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Diving location and depth of breeding chinstrap penguins during incubation and chick-rearing period in King George Island, Antarctica

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Breeding birds can increase their foraging efforts to feed chicks after hatching. We investigated how chinstrap penguins (*Pygoscelis antarctica*) differ foraging diving behaviors with breeding stages. During incubation and chick-rearing period, from December 2015 to January 2016 on King George Island, Antarctica, diving characteristics of breeding chinstrap penguin parents were recorded by deploying GPS and Time-Depth Recorder (TDR). Our results showed that chinstrap penguins have wider-range diving areas and longer foraging trips during incubation period while they dive in on-shore areas for a short trip hours during chick-rearing period. In addition, chinstrap penguins exhibited deeper dive depths during chick-rearing than during incubation. Our results suggest that chinstrap parents change their foraging area and dive depth between incubation and chick-rearing, possibly due to the increased need of chick-feeding and the temporal changes in prey availability between the two reproduction stages.

key words: diving behavior, incubation, chick-rearing, Chinstrap penguin

Introduction

Breeding seabirds could adjust their foraging behaviors with the breeding stages to meet the need of offspring (Weimerskirch et al. 1994; Meyer et al. 1997; Ito et al. 2010). During incubation period, parents are responsible for self-maintenance and for keeping eggs with their mates (Watanuki et al. 1997). After egg-hatching, parent birds need to acquire food for themselves and their chicks. Therefore, parents are expected to adjust their foraging behavior to optimize foraging efficiency by behavioral shift with the reproduction stages (Shaffer et al. 2003; Shoji et al. 2016). However, it is still not clear how birds change their foraging behaviors between incubation and chick-rearing with the temporal changes in prey availability (Ito et al. 2010).

Chinstrap penguins (*Pygoscelis antarctica*) are diving seabirds breeding from sub-Antarctic to Antarctic regions. Male and female parents alternate incubating and share chick-feeding. Recent studies showed that breeding penguins change their diving patterns and foraging locations over the breeding periods aided by technological advances on bio-logging devices, such as GPS and Time-Depth Recorder

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(TDR) (reviewed in Bograd et al. 2010). Especially, related with the prey distribution, previous studies revealed that penguins may consume different food items with the breeding stages (in Adélie penguins *Pygoscelis adeliae*, Puddicombe and Johnstone 1988; in Yellow-eyed penguins *Megadyptes antipodes*, Moore 1999; in Magellanic penguins *Spheniscus magellanicus*, Scioscia et al. 2014; in Gentoo penguins *Pygoscelis papua*, Handley et al. 2016). To our knowledge, however, chinstrap penguins have not been studied on their foraging behavioral shift between incubation and chick-rearing yet.

In this study, we investigated dive tactics of chinstrap penguins in King George Island, Antarctica, during incubation and chick-rearing period. By deploying GPS and TDR on breeding parents, we aimed to compare foraging dive locations and dive depth between incubation and chick-rearing in chinstrap penguin parents.

Materials and methods

We studied a chinstrap penguin population at Narębski Point (Antarctic Specially Protected Area, No. 171) on King George Island, South Shetland Islands, Antarctica (62°14.3'S, 58°46.5'W). Approximately 3,000 breeding pairs have been annually recorded since 2005 in our study site.

To determine diving locations of chinstrap penguins, we used a GPS tracking device (GPL400; 57 g with battery (1.4% of average penguin body mass), cylinder type: 20 mm diameter and 103 mm length; Little Leonardo, Japan) which records location data on water surface from satellites every second for approximately 40 hours. During incubation period, in 12th and 13th December 2015, we randomly captured 6 breeding individuals from 6 nests which were leaving their nest sites to the sea for foraging and, during chick-rearing period, in 30th December 2015 and in 4th, 6th, 7th January 2016, we randomly captured 8 breeding individuals from 8 nests (Table 1). Totally 14 GPS deployments were conducted (6 in incubation and 8 in chick-rearing) with Tesa tape on the back and retrieved the devices when the penguin returned from the sea near the nest site.

