

## Diel diving behavior of breeding gentoo penguins on King George Island in Antarctica

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(Received 15 March 2015; received in revised form 1 June 2015; accepted 3 July 2015)

Many marine birds dive to catch prey in water. The gentoo penguin (*Pygoscelis papua*), a specialized diving seabird that preys on krill and fish, is distributed from the sub-Antarctic islands to Antarctic regions. Here, we observed the diving behavior of breeding gentoo penguins on King George Island, South Shetland Islands, Antarctica. Using a time–depth recorder, we collected diving depths every second from seven gentoo breeders for 5–21 days during the chick-rearing period and analyzed their diving characteristics. Most dives occurred in shallow water, although the dive efficiency (=bottom duration time/[dive duration + post-dive surface time]) was highest at depths of 30–35 m and decreased as the penguins dove deeper. Gentoo penguins did not dive more frequently during the day than at night, but during nighttime, most dives occurred in shallow water (<20 m) and the dive efficiency was also higher at this time. As penguins repeated their foraging trips, the number of dives, depth of dives, and trip duration did not change significantly. Our results suggest that the diel dive patterns of gentoo penguins might be related to the vertical migration of krill (upward to the surface at night). In addition, we observed that gentoo penguins could perform active diving behavior even at night, possibly aided by civil twilight during the chick-rearing period in Antarctic regions.

**KEYWORDS:** bio-logging; diving behavior; foraging behavior; gentoo penguin; *Pygoscelis papua*

### Introduction

Many marine birds have evolved diving ability to catch prey in water (Butler & Jones 1997; Kooymann & Ponganis 1998). Among them, Antarctic penguins are one of the most specialized diving species, feeding on krill or fish in the sea (Williams, Briggs et al. 1992; Williams, Kato et al. 1992; Wilson et al. 1992; Ainley 2002; Kokubun et al. 2010). Because their feeding occurs mostly in water, studying their underwater behavior is very important. Thus, many researchers have used bio-logging devices, such as time–depth recorders (TDRs), to collect behavioral data from diving animals (Womble et al. 2013).

The gentoo penguin (*Pygoscelis papua*), which is distributed from the sub-Antarctic islands to Antarctic regions, feeds on krill and fish (Robinson & Hindell 1996; Kokubun et al. 2010). Several studies have described gentoo penguin's general diving behaviors both in Antarctic (Williams, Briggs et al. 1992; Williams, Kato et al. 1992; Wilson et al. 1996; Miller et al. 2009) and sub-Antarctic (Bost et al. 1994), but only a few studies described the diel patterns of diving characteristics (but see Croxall et al. 1988; Williams, Briggs et al. 1992; Lescroël & Bost 2005; Wilson 2010). During chick-rearing, penguins dive to forage in water and feed their offspring by regurgitating the food (Williams 1995). Gentoo penguins usually conduct deep dives (>30 m depth) for feeding and shallow dives (<20 m) for search or traveling (Williams, Briggs et al. 1992).

In the previous studies, gentoo penguins have been reported to display different diving behaviors between the sub-Antarctic islands and Antarctica. Dives occurred largely during daylight hours in sub-Antarctic regions (at South Georgia, 100% in Croxall et al. 1988 and 92% in Williams & Rothery 1990; at Macquarie Island, 84% in Robinson & Hindell 1996; and at Kerguelen Archipelago, 83–95% in Lescroël & Bost 2005), whereas these were concentrated on early and mid-morning and dispersed during both day and nighttime hours in an Antarctic region (at Ardley Island, actual values were not provided, see Wilson et al. 1993 and Wilson 2010). Although main prey items are krill and fish both in Antarctic and sub-Antarctic gentoo penguins (reviewed in Robinson & Hindell 1996; Kokubun et al. 2010), there is a latitudinal difference between two regions so that sub-Antarctic islands (46°–60°) have longer daily hours than Antarctica (South of 60° S) from December to January in austral summer.

