated value	t	p
Non-reproductive/Nest	0.02	0.18	0.85
Non-reproductive/Incubation	0.048	0.83	0.41
Non-reproductive/Early chick-rearing	-0.088	-1.16	0.25
Non-reproductive/Late chick-rearing	-0.508	-6.86	<0.05
Non-reproductive/Pre-molt	-3.067	-5.57	<0.05
Non-reproductive/Molting	-0.062	-1.09	0.27
Nest/Incubation	-0.068	-0.74	0.46
Nest/Early chick-rearing	-0.108	-1.04	0.3
Nest/Late chick-rearing	-0.529	-5.14	<0.05
Nest/Pre-molt	-3.087	-5.56	<0.05
Nest/Molting	-0.082	-0.9	0.37
Incubation/Early chick-rearing	-0.039	-0.46	0.65
Incubation/Late chick-rearing	-0.461	-5.4	<0.05
Incubation/Pre-molt	-3.019	-5.46	<0.05
Incubation/Molting	-0.014	-0.2	0.84
Early chick-rearing/ Late chick-rearing	-0.42	-4.28	<0.05
Early chick-rearing/Pre-molt	-2.979	-5.37	<0.05
Early chick-rearing/Molting	0.026	0.3	0.77
Late chick-rearing/Pre-molt	-2.558	-4.62	<0.05
Late chick-rearing/Molting	0.446	5.3	<0.05
Pre-molt/Molting	3.004	5.44	<0.05

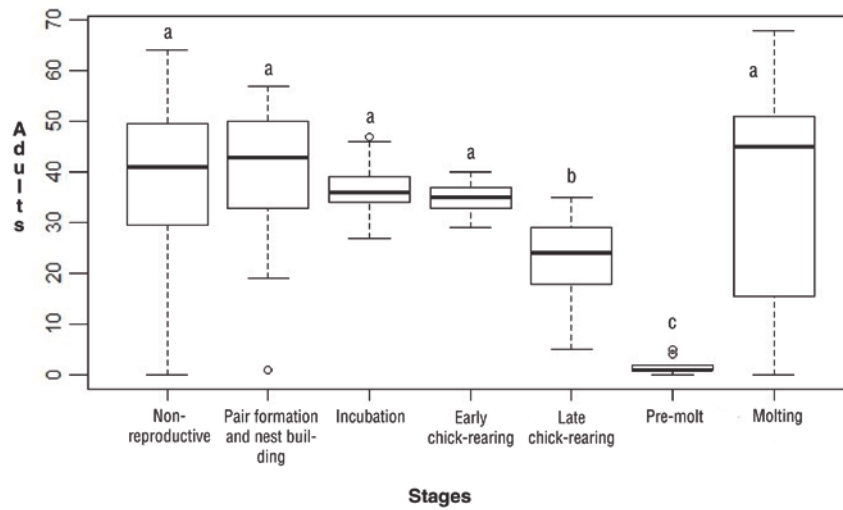
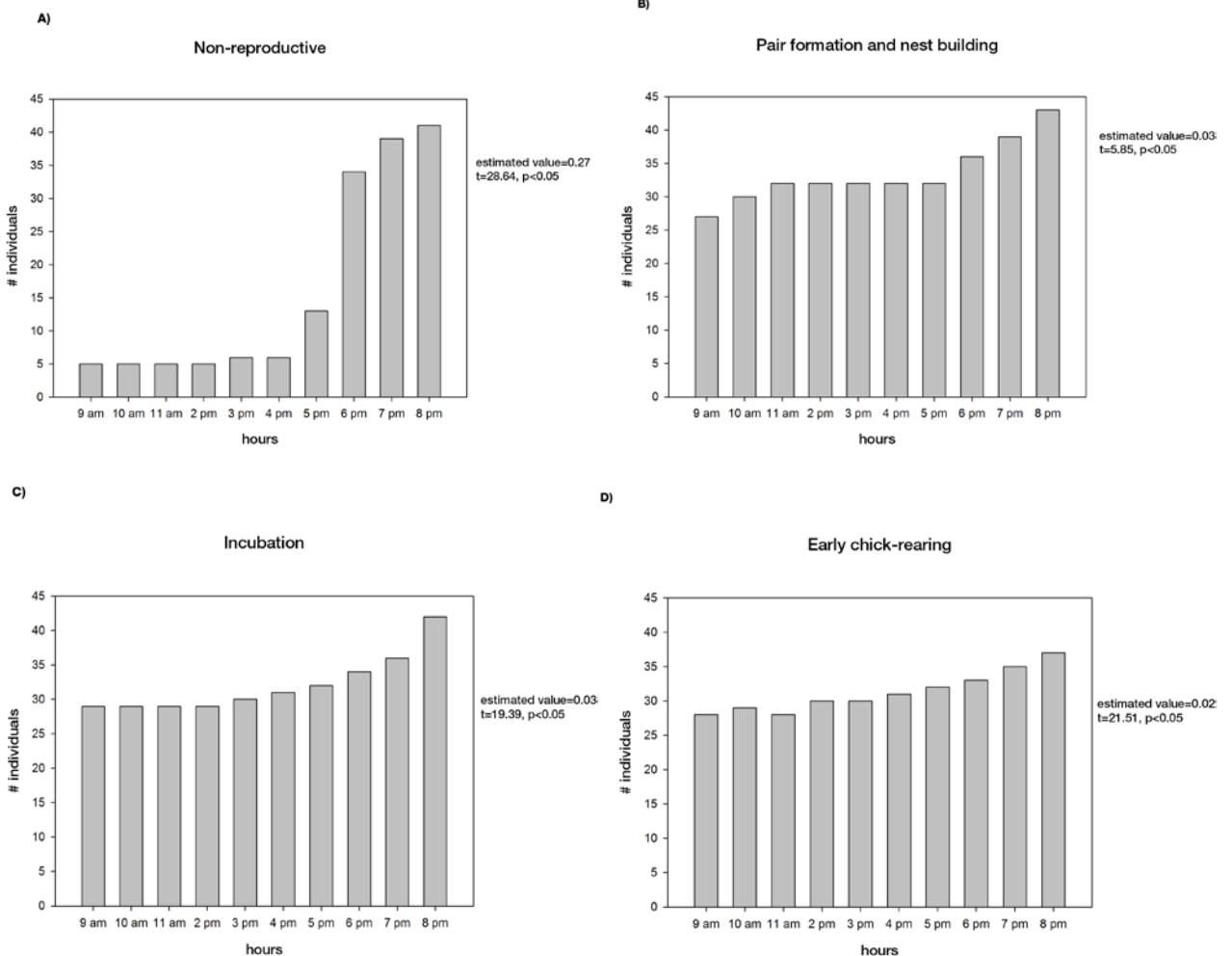