To estimate dive depths of chinstrap penguins, we used a TDR device (M190-DT; 14 g with battery (0.3% of average penguin body mass), cylinder type: 15 mm diameter and 48 mm length; Little Leonardo, Japan). This device records dive depths of penguins every second for maximally 20 days. We captured 6 breeding individuals from 6 nests during incubation in December 2015 and 10 penguins from 6 nests at day 1-3 after hatching in late December and early January (Table 2), and deployed TDR with a similar manner as we did with GPS. Using IGOR Pro version 6.2.2.2 (Wave Metrics, Lake Oswego, OR, USA), we calculated dive depth and foraging trip duration. These TDR birds were different individuals with the ones that we deployed GPS tags. When deploying the loggers, we also measured bill length and depth and determined the sex of penguins (Table 1 and 2) following Lee et al. (2015)'s discriminatory functions.

From raw GPS data points, we acquired kernel density distributions to visualize their main foraging area (50% of kernel density; Hamer et al. 2007, Kokubun et al. 2010) and calculated maximum distances in ArcGIS pro version 1.1.0 (ESRI, Redlands, CA, USA). In ArcGIS PRO program, default search radius (bandwidth) algorithm was determined follow the formular ('min' means that a smaller value will be used between the

two values; ‘SD’ is the standard distance; D_m is the median distance; n is the number of points):

$$\text{Search radius} = 0.9 \times \min\left(SD, \sqrt{\frac{1}{\ln(2)}} \times D_m \right) \times n^{-0.2}$$

Table 1. Information of chinstrap penguins which were deployed with GPS tags during incubation ($n = 6$) in mid December 2015 and chick-rearing period ($n = 8$) in late December 2015 and early January 2016.

| ID | Period | Sex | Mass (kg) | Recording days | Maximum distance (m) |
|-----|---------------|-----|-----------|----------------|----------------------|
| 06I | Incubation | M | 4.7 | 3 | 63,741 |
| 07I | Incubation | M | 4.2 | 3 | 65,232 |
| 08I | Incubation | F | 3.9 | 3 | 60,124 |
| 09I | Incubation | F | 3.8 | 3 | 49,378 |
| 10I | Incubation | M | 4.1 | 2 | 63,736 |
| 11I | Incubation | M | 4.7 | 3 | 37,546 |
| 14C | Chick-rearing | F | 3.5 | 2 | 3,969 |
| 15C | Chick-rearing | F | 4.4 | 2 | 34,209 |
| 16C | Chick-rearing | M | 5.5 | 2 | 11,684 |
| 18C | Chick-rearing | F | 4.4 | 3 | 39,337 |
| 19C | Chick-rearing | F | 4.1 | 3 | 30,976 |
| 24C | Chick-rearing | M | 4.0 | 2 | 11,962 |
| 27C | Chick-rearing | F | 4.2 | 2 | 20,876 |
| 28C | Chick-rearing | M | 4.5 | 2 | 44,823 |