Among other possible factors which can affect diving behavior of breeding gentoo penguins, chick age can induce the escalation of foraging effort (gentoo penguins in Williams & Rothery 1990; Rhinoceros Auklet *Cerorhinca monocarata* in Bevan et al. 2002; Wandering Albatross *Diomedea exulans* in Shaffer et al. 2003). It was previously suggested that gentoo penguins increased duration time for foraging trip during chick-rearing (Williams & Rothery 1990; Williams, Briggs et al. 1992) or total

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amount of food delivery (Jablonski 1985) with chick age throughout the chick-rearing period, possibly to meet the increased food demand of chicks.

In this study, we observed the diving behavior of breeding gentoo penguins using TDRs for a period of up to 3 weeks in the South Shetland Islands, Antarctica. Using the depth data, we examined how gentoo penguins dived during both day and night and investigated changes in their diving patterns as the chicks grew. Although gentoo penguins are one of well-studied systems among Antarctic birds, it is surprising that only one depth recording (1991–1992 at Ardley Island, by Wilson et al. 1993 and Wilson 2010) was conducted on their diel diving of gentoo penguins, excluding the studies at sub-Antarctic islands. To best our knowledge, this study is the second description on the diel patterns of gentoo diving behavior in Antarctic areas.

### Materials and methods

The study was conducted in a gentoo penguin colony at Naręski Point (62°14.3'S, 58°46.5'W, Antarctic Specially Protected Area No. 171) on King George Island in the South Shetland Islands, during the chick-rearing period (December 2013–January 2014). We captured either of the adult gentoo parents and sampled blood from a foot vein when the birds alternated between foraging and brooding at the nest sites. To observe their diving behavior, we deployed a TDR (M190-DT, 48 mm length, 15 mm diameter, 14 g; Little Leonardo Corporation, Tokyo, Japan). The resolution was  $\pm 0.1$  m and the accuracy was  $\pm 0.5$  m. To improve the accuracy of data regarding the recording intervals (Wilson et al. 1995), we recorded diving depths with a 1-s interval (compared to 15 s in Williams, Briggs et al. 1992; Williams, Kato et al. 1992; 10 s in Bost et al. 1994; 15 s in Wilson et al. 1996; and 5 s in Miller et al. 2009). We randomly selected seven breeding pairs with two chicks (at day 0–5 after hatching) and attached the TDR device on the back of either parent using waterproof Tesa tape (a picture of gentoo penguin with a TDR on the back is shown in

Figure 1S, for details see Wilson & Wilson 1989; Wilson et al. 1996). Thus the seven individuals were chosen randomly in either of parents from seven different nests during chick-rearing. Because we deployed the loggers at various times (from early dawn until late afternoon) during the day, the start times of the recordings were distributed from 03:10 to 16:55 among the seven individuals (Table 1).

After the loggers were collected from the birds, we analyzed the diving patterns using IGOR Pro (version 6.2.2.2). From the depth data, we calculated foraging trip duration defined by the time between the start of the first dive ( $>1$  m depth) after departure from the colony and the end of the last dive before returning to the colony. We also calculated dive parameters such as diving depth and duration, vertical movements (ascending and descending speed), bottom duration and post-surface time before the next dive (see Figure 2S). We excluded data for dives shallower than 5 m, because they held majority of dive ( $62.1 \pm 12.2\%$ , SD) in number but accounted for only a small portion of the total dive duration ( $9.4 \pm 3.5\%$ , SD) so that we assumed that these shallower dives ( $<5$  m) are likely to constitute not foraging dives but traveling dives (Takahashi et al. 2003; Kokubun et al. 2010). The long recordings enabled us to observe each individual during day and nighttime periods (Figure 3S).