Fig. 2. Differences between stages in the colony attendance at 19 pm. Different letters indicate significant differences between these stages.



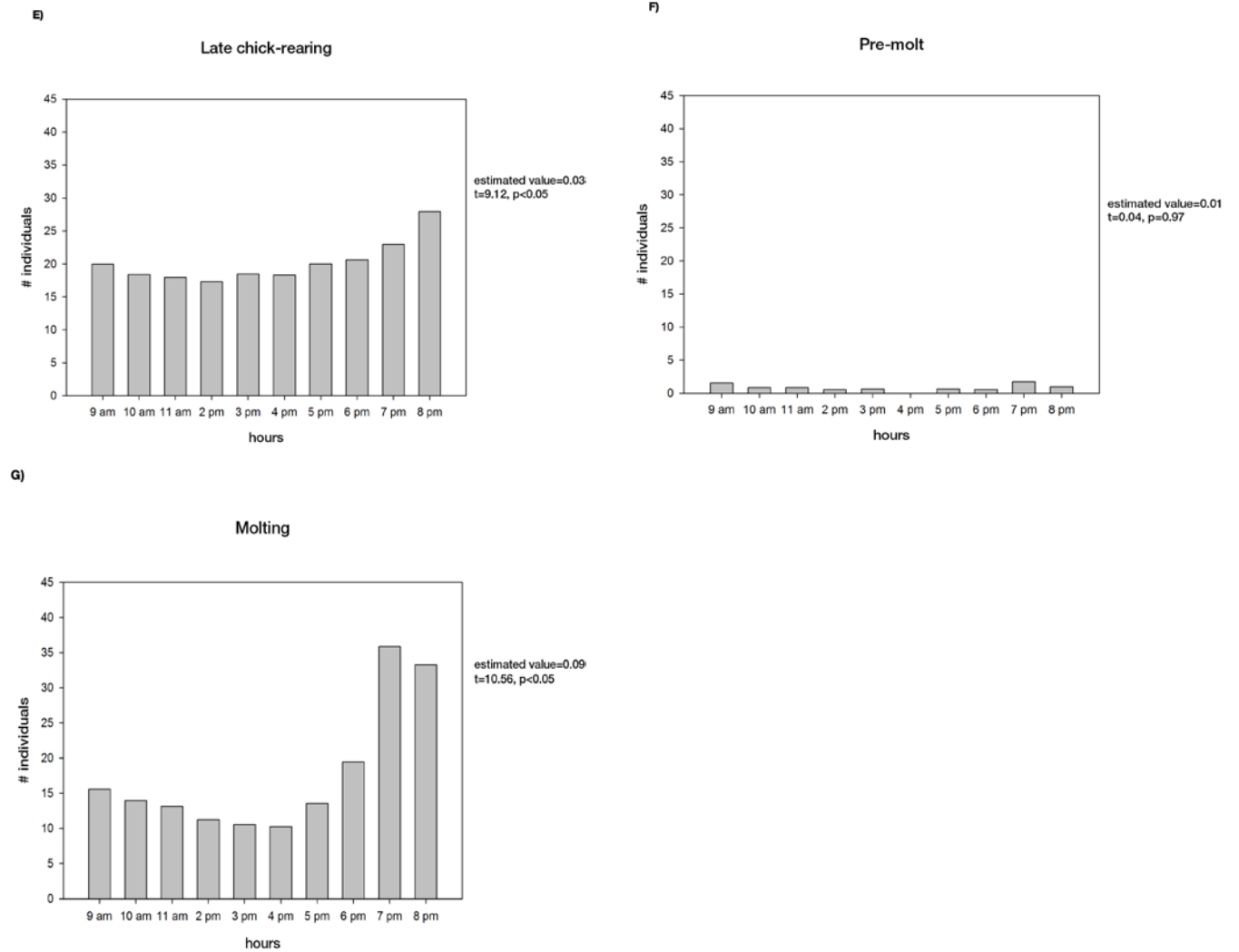


Fig 3. Colony attendance throughout the day within each stage. The results of the generalized linear mixed model are indicated.

Table 2. Generalized linear models using the Akaike Information Criterion. K, number of estimated parameters; AICc, Akaike's information Criterion corrected for small samples; Δ AICc, differences in AICc; w_i , Akaike weight. All candidate models and the null model are presented, listed in decreasing order of Δ AICc.

Response variable	Model	K	AICc	Δ AICc	w_i
Differences between the arrival time at the colony and hour of sunrise	duration+duration ²	4	281.8	0.00	0.363
	duration+duration ² +temperature ²	5	282.2	0.39	0.298
	duration+duration ² +temperature	5	283.2	1.38	0.182
	duration+duration ² +temperature+temperature ²	6	283.5	1.7	0.155
	duration ²	3	293.7	11.93	0.001
	duration ² +temperature ²	4	294.3	12.53	0.001
	duration ² +temperature+temperature ²	5	295.2	13.37	0.00
	duration ² +temperature	4	295.3	13.54	0.00
	duration	3	309	27.17	0.00
	duration+temperature ²	4	309.4	27.62	0.00
	duration+temperature+temperature ²	5	310.2	28.42	0.00
	duration+temperature	4	310.5	28.71	0.00
	temperature ²	3	513.3	231.51	0.00
	temperature	3	514.1	232.29	0.00
	temperature+temperature ²	4	515.1	233.29	0.00
	null	2	530.2	248.49	0.00

References

- Boersma P.D., Stokes D.L., Yorio P.M. (1990) Reproductive variability and historical change of Magellanic penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. In 'Penguin biology' (Eds L.S. Davis and J.T. Darby) pp 15-43. (Academic Press: San Diego, USA.)
- Boersma, P. D. and Rebstock, G. A. (2009). Foraging distance affects reproductive success in Magellanic Penguins. *Marine Ecology Progress Series* 375, 263–275. doi:10.3354/meps07753.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24, 127–135.
- Bost, C.A. and Jouventin, P. (1990). Evolutionary ecology of Gentoo Penguins (*Pygoscelis papua*). In 'Penguin biology' (Eds L.S. Davis and J.T. Darby) pp. 85–112. (Academic Press: New York)
- Bost, C.A. and Clobert, J. (1992). Gentoo Penguin *Pygoscelis papua*: factors affecting the process of laying a replacement clutch. *Acta Ecológica* 13, 593–605.