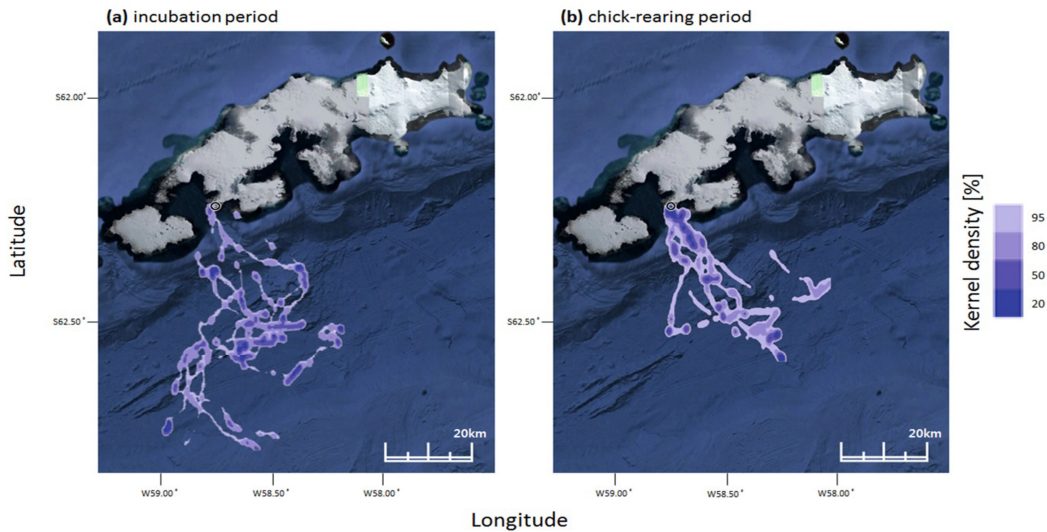


Fig. 1. Diving locations of chinstrap penguins acquired from kernel density contours of 20, 50, 80, and 95% (a) during incubation period (left, $n = 6$) and (b) during chick-rearing period (right, $n = 8$). Black circles indicate the nest sites of penguins.

To differentiate foraging areas, we acquired kernel density line of 20, 50, 80 and 95% contour in R package 'spatialEco' (Evans 2016) and the lines were presented (Fig. 1) on Google Earth map version 7.1.5.1557 (Google inc., Mountain View, CA, USA)

Table 2. Information of chinstrap penguins which were deployed with TDR (Time-Depth Recorder) tags during incubation (n = 6) in December 2015 and chick-rearing period (n = 10) in late December 2015 and January 2016.

| ID | Period | Sex | Mass (kg) | Recording days | No. of dive | No. of foraging trips | Trip duration (h) | Dive depth (mean \pm SD, m) | Dive duration (mean \pm SD, s) |
|-----|---------------|-----|-----------|----------------|-------------|-----------------------|-------------------|-------------------------------|----------------------------------|
| 01B | Incubation | M | 4.1 | 8 | 1,437 | 1 | 76.07 | 27.34 \pm 18.19 | 75.85 \pm 32.01 |
| 01W | Incubation | F | 4.1 | 8 | 2,755 | 1 | 16.08 | 26.71 \pm 17.76 | 63.17 \pm 33.51 |
| 02W | Incubation | F | 3.6 | 14 | 4,575 | 1 | 104.63 | 36.21 \pm 19.44 | 80.1 \pm 27.38 |
| 03B | Incubation | M | 4.0 | 12 | 5,359 | 2 | 90.23 \pm 6.95 | 29.03 \pm 21.73 | 73.66 \pm 31.14 |
| 04B | Incubation | F | 3.8 | 15 | 8,819 | 1 | 67.97 | 21.7 \pm 16.71 | 55.92 \pm 28.61 |
| 04W | Incubation | M | 3.5 | 15 | 3,985 | 1 | 90.90 | 26.33 \pm 19.74 | 75.99 \pm 28.3 |
| 01B | Chick-rearing | M | 3.7 | 18 | 5,253 | 11 | 19.22 \pm 9.31 | 40.3 \pm 27.03 | 89.55 \pm 38.14 |
| 02B | Chick-rearing | M | - | 12 | 4,173 | 9 | 12.44 \pm 8.82 | 47.39 \pm 39.08 | 90.11 \pm 56.79 |
| 02W | Chick-rearing | F | 4.0 | 13 | 5,207 | 9 | 14.59 \pm 9.28 | 36.96 \pm 31.03 | 84.63 \pm 41.69 |
| 03W | Chick-rearing | F | 4.0 | 16 | 12,750 | 14 | 14.15 \pm 11.08 | 32.91 \pm 27.51 | 80.75 \pm 38.48 |
| 04B | Chick-rearing | F | - | 16 | 11,427 | 10 | 19.05 \pm 9.81 | 30.89 \pm 24.76 | 69.14 \pm 39.39 |
| 04W | Chick-rearing | M | 3.5 | 8 | 3,727 | 5 | 24.45 \pm 6.45 | 25.34 \pm 23.12 | 74.73 \pm 38.96 |
| 12B | Chick-rearing | M | 4.6 | 18 | 7,047 | 10 | 20.76 \pm 6.97 | 30.35 \pm 21.4 | 86.51 \pm 37.53 |
| 12W | Chick-rearing | F | 3.6 | 19 | 7,866 | 11 | 19.13 \pm 7.17 | 30.28 \pm 26.2 | 70.72 \pm 39.85 |
| 20B | Chick-rearing | M | 3.6 | 13 | 4,926 | 9 | 13.67 \pm 4.12 | 38.03 \pm 33.43 | 84.04 \pm 45.45 |
| 20W | Chick-rearing | F | 3.0 | 7 | 2,403 | 4 | 19.18 \pm 5.28 | 44.16 \pm 25.54 | 97.78 \pm 42.56 |