During the recording period (20 December 2013–10 January 2014) sunrise was between 02:58 and 03:31 and sunset was between 22:35 and 22:50 (<http://www.suncalc.net/>). Here we defined “night” as the period between sunset and sunrise and “day” as the period between sunrise and sunset. Because the number of depth wiggles (number of zigzag during a dive) correlates with the number of predation attempts for prey (Takahashi et al. 2004; Bost et al. 2007), we assumed that diving with depth wiggles during the period at the bottom indicated attempts to forage for prey. In penguin diving behavior, the depth wiggles are interpreted as prey pursuit (Rodary et al. 2000). A dive cycle consists of descending, bottom duration, ascending and post-surface (Figure 3S). Following Ydenberg and Clark (1989), we defined the

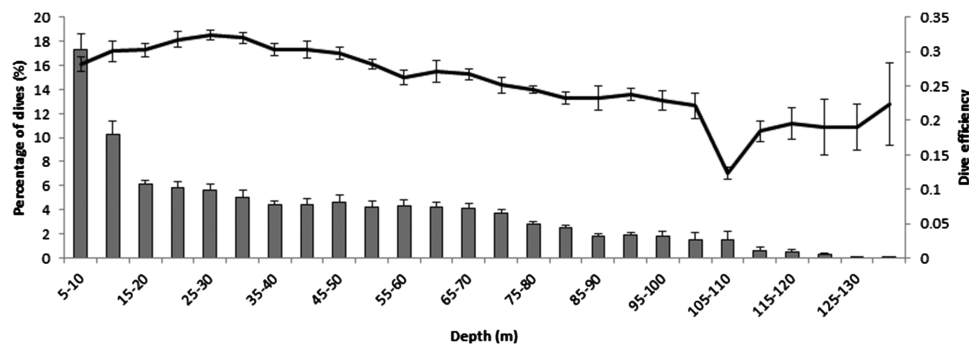


Figure 1. Percentage of dives (mean  $\pm$  SE, in gray bars) and dive efficiency (mean  $\pm$  SE, in solid line) at different depths (5-m intervals), excluding dives with depths of less than 5 m, based on data from seven gentoo individuals.

Table 1. Foraging trips and diving characteristics of seven breeding gentoo penguins on King George Island, Antarctica, during the chick-rearing period (recorded at days 0–5 after hatching, between 20 December 2013 and 10 January 2014).

ID	Sex	Mass (kg)	Recording start time (h)	Recording (days)	No. of foraging trips	Duration of trip (h)	Max dive depth (m)	Mean dive depth (m)	Mean dive duration (s)
108	F	5.2	10:59	21	21	11.2 ± 2.5	148.8	38.6 ± 31.0	98.2 ± 46.5
111	F	4.8	13:07	20	28	8.4 ± 3.4	132.6	41.0 ± 27.7	95.9 ± 42.4
121	M	5.7	10:55	6	6	13.0 ± 2.4	114.2	43.1 ± 29.4	108.1 ± 49.0
123	M	5.9	03:10	19	22	10.4 ± 4.3	142.0	35.9 ± 27.4	92.3 ± 39.5
166	F	5.9	16:55	5	7	13.4 ± 5.4	182.6	52.2 ± 37.4	106.1 ± 44.2
168	M	6.4	11:21	18	20	12.5 ± 3.2	123.1	40.7 ± 33.5	109.6 ± 54.6
170	M	5.6	04:00	16	17	11.2 ± 5.0	131.0	37.9 ± 25.7	95.5 ± 43.0

Note: The values are mean ± SD.

dive efficiency as the proportion of diving bottom time in a dive cycle [i.e. dive efficiency = bottom duration/(dive duration + post-dive surface time)], excluding diving events with more than 200 s of post-surface time (see Kokubun et al. 2010; Pichegru et al. 2011). This dive efficiency is a function to show how a diving animal distributes time for bottom duration on each dive cycle (Dewar 1924) and this can be used to predict the optimal diving physiologically (Elliott et al. 2013).

Each individual was recorded for 17–21 days after the first egg hatched. The depths obtained by two of the seven individuals (ID 121 and 161) were not correctly recorded after 6–7 days due to a mechanical problem with the loggers. Therefore, we excluded data collected after day 7 for ID 121 and after day 6 for ID 161. Thus, the average recording period was 15 days (±6.7 SD).