307 BOST, C. A. and LE MAHO, Y. (1993). Seabirds as bio-indicators of changing marine ecosystems: new perspectives.
308 *Acta Ecológica* 14, 463–470.

309 Clausen, A.P. (2000). Falkland Islands Seabird Monitoring Programme Annual Report 1999/00. Falklands Conservation,
310 Stanley, Falkland Islands.

311 Clausen, A.P. (2001). Falkland Island Seabird Monitoring Programme Annual Report 2000/01. Falklands Conservation,
312 Stanley, Falkland Islands.

313 Clausen, A.P. and Pütz, K. (2002). Recent trends in diet composition and productivity of gentoo, magellanic and
314 rockhopper penguins in the Falkland Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12, 51–61.

315 Clausen, A.P. and Pütz, K. (2003). Winter diet and foraging range of gentoo penguins (*Pygoscelis papua*) from Kidney
316 Cove, Falkland Islands. *Polar Biology* 26, 32–40. doi 10.1007/s00300-002-0443-2

317 Crawley, M.J. (2007). The R book . (Imperial College London: Silwood Park, UK.). Pp 511-526.

318 Davoren, G. K. and Montevecchi, W. A. (2003). Consequences of foraging trip duration on provisioning behaviour and
319 fledging condition of Common Murres *Uria aalga*. *Journal of Avian Biology* 34, 44–53. doi:10.1034/j.1600-
320 048X.2003.03008.x.

321 Einoder, L. D. (2009). A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries*
322 *Research* 95, 6-13.

323 Forcada, J. and Trathan, P. N. (2009). Penguin responses to climate change in the Southern Ocean. *Global Change*
324 *Biology* 15, 618-30.

325 Ghys, M. L., Raya Rey, A., Schiavini, A. (2008). Population trend and breeding biology of gentoo penguin in Martillo
326 Island, Tierra del Fuego, Argentina. *Waterbirds* 31, 625-31.

327 Huffeldt, N.P. and Merkel, F.R. (2013). Remote Time-lapse Photography as a Monitoring Tool for Colonial Breeding
328 Seabirds: A Case Study Using Thick-billed Murres (*Uria lomvia*). *Waterbirds* 36, 330-341.

329 Jansen, J.K., Boveng, P.L., Bengtson, J.L. (1998). Foraging modes of chinstrap penguins: contrasts between day and
330 night. *Marine Ecology Progress Series* 165, 161–172.

331 Kitaysky, A. S., Hunt, G. L. JR, Flint, E. N., Rubega, M. A., Decker, M. B. (2000). Resource allocation in breeding
332 seabirds: responses to fluctuations in their food supply. *Marine Ecology Progress Series* 206, 283–296.
333 doi:10.3354/meps206283.

334 Lescroël, A. and Bost, C. A. (2005). Foraging under contrasting oceanographic conditions: the Gentoo Penguin at
335 Kerguelen Archipelago. *Marine Ecology Progress Series* 302, 245-261.

336 Lescroël, A. and Bost, C. A. (2006). Recent decrease in Gentoo Penguin populations at Iles Kerguelen. *Antarctic Science*
337 18, 171-174.

338 Lescr  el, A., Bajzak C., Bost C. A. (2009). Breeding ecology of the gentoo penguin *Pygoscelis papua* at Kerguelen
 339 Archipelago. *Polar Biology* 32, 1495-1505.

340 Lynch, H.J., Fagan W. F., Naveen R., Trivelpiece S. G., Trivelpiece W. Z. (2009). Timing of clutch initiation in
 341 *Pygoscelis* penguins on the Antarctic Peninsula: Towards an improved understanding of off-peak census correction
 342 factors. *CCAMLR Science* 16, 49-65.

343 Lynch, H. (2013). Gentoo penguin. In 'PENGUINS: Natural History and Conservation'. (Eds Garc  a P.G. Borboroglu and
 344 P.D. Boersma) pp 73-88. (University of Washington Press: Seattle, U.S.A.)