We used generalized linear mixed models (GLMMs, PROC MIXED in SAS version 9.3 (SAS institute, Cary, NC, USA)) to estimate if breeding periods (incubation and chick-rearing) affected 1) maximum distance, 2) trip duration and 3) dive depth. In three GLMM models, explanatory variables were breeding period (binary coded as incubation or chick-rearing) and sex (binary as M or F). Individual ID was treated as a random factor. From the initial models of main effects and two-way interactions, we chose best models by stepwise backward elimination (Crawley 1993) based on P-value (<0.05). In the results, the values were provided with average \pm standard deviation.

Results

From GPS track points for 14 foraging trips (6 trips for incubation and 8 trips for chick-rearing), incubating chinstrap penguin parents had higher maximum distances (56,626 m \pm 10,991) than chick-rearing birds (24,729 m \pm 14,760) (Table 1 and 3, Fig 1; GLMM, F = 19.66, P < 0.001). Kernel

density images visualized their foraging areas (which were lined in 95% kernel density contours) and main foraging areas (in 50% kernel density contours), and the maximum distances from the breeding site to the main foraging areas were 63,935 m during incubation and 47,467 m during chick-rearing. From TDR data during incubation and chick-rearing period for 99 foraging trips (7 trips for incubation and 92 trips for chick-rearing), totally 42,584 dive events were recorded (Table 2). Dive depths revealed that the penguins dived deeper during chick-rearing ($35.65 \text{ m} \pm 6.93$) during incubation ($27.89 \text{ m} \pm 4.75$) (Table 2 and 3; GLMM, $F = 707.95$, $P < 0.001$). Foraging trip duration was shorter during chick-rearing ($17.22 \text{ h} \pm 8.05$) than during incubation ($76.59 \text{ h} \pm 29.29$) (Table 2 and 3; GLMM, $F = 199.14$, $P < 0.001$). Sex was removed in the process of selecting best models in the three GLMMs.

Table 3. Summary of three minimal models of GLMMs for estimating 1) maximum distance, 2) trip duration and 3) dive depth. In the three models, breeding period (binary coded as incubation or chick-rearing) and sex (binary as M or F) were included in the initial full models and Individual ID was treated as a random factor. From the initial models of main effects and two-way interactions, we chose best models by stepwise backward elimination.

| | Response variable | Explanatory variable | Numerator DF | Denominator DF | F value | P value |
|---------|-------------------|----------------------|--------------|----------------|---------|---------|
| Model 1 | Maximum distance | Breeding period | 1 | 12 | 19.66 | 0.0008 |
| Model 2 | Trip duration | Breeding period | 1 | 14 | 199.14 | <0.0001 |
| Model 3 | Dive depth | Breeding period | 1 | 14 | 707.95 | <0.0001 |

Discussion

Our results showed that chinstrap penguins foraged in longer distances and spent more time for foraging trip during incubation than during chick-rearing. One possibility for the trip duration difference between incubation and chick-rearing is that adult birds require more energy gain after fasting with courtship and laying when there is no need for feeding their chicks (Green et al. 2009; Raya Rey et al. 2012). Thus, incubating birds could perform foraging trips for longer distances. Another possibility is that different food availability and prey distributions could affect the changes of foraging behaviors of penguins (Lescroël et al. 2004, 2005). Since our observation on foraging behavior during incubation and chick-rearing were conducted at different time periods, it needs to be clarified if prey availability changes between the two periods or if there were temporal changes in environments over the periods, such as sea-ice extension in Adélie penguins in east Antarctica (Clarke et al. 2006), which could constrain the birds' movements. Although such dramatic changes are not expected for one month period between incubation and chick-rearing in our field site, we do not exclude possibilities of certain changes between the two breeding periods. In our chinstrap penguin colony, incubation was mostly from November to late December and chick-rearing was from late December to early February, prey could shift their main habitats between incubation and chick-rearing of penguins. Shorter trip duration during chick-rearing than incubation (59.37 hour difference between the two periods) may be related with the