From the blood samples, we performed molecular sexing using the 2550F and 2718R primers (Fridolfsson & Ellegren 1999) and morphological sexing by bill and middle toe size measurements (Lee et al. 2015), and determined the sex of all seven individuals (see Table 1).

We did not include values for the frequency and efficiency of dives over 135 m because only a small number of dives (a total of 52 dive events, 0.36% mean percentage among total dives) were recorded from three individuals. We have presented data as a mean value ± SD in the Results and Discussion sections. Throughout the text, we used the diving tactic terms as below:

*Diving frequency* – the number of dives per hour.

*Dive efficiency* – proportion of bottom duration time in one dive cycle (calculated as bottom duration time/(dive duration + post-dive surface time)).

*Trip duration* – duration time after entering into the water and before finishing the swim.

*Dive timing* – it was binary coded if it is night dive or day dive, according to sunrise and sunset times

We used generalized linear mixed models (GLMMs, PROC MIXED in SAS 9.3) to determine which variables affect dive depth and dive efficiency. For estimating the effects on dive depth, explanatory variables were dive timing (day or night), sex of individuals (male or

female), and recording dates. The individual identity and the foraging trip identity were included as random factors. For dive efficiency, we also included dive timing, sex, and recording dates as explanatory variables and included the individual identity and the foraging trip identity as random. In this model, we dive depth was included as a covariate. Using GLMM, we also estimated if any changes occurred in the diving patterns as the penguins affect the number of their foraging trips. Response variables were the number of dives per trip, average dive depth, trip duration (h) and sex. The number of foraging trips (i.e. with the chick growth) was included as an explanatory variable and individual identity was included as a random variable in the model. In the three GLMM models, we selected best models by stepwise backward elimination procedures (Crawley 1993) from the initial models of the main effects and two-way interactions based on  $P$ -value < .05.

## Results

We recorded 24,087 dives (with a depth of more than 5 m) during 121 foraging trips from 7 gentoo penguins. During the foraging trips, the penguins performed  $211.0 \pm 39.8$  dives per trip, and each trip lasted for  $11.4 \pm 1.7$  h. The mean depth of each dive was  $16.5 \pm 5.0$  m with a mean duration of  $41.4 \pm 11.2$  s, and the maximum dive depth varied substantially among the individuals (114–182.6 m), although the sample size was not large enough to statistically evaluate the variance (Table 1). Among the all dives,  $82.9 \pm 7.1\%$  were performed during daytime and  $17.0 \pm 7.1\%$  were performed during nighttime.

Dives occurred most frequently (17%) near the surface (5–10 m) and the proportion of deeper dives decreased sharply to 4–6% at depths of 15–20 m depth, which was maintained until depths of 70–75 m (Figure 1). Dive efficiency had a peak around 25–30 m and both shallower and deeper dives had lower values (Figure 1). Gentoo penguins displayed similar dive frequency between daytime (between sunrise and sunset) and nighttime (after sunset and before sunrise) (Figure 2(a), the mean dive frequency

per hour were  $3.6 \pm 1.7\%$  for nighttime and  $4.3 \pm 0.3\%$  for daytime; paired *t*-test,  $t = -0.92$ ,  $df = 6$ ,  $P = .39$ ). The birds dived shallower at nighttime compared to daytime ( $16.6 \pm 2.9$  m at night and  $45.8 \pm 7.1$  m during the day; GLMM,  $F = 1188.78$ ,  $P < .001$ ; Figure 2(b)). Notably, the dive

efficiency during nighttime was higher than that during daytime ( $0.35 \pm 0.07$  at night and  $0.27 \pm 0.01$  during the day; GLMM  $F = 103.72$ ,  $P < .001$ ; Figure 2(c)). We categorized all dives into day and night dives and compared the diving frequency and dive depth between day and

