The influence of preceding dive cycles on the foraging decisions of Antarctic fur seals

T. Iwata1,2,†, K. Q. Sakamoto3, E. W. J. Edwards4, I. J. Staniland4, P. N. Trathan4, Y. Goto1, K. Sato1, Y. Naito5 and A. Takahashi2,5

1Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan
2The Graduate University for Advanced Studies, Hayama, Miura, Kanagawa 240-0193, Japan
3Graduate School of Veterinary Medicine, Hokkaido University, Kita 8, Nishi 5, Kita, Sapporo 060-0818, Japan
4British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK
5National Institute of Polar Research, 10-3, Midoricho, Tachikawa, Tokyo 190-0014, Japan

The foraging strategy of many animals is thought to be determined by their past experiences. However, few empirical studies have investigated whether this is true in diving animals. We recorded three-dimensional movements and mouth-opening events from three Antarctic fur seals during their foraging trips to examine how they adapt their behaviour based on past experience—continuing to search for prey in the same area or moving to search in a different place. Each dive cycle was divided into a transit phase and a feeding phase. The linear horizontal distance travelled after feeding phases in each dive was affected by the mouth-opening rate during the previous 244 s, which typically covered two to three dive cycles. The linear distance travelled tended to be shorter when the mouth-opening rate in the previous 244 s was higher, i.e. seals tended to stay in the same areas with high prey-encounter rates. These results indicate that Antarctic fur seals follow decision-making strategies based on the past foraging experience over time periods longer than the immediately preceding dive.

1. Introduction

Animals should make optimal decisions about where and how to forage to maximize energy intake rates [1]. Several predictions about how predators should adjust their movements in response to prey capture have been made [2]. In a patchy environment, it is expected that predators should increase their search effort after capturing prey because of the high probability of encountering other prey nearby [3]. Although these decision-making processes have been investigated in terrestrial animals [4], few empirical data exist for breath-holding diving animals. Prey-searching behaviour of diving animals is constrained by the requirement to return to the surface at regular intervals to breathe, which means animals cannot remain within prey patches at depth [5,6].

Recent studies have investigated foraging behaviour using animal-borne data loggers [7]. Three-dimensional dive paths have been reconstructed from triaxial magnetic and acceleration data loggers [8], whereas prey-capture signatures detected by accelerometers [9–11] and mouth-opening events detected by acceleration data loggers attached to the lower jaw [12,13] have been used as a prey-encounter indices. The Antarctic fur seal Arctocephalus gazella is a diving predator that has a specialized diet at South Georgia, consisting almost entirely of a patchily distributed prey-source, Antarctic krill Euphausia superba [14]. We used this species as a subject to examine possible foraging decision-making strategies in diving...
predators. According to the predictions from theoretical studies [3], foraging decisions in fur seals should be based on their past prey-capture experiences. However, it remains unclear over what time period animals decide their next movement. These decisions are important as they determine whether it is more beneficial for them to stop or continue diving if they cannot catch prey within a preceding dive. According to the marginal value theorem in optimal foraging [1], if they continue diving, then they must decide for how long to do so and such decisions must be based on their past foraging experience. In this study, we examined preceding prey-encounter rates and travelling distances between individual dives made by Antarctic fur seals in order to understand how decision-making takes place.