need for more available food resources, such as Antarctic krill (*Euphausia superba*), which is a main food source of chinstrap penguins in our population (Kokubun et al. 2010), for feeding chicks more frequently. Fat-based food value can be a factor to affect foraging behavioral changes (Puddicombe and Johnstone 1988; Tierney et al. 2008) since parents spend higher metabolic expenditure for foraging during chick-rearing than during incubation (Chappell et al. 1993) and more sensitive to changes in food density (Harding et al. 2007). We expect that both the increased energy expenditure and flexible prey availability after hatching could affect the short trip duration and shallow dives during the chick-rearing period, compared with during the incubation.

We also found that incubating chinstrap penguins performed shallower dive depth. Vertical prey distribution may explain such different dive depths between incubating and chick-rearing chinstrap penguins (Jakubas et al. 2014). Because chinstrap penguins mainly forage on Antarctic krill species at our study site (Kokubun et al. 2010), vertical migration of the krill (Hopkins and Arnould 2013) could be responsible for the penguins behavioral change in depth. Although other penguin studies reported sexual differences in foraging characteristics (in Royal penguins *Eudyptes schlegeli*, Hull 1997; in macaroni penguins *Eudyptes chrysolophus*, Barlow and Croxall 2002; in gentoo penguins, Bearhop et al. 2006; in Magellanic penguins, Raya Rey et al. 2012), we did not detect differences in maximum distance, trip duration and dive depth in chinstrap penguins. Considering different bill size and bill length between the sexes, it is still worth to examine their sexual differences in prey type and size while foraging. Future studies on different food items and prey distribution during incubation and chick-rearing may provide more accurate information for studying the foraging strategies of chinstrap penguins with the breeding cycles.

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References

- Barlos K.E. and J.P. Croxall. 2002 Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. Marine Ecology Progress Series 232: 291-304
- Bograd S., B.A. Block, D.P. Costa and B.J. Godley. 2010 Biologging technologies: new tools for conservation. Introduction. Endangered Species Research 10: 1-7