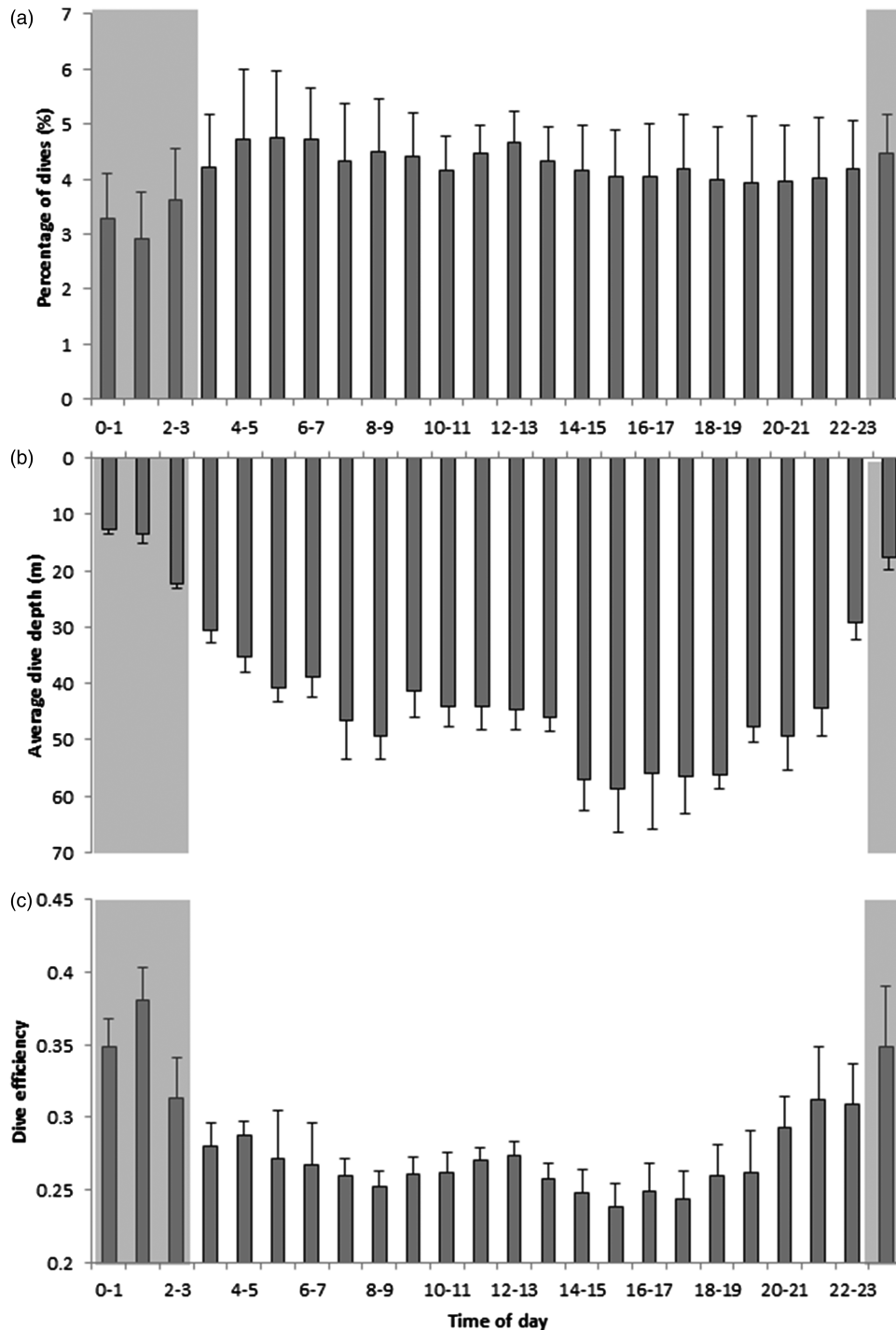


Figure 2. Percentage of dives (mean + SE) in gray bars (a), average depth of diving events (mean + SE) in gray bars (b), and dive efficiency (mean + SE) in gray bars (c) made at different times of the day (in 1-h intervals, from 0 to 24), based on data from seven gentoo individuals. Gray square areas indicate nighttime hours during the recording period.

