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Distribution of emperor penguins' dive directions under the fast sea ice

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ABSTRACT

Emperor penguins *Aptenodytes forsteri* feed mainly on *Pleurogramma antarcticum* and *Pagothenia borchgrevinki* in the sea of Antarctica. Because these prey are not distributed uniformly, prey encounter rates during a dive change depending on where emperor penguins dive. In limited time and space, they should select areas in which prey are expected to be abundant. We hypothesized that the distribution of emperor penguins' dive directions was not uniform due to their selective dives. In order to test this hypothesis, dive paths were calculated with the data recorded by data loggers. Dive direction was obtained for each dive path, and the distribution of the dive directions was investigated. In five experiments of the total of six experiments, the dive directions were not distributed uniformly. This suggested that the emperor penguins had a preference about their dive directions. The dive directions were not related with ocean current direction, which was considered to be one of the factors affecting penguins' diving behavior. The emperor penguins may have decided where they dived according to their knowledge about prey distribution and/or the behavior of conspecific individuals.

KEYWORDS: emperor penguin, dive direction, foraging strategy, data logger, sea ice

INTRODUCTION

Emperor penguins *Aptenodytes forsteri* dive routinely for foraging in the sea of Antarctica. This species is an excellent diver with the recorded longest dive greater than 20 min (Wienecke *et al*. 2007). Their main prey are *Pleurogramma antarcticum* and *Pagothenia borchgrevinki* (Green 1986, Cherel and Kooyman 1998). Because these prey are not distributed uniformly (cf. Guglielmo *et al.* 1998), prey-encounter rates during a dive change depending on where emperor penguins dive. This condition makes their selection of the foraging space crucial for their foraging strategies. Additionally, emperor penguins are often forced to dive under the thick sea ice. Therefore, their foraging space is constrained around the ice hole or crack for exit unlike in the open water. In limited time and space, they should dive selectively to areas in which prey are expected to be abundant.

We hypothesized that the distribution of emperor penguins' dive directions was not uniform due to their selective dives. In order to test this hypothesis, dive paths of emperor penguins were calculated from data obtained with the miniature data logger.

MATERIALS AND METHODS

In this study, new analyses were conducted on the data of dive paths of three emperor penguins (bird; A, B, C, Shiomi *et al.*2008).

They were captured near the sea ice edge of the east McMurdo Sound, Antarctica, and were maintained in a corral (77°43'S, 166°07'E). A southward-flowing current was found to predominate near the site (77°49'S, 166°7'E; Barry & Dayton 1988). A data logger (W1000L-3MPD3GT: 26 mm in diameter, 174 mm in length, 120 g weight in air; Little Leonardo Co., Tokyo, Japan) was attached on the back of each bird one to three times with the water proof tape (Tesa tape) and the instant glue (Loctite) (deployments named A-1, A-2, A-3, B-1, B-2, and C, respectively; Table 1). They foraged daily beneath the sea ice, diving in and out of the sea only through two isolated ice holes (see Sato *et al.* 2005 for detail). Dive paths of the penguins were calculated with the magnetic, gravitational acceleration, depth and swimming speed data recorded by the loggers (Shiomi *et al.* 2008).

The maximum depth during each dive was defined as the dive depth, and the distance on the horizontal plane between the farthest point and the start point of a dive as the horizontal distance. Only dives in which the dive depth was >25 m and the horizontal distance was >100 m were used for the directional analysis. We considered the other dives not to be suitable for the analysis. In those dives, they swam tortuously and irregularly near the dive holes, so it was not sure that the penguins dived for foraging. The direction of a dive was defined as the direction of the farthest point relative to the start point. The uniformity of the distribution of dive directions in each deployment was examined by Rayleigh test (Zar 1999, chap 27), and the mean angles of dive directions were compared among all deployments and among deployments with each bird using the Watson-Williams test (Zar 1999, chap 27).

Results are presented as mean ± the standard deviation, and the results of tests were assumed to be significant at $P < 0.05$.

Table 1. Information about deployments on emperor penguins.

Deployment	Logger-attachment date and time		Deployment duration (h)	Number of dives (n)	Number of dives for directional analysis (n)
A-1	Nov. 19, 2004	11:09	50.3	175	54
A-2	Nov. 29, 2004	13:22	48.3	86	41
B-1	Nov. 14, 2004	8:02	38.0	131	34
B-2	Nov. 22, 2004	9:02	52.5	119	37
B-3	Dec. 2, 2004	8:05	60.4	134	46
C	Nov. 25, 2004	10:26	55.6	133	33

RESULTS

The three penguins performed 778 dives in six deployments, and three-dimensional dive paths of 662 dives were calculated. Those of the remaining dives (i.e. 116 dives) could not be reconstructed due to a stall of the propeller rotation for measuring the swimming speed. Of the calculated dive paths, 245 dives were >25 m in dive depth and >100 m in horizontal distance, and those were analyzed here.

The distribution of the dive directions in the deployment A-1 and C were not uniform (Rayleigh test; $P < 0.01$ for A-1, $P < 0.05$ for C), that in B-1, B-2, and B-3 was diametrically bimodal (Rayleigh test using the doubling angle; $P < 0.001$ for B-1, $P < 0.05$ for B-2 and B-3), while that in A-2 was not biased (Fig. 1). The mean angles of the dive direction were significantly different among deployments (Watson-Williams test; $F = 8.84$, $P < 0.001$). For bird B, the mean angles were not significantly different among the three deployments (Watson-Williams test; $F = 0.26$, $P > 0.05$).