- Chappell M.A., Janes, D.N., Shoemaker, V.H., Bucher, T.L. and T.L. Maloney. 1993. Reproductive effort in Adélie penguins. *Behavioral Ecology and Sociobiology* 33: 173-182
- Clarke J., L.M. Emmerson and P. Otahal. 2006 Environmental conditions and life history constraints determine foraging range in breeding Adélie penguins. *Marine Ecology Progress Series* 310: 247-261
- Crawley M.J. 1993 GLIM for ecologists. Oxford: Blackwell Scientific Publications
- Evans J.S. 2016 spatialEco. R package version 0.0.1-4, <http://CRAN.R-project.org/package=spatialEco>
- Green J.A., R.P. Wilson, I.L. Boyd, A.J. Woakes, C.J. Green and P.J. Butler. 2009 Tracking macaroni penguins during long foraging trips using 'behavioural geolocation'. *Polar Biology* 32: 645-653
- Hamer K.C., E. M. Humphreys, S. Garthe, J. Hennenke, G. Peters, D. Gremillet, R.A. Phillips, M.P. Harris, and S. Wanless. 2007 Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology Progress Series* 338: 295-305
- Handley, J.M., A.M.M. Baylis, P. Brickle and P. Pistorius. 2016 Temporal variation in the diet of gentoo penguins at the Falkland Islands. *Polar Biology* 39: 283-296
- Harding A.M.A., J.F. Piatt and J.A. Schmutz. 2007 Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. *Marine Ecology Progress Series* 352: 269-274.
- Hopkins A.J. and J.P.Y. Arnould. 2013 Temporal allocation of foraging effort in female Australian Fur Seals (*Arctocephalus pusillus doriferus*). *PLoS ONE* 8:e79484
- Hull, C.L. 1997 The effect of carrying devices on breeding royal penguins. *The Condor* 99: 530-534
- Ito M., A. Takahashi, N. Kokubun, A.S. Kitaysky and Y. Watanuki. 2010 Foraging behavior of incubating and chick-rearing thick-billed murres *Uria lomvia*. *Aquatic Biology* 8: 279-287
- Jakubas D., K. Wojczulanis-Jakubas, L. Iliszko, M. Darecki and L. Stempniewicz. 2014 Foraging strategy of the little auk *Alle alle* throughout breeding season – switch from unimodal to bimodal pattern. *Journal of Avian Biology* 45: 551-560
- Kokubun N., A. Takahashi, Y. Mori, S. Watanabe, H.C. Shin. 2010 Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Marine Biology* 157: 811-825
- Lee W.Y., J.W. Jung, Y.D. Han, H. Chung and J.H. Kim. 2015 A new sex determination method using morphological traits in adult chinstrap and gentoo penguins on King George Island, Antarctica. *Animal Cells and Systems* 19: 156-159
- Lescroëel A., V. Ridoux and C.A. Bost. 2004 Spatial and temporal variation in the diet of the Gentoo penguin (*Pygoscelis papua*) at Kerguelen Islands. *Polar Biology* 27: 201-216
- Lescroëel A. and C.A. Bost. 2005 Foraging under contrasting oceanographic conditions: the Gentoo penguin at Kerguelen Archipelago. *Marine Ecology Progress series* 302: 245-261
- Meyer W.R., J.L. Bengston, J.K. Jansen and R.W. Russell. 1997 Relationships between brood size and parental provisioning performance in chinstrap penguins during the chick guard phase. *Polar Biology* 17: 228-234
- Moore P.J. 1999 Foraging range of the Yellow-eyed Penguin *Megadyptes antipodes*. *Marine Ornithology* 27: 49-58
- Puddicombe R.A. and G.W. Johnstone. 1988 The breeding season diet of Adélie penguins at the Vestfold Hills, East Antarctica. *Hydrobiologia* 165: 239-253
- Raya Rey A., K. Pütz, G. Scioscia, B. Lüthi and A. Schiavini. 2012 Sexual differences in the foraging behaviour of Magellanic Penguins related to stage of breeding. *Emu* 112: 90-96
- Scioscia G., A.R. Rey, R.A.S. Samaniego, O. Florentín and A. Schiavini. 2014 Intra- and interannual variation in the diet of the Magellanic penguin (*Spheniscus magellanicus*) at Martillo Island, Beagle Channel. *Polar Biology* 37: 1421-1433

- Shaffer S.A., D.P. Costa and H. Weimerskirch. 2003 Foraging effort in relation to the constraints of reproduction in freeranging albatrosses. *Functional Ecology* 17: 66-74
- Shoji A., S. Aris-Brosou, E. Owen, M. Bolton, D. Boyle, A. Fayet, B. Dean, H. Kirk, R. Freeman, C. Perrins and T. Guilford. 2016 Foraging flexibility and search patterns are unlinked during breeding in a free-ranging seabird. *Marine Biology* 163:72
- Tierney M., P.D. Nichols, K.E. Wheatley and M.A. Hindell. 2008 Blood fatty acids indicate inter- and intra-annual variation in the diet of Adélie penguins: Comparison with stomach content and stable isotope analysis. *Journal of Experimental Marine Biology and Ecology* 367: 65-74
- Watanuki Y., A. Kato, G. Robertson and S. Robinson. 1997 Diving and foraging behaviour of Adélie penguins in areas with and without fast seaice. *Polar Biology* 17: 296-304
- Weimerskirch H., O. Chastel, L. Ackermann, T. Chaurand, F. Cuenot-Chaillet, X. Hindermeyer and J. Judas. 1994 Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour* 47: 472-476