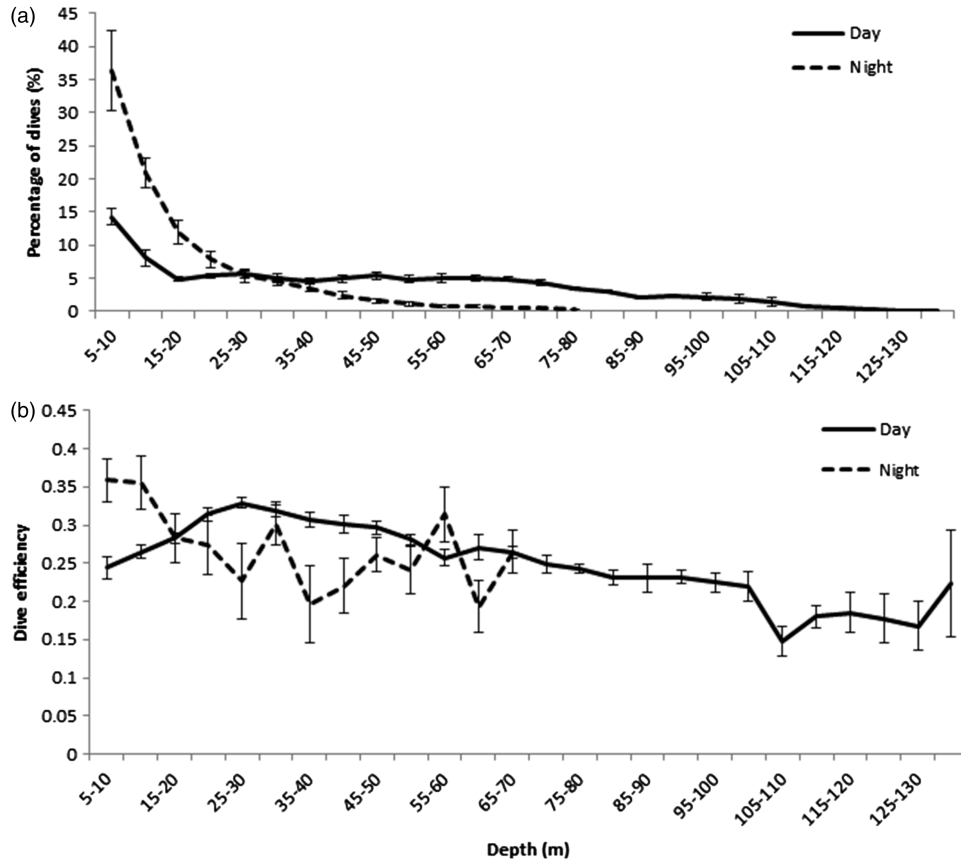


Figure 3. Percentage of day dives (solid line, mean  $\pm$  SE) and night dives (dotted line, mean  $\pm$  SE) (a) and dive efficiency of day dives (solid line, mean  $\pm$  SE) and night dives (dotted line, mean  $\pm$  SE) (b) expressed in 5-m depth intervals, excluding dives at depth of less than 5 m, based on data from seven gentoo individuals.

night dives. Night dives occurred mostly at near surface (5–10 m,  $31.3 \pm 18.4\%$  of total dives), whereas day dives were evenly distributed between depths from 20 to 80 m (Figure 3(a)). The dive efficiency during day slightly increased with depth with a peak at depths around 25–30 m, but night dive efficiency was highest near the surface and decreased with depth with a high variation at depths below 30 m (GLMM,  $F = 76.55$ ,  $P < .001$ , estimate =  $-0.0003 \pm 0.0004$  (SE) at day and  $-0.0020 \pm 0.0002$  at night; Figure 3(b)). The number of dives, depth of dives, and trip duration time did not change as the chicks grew; the average number of dives per trip (GLMM,  $F = 0.64$ ,  $P = .42$ ), the average depth of dives (GLMM,  $F < 0.001$ ,  $P = .99$ ), and the trip duration (GLMM,  $F < 0.001$ ,  $P = .99$ ) were not affected by the number of foraging trips.