DISCUSSION

In five of all the deployments, the distribution of the dive directions was biased significantly (Fig. 1). This result suggested that the emperor penguins dived in a direction not randomly but selectively; this supported our hypothesis.

The mean angles of the dive directions were significantly different among the six deployments. The selection of dive directions may be affected by the ocean drift, prey distribution, and/or the presence of other individuals, which may have varied depending on time. However, for bird B, the dive directions distributed similarly in all the three deployments; the mean angles of the dive directions were not significantly different, and the distributions were diametrically bimodal. This may mean that the bird had decided the dive directions based on time-independent factors at least for about half a month (e.g. an experience of successful foraging).

The mean angles of dive directions were deviated from the major axis of the current, identified by principle component analysis (see Fig. 3a in Barry & Dayton 1988). Under the conditions of this study, the emperor penguins had to return the same hole. So, even if they could save energy use by swimming with current in either outward or inward journey, they had to swim against current in either journey. This perhaps explained why the dive directions were not related to current direction. The relationship of the prey distribution and inter-individual interaction with the dive directions will become clearer by obtaining the data of prey distribution around the experimental site and by attaching the data loggers on some individuals at the same time. In addition, the contribution of experience can be examined by attaching the logger many times on one bird from the arrival at the experimental site.

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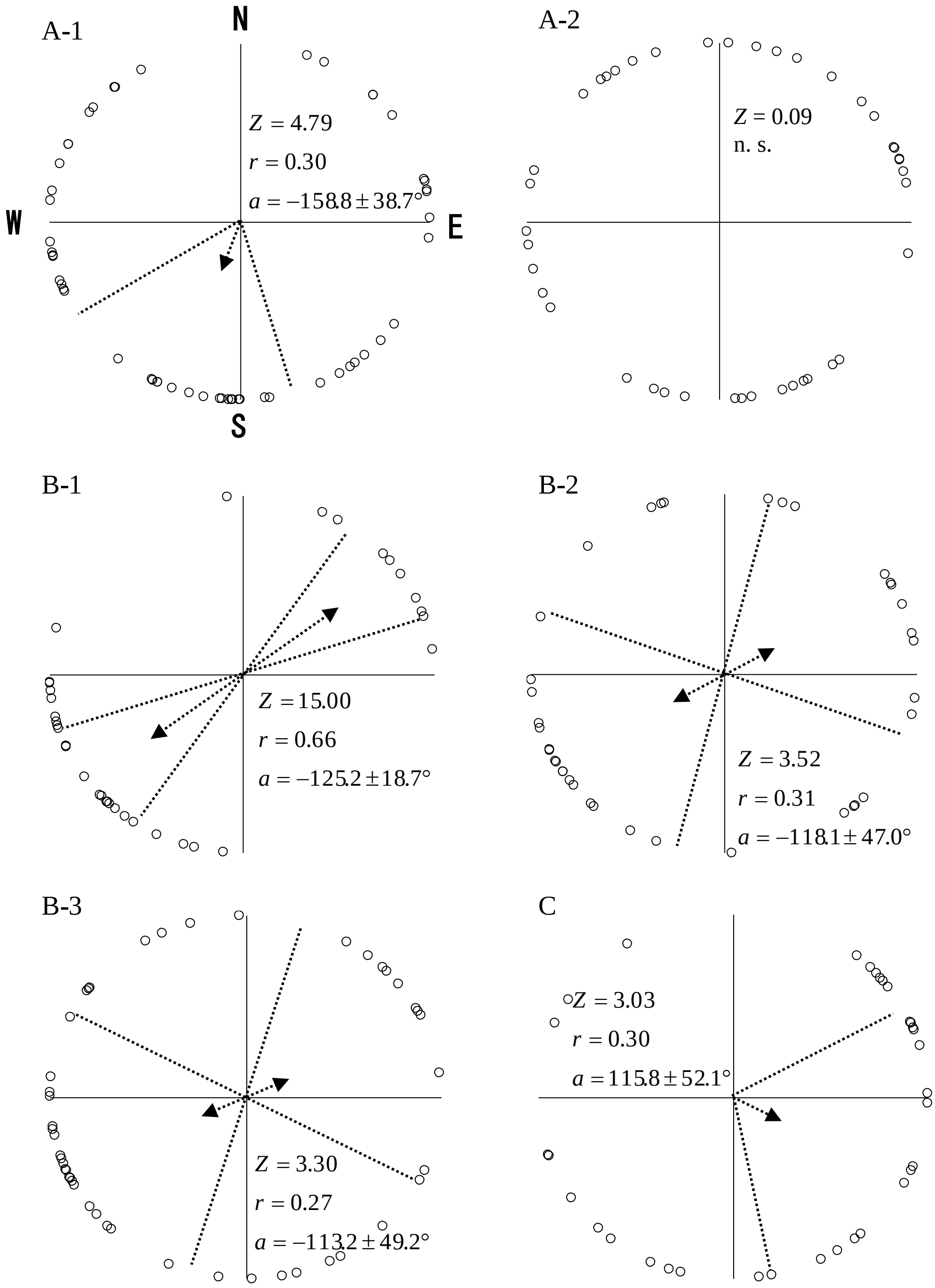

Fig. 1: The distribution of the dive directions in each deployment. *r* is Rayleigh's *r*, *a* the mean angle. The dashed arrows represent the mean vectors. The length of the vector is drawn proportional to the radius of the circle=l. The confidence limit for the mean angle was marked by dashed lines. n. s.: the mean angle was not significant**.**