345 Mallory, M. L., Robinson, S. A., Hebert, C. E., Forbes, M. E. (2010). Seabirds as indicators of aquatic ecosystem
 346 conditions: a case for gathering multiple proxies of seabird health. *Marine Pollution Bulletin* 60, 7-12.

347 Newbery, K. B., and Southwell, C. (2009). An automated camera system for remote monitoring in polar environments.
 348 *Cold Regions Science and Technology* 1, 47-51.

349 Otley, H.M., Clausen, A.P., Christie, D.J., P  tz, K. (2005). Aspects of the breeding biology of the Gentoo Penguin
 350 *Pygoscelis papua* at Volunteer Beach, Falkland Islands, 2001/02. *Marine Ornithology* 33, 167–171.

351 Piatt, J. F., Sydeman, W. J., Browman, H. I. (2007). Seabirds as indicators of marine ecosystems. *Marine Ecology*
 352 *Progress Series* 352, 199-309.

353 Pinheiro, J. C. and Bates, D.M. (2000). Mixed-effects models in S and S-PLUS. *Springer, New York* 528pp.

354 P  tz, K., Ingham, R.J., Smith, J.G., Croxall, J.P. (2001). Population trends, breeding success and diet composition of
 355 gentoo *Pygoscelis papua*, magellanic *Spheniscus magellanicus* and rockhopper *Eudyptes chrysocome* penguins in the
 356 Falkland Islands. *Polar Biology* 24, 793–807.

357 R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing,
 358 Vienna, Austria. URL <http://www.R-project.org/>

359 Raya Rey A., Trathan P., Schiavini A. (2007) Inter-annual variation in provisioning behaviour of Rockhopper Penguins
 360 *Eudyptes chrysocome chrysocome* at Staten Island. *Ibis* 149, 826-835

361 Raya Rey, A., Rosciano, N., Liljestr  m, M., Samaniego, R. S., Schiavini, A. (2014). Species-specific population trends
 362 detected for penguins, gulls and cormorants over 20 years in sub-Antarctic Fuegian Archipelago. *Polar Biology* 37, 1343-
 363 1360.

364 Schiavini, A., Yorio, P., Gandini, P., Raya Rey, A., BOERSMA, D. (2005). Los ping  inos de las costas argentinas: estado
 365 poblacional y conservaci  n. *El Hornero* 20, 5–23.

366 Southwell, C., and Emmerson, L. (2015). Remotely-operating camera network expands Antarctic seabird observations of
 367 key breeding parameters for ecosystem monitoring and management. *Journal for Nature Conservation* 23, 1-8.

368 Trivelpiece, W. Z., Trivelpiece S. G., Volkman N. J. (1987). Ecological segregation of Adélie, gentoo, and chinstrap
369 penguins at King George Island, Antarctica. *Ecology* 68, 351- 61.

370 Viquerat, S (2015). An open source software facilitating the analysis of count data from still images. 29th Conference of
371 the European Cetacean Society.

372 Walker, B. G., and Boersma, P. D. (2003). Diving behavior of Magellanic Penguins (*Spheniscus magellanicus*) at Punta
373 Tombo, Argentina. *Canadian Journal of Zoology* 81:1471–1483.

374 Williams, A.J. (1982). Chick-feeding rates of Macaroni and Rockhopper Penguins at Marion Island. *Ostrich* 53, 129–134.

375 Williams, T.D., (1990). Annual variation in breeding biology of gentoo penguins, *Pygoscelis papua*, at Bird Island, South
376 Georgia. *Journal of Zoology*, London 222:247–258.

377 Williams, T. D. (1995). Bird Families of the World: The Penguins. (Oxford University Press: Oxford.)

378 Wilson, R.P., Culik, B., Coria, N.R., Adelung, D., Spairani, H.J. (1989). Foraging rhythms in Adélie penguins (*Pygoscelis*
379 *adeliae*) at Hope Bay, Antarctica; determination and control. *Polar Biology* 10, 161–165.

380 Wilson, R.P., Pütz, K., Bost, C.A., Culik, B.M., Bannasch, R., Reins, T. Adelung, D. (1993). Diel dive depth in penguins
381 in relation to diel vertical migration of prey: whose dinner by candlelight? *Marine Ecology Progress Series* 94, 101–104.

382 Woehler, E. J. (1993). The distribution and abundance of Antarctic and Subantarctic penguins. Scientific Committee on
383 Antarctic Research, Cambridge.