**Discussion**

Despite the small number of individuals studied, the large amount of recorded data allowed us to investigate the diel diving patterns of gentoo penguins. Our results identified several details of their diving characteristics. Gentoo penguins dove most frequently in shallow water (<20 m),

and the dive efficiency was highest at depths of 25–30 m. Because the dives consist of vertical movements, foraging (i.e. bottom duration) and time spent searching for prey under limited diving capacities, penguins cannot spend longer time for bottom duration in deeper dives (Butler & Jones 1997). In this study, therefore, the smaller dive efficiency values in the dives deeper than 30 m may be attributed to the physiological limitation of the penguins. Dive efficiency in the depths shallower than 30 m showed a contrasting trend between the day and night dives (Figure 3(b)). This opposite pattern suggests the different dive pattern of gentoo penguins depending on the time. Penguins spent a longer bottom duration time in a dive at near surface at night and they decreased the proportion of bottom duration in deeper water. On the other hand, at daytime they increased bottom duration from the surface to 25–30 m depth. Since the bottom duration is considered as an indicator of foraging (Croll et al. 1992; Charrassin et al. 1998), this may reflect the active foraging activity at near surface during nighttime and at 25–30 m during daytime. Also, at daytime, dive efficiency can be lower in shallow water because penguins may dive for other purposes near the surface, such as searching and

exploring/traveling, rather than foraging itself (Trivelpiece et al. 1986; Williams, Briggs et al. 1992).

In contrast to the results of earlier studies in the sub-Antarctic areas (Bird Island, South Georgia; Macquarie Islands; Kerguelen Archipelago) that gentoo penguins mostly dive at daytime (Croxall et al. 1988; Williams, Briggs et al. 1992) or dive only at shallow water (<10 m) with small frequencies (Robinson & Hindell 1996; Lescroël & Bost 2005), our observations indicated that penguins actively dived during the nighttime. Dives were distributed throughout all periods of the day. The results indicated that gentoo penguins in the Antarctic area more actively dived at night and were possibly foraging in shallow water. Many gentoo penguins were observed to be fed by leopard seals (*Hydrurga leptonyx*) during the chick-rearing period near the sea shore. If penguins have difficulty in detecting the presence of predator under darkness, they could have fear of predation and avoid foraging at night (Ainley & Ballard 2012). However, the frequent night dives in this population are not fully explained by the predation. Instead, one possible explanation would be with the light condition at night. According to the definition of "civil twilight," total darkness does not occur when the sun is between 0° and 6° below the horizon. Throughout our measurement period (20 December 2013–10 January 2014), civil twilight continued from the time between sunset and sunrise. Because penguins are largely dependent on visual ability in water (Martin 1990), light levels from 3.4 to 400 lux (Bond & Henderson 1963; Ballard et al. 2010) may enabled penguins to avoid darkness at night during the recording period. The dive depth of gentoo penguins was shallow at night (<20 m) and relatively deeper during the day. Although Antarctic penguins also feed in the dark (Lishman 1985; Rodhouse et al. 1998), the brighter condition with civil twilight could contribute to the active diving for foraging at night. The main finding of this study is that dive depth of gentoo penguins was concentrated in shallow water at night (<20 m) and relatively deeper at day like Wilson et al.'s study (1993). Diving depth and time of Antarctic diving animals are possibly influenced by the vertical migration of krill (Fraser et al. 1989; Bengtson & Stewart 1992; Hopkins & Arnould 2013). The main prey item of breeding gentoo penguins in our study area is mostly krill (Miller et al. 2009; Kokubun et al. 2010). Considering the vertical migration of krill moving up to shallower depths surface at night for food sources (Brierley 2008; Gaten et al. 2008), our results corresponded to the diel vertical krill distribution with depth (Brierley 2008; Gaten et al. 2008). Kalinowski and Witek (1980) presented that krill in the western Antarctica moved up to 10 m depth during nighttime and down to 30–60 m at daytime. Thus, the diel pattern of gentoo penguin diving may support the hypothesis that the gentoo penguin dives are closely related to the vertical movement of prey (Croxall et al. 1988; Williams, Briggs et al. 1992).

Although we expected foraging efforts to increase as penguin chicks grew (Williams & Rothery 1990; Williams, Briggs et al. 1992), the trip duration, number of dives, and diving depths were not changed with the chick age. Rather than the increased food requirements for chick development, other factors, such as food availability and wave conditions, are likely to be crucial for determining foraging behavior. From our observations in the field, gentoo penguins seemed to hesitate to get into diving and spend less time when there were strong winds at the sea shore. As previous studies showed in other gentoo populations (Croxall et al. 1988; Williams, Briggs et al. 1992), there was no sexual difference in dive parameters. Their diving capacities do not seem to differ between the sexes although male gentoo penguins are known to be slightly larger than females (Williams 1995).

Our results showed the diel pattern of diving behavior in Antarctic gentoo penguins. Here, we described that the penguins conducted diving in shallow water during nighttime as frequent as they did during daytime. We expect that these results can provide important data to understand the diving behavior throughout the whole 24 h period in Antarctic gentoo penguins, compared to previous results in sub-Antarctic areas (e.g. Croxall et al. 1988; Williams & Rothery 1990; Robinson & Hindell 1996; Lescroël & Bost 2005). In our study area, chinstrap penguins (*Pygoscelis antarctica*) are also present, and they sympatrically breed with gentoo penguins in austral summer. A competitive relationship for foraging habitats between the two species (Kokubun et al. 2010) may also influence their diving behavior. In future studies, comparing the diving patterns of the two species would be useful. In addition, if data from both parents within a breeding pair are collected, it would enable an understanding of how the parents allocate time between foraging and chick brooding duties. Because the penguins in our study were randomly chosen in either of parents, it is difficult to examine the parental role and investment during chick-rearing. Although we did not find any sexual influences on dive depth and dive efficiency, gentoo penguins may have different diving traits between the sexes (possibly related with their sex-specific diving depth, Bearhop et al. 2006). Although, there were no sexual differences in dive parameters in a few studies (Croxall et al. 1988; Williams & Rothery 1990; Williams, Briggs et al. 1992), male gentoo penguins are known to be slightly larger than females (5–16%, Williams 1995). Considering that a larger sex dived deeper and longer in a diving bird (Japanese Cormorants, *Phalacrocorax capillatus*, Watanuki et al. 1996), it is still worth to estimate the sexual difference. Examining parental qualities and correlating them with diving behavior and food delivery rates would also be interesting. Flexible foraging characteristics of gentoo penguins have been observed in Antarctica from multiple sampling data (Miller et al. 2009). We anticipate that long-term monitoring of diving

behavior would provide basic information regarding the foraging strategy of penguins and its relationship with the distribution of their prey in Antarctic regions.

### Acknowledgements

We specially thank to Dr Eric Potvin for English correction and for helpful comments on the manuscript. We thank Hankyu Kim and Minsoo Jung for the technical assistance during fieldwork.

### Disclosure

No potential conflict of interest was reported by the authors.

### Supplemental data

Supplemental data for this article can be accessed here [10.1080/19768354.2015.1074107](https://doi.org/10.1080/19768354.2015.1074107)

### Funding

This research was supported by the Long-Term Ecological Researches on King George Island to Predict Ecosystem Responses to Climate Change (PE14020) funded by Korea Polar Research Institute. Also, this work was partly supported by Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education, Science and Technology (NRF-2014 R1A6A3A01008495). This was also partly supported by NIPR visiting scientist program for polar sciences from Asian countries in 2014.

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