2. Material and methods

Three female Antarctic fur seals, observed nursing a pup, were captured at Bird Island, South Georgia (54°00′S, 38°03′W) in January and February 2009. Females were restrained by methods previously described [15]. Data loggers (see below) were attached by cable ties to nylon webbing, which was then glued to the fur using a quick-setting epoxy. The data loggers were recovered after a single foraging trip by recapturing the animal and cutting the cable ties. We used three types of data loggers: M190-D2GT (diameter 15 ± 53 mm; 17 g in air; Little Leonardo Ltd, Japan), which recorded diving depth, temperature and two-axial acceleration; W1000L-174G (diameter 26 × 174 mm; 135 g in air), which recorded diving depth, temperature, swimming speed, triaxial acceleration and geomagnetism; and GPS data loggers (90 × 50 × 22 mm; 105 g in air; Sirtrack Ltd, New Zealand). The D2GT were attached to the lower mandible to detect mouth-opening events, which were used as a proxy of prey-encounter [12]. We used only mouth-opening events when seals were deeper than 2 m because of difficulty in distinguishing between prey-capture attempts and breathing near the surface. Both 3MPD3GT and GPS loggers were attached to the dorsal fur of animals and used to reconstruct the three-dimensional dive paths and the animal’s location between dives. Three-dimensional dive paths reconstructed by 3MPD3GT include some errors owing to water currents and sampling intervals [8]. The horizontal positions obtained by GPS tracking data on the surface were used to correct the three-dimensional dive path. A dive was defined as any excursion below the surface to a depth of more than 2 m. Each dive cycle was subdivided into two phases: a transit phase (ascent, surface and descent) and a feeding phase (the dive bottom duration between descent and ascent; figure 1). We used dives with the maximum depth deeper than 2 m as criteria following the definition of foraging in shallow dives. The diving data were separated into dive bouts using a 74 s bout ending criterion, which is the difference in surface duration between two successive dives estimated by sequential difference analysis [16]. Moreover, to investigate the effect of preceding foraging experiences we used dive bouts longer than 25 min (1500 s) for analysis as previous studies have shown this value to be the approximate mean duration of bouts in Antarctic fur seals [17,18]. The linear horizontal distance travelled after a feeding phase was determined as the horizontal straight-line distance between the end of the feeding phase and the start of the next feeding phase (figure 1). The linear horizontal distance data after the last dive of each dive bout was not used. During dive bouts, we tested the effect of the preceding mouth-opening rate on the linear horizontal distance travelled after the feeding phase during a dive using generalized linear mixed models (GLMMs) with Gaussian distribution and identity links; we set the identity of individuals as a random factor. The response variable was the logarithmic value of the linear horizontal distance travelled after the feeding phase. The mouth-opening rate was set to an explanatory variable, which was calculated by dividing the number of mouth-opening events over the period from 1 to 1500 s, respectively. We selected the mouth-opening rate that best corresponded to the explanatory variables by comparing the Akaike’s information criterion (AIC) for each GLMM. We then calculated the value of the conditional R² for GLMMs. Statistical analyses were carried out using R software v. 3.1.2 [19], with the GLMMs fitted and conditional R² calculated in the package ‘lme4’ and ‘MuMIn’, respectively [20]. Means ± s.d. are presented unless otherwise indicated.

3. Results

All data loggers were recovered from our study animals. Twenty-seven dive bouts were identified from sequential difference analysis: these lasted from 0.42 to 7.70 h (10–273 dives). A dive cycle was composed of a dive duration (108 ± 38 s) and a surface duration (42 ± 25 s; n = 1026 dives from three seals). The dive duration was divided into a descent (27 ± 16 s), a feeding-phase (62 ± 19 s) and an ascent (20 ± 14 s). The mean mouth-opening depth was 42 ± 23 m (n = 20993 events by three seals).

Our statistical analysis clearly indicated that the linear horizontal distance travelled was related to the preceding mouth-opening rate. The AIC was lowest when the explanatory variable was calculated over the previous 244 s (figure 2a). The values of AIC changed periodically (figure 2a). We carried out the autocorrelation analysis to determine the periodicity of the fluctuation in AIC. Values of AIC changed periodically (figure 2a). The autocorrelation analysis indicated the frequency of periodicity of AIC. The peak of periodicity in AIC was about 45 s (figure 2b) indicated the cycle was 145 s, which is similar to the duration of a typical dive cycle (150 s = 108 s + 42 s). Moreover, linear horizontal distance travelled was significantly shorter when the mean value of the mouth-opening rate in the previous 244 s was higher (p < 0.001, conditional R² = 0.60, GLMM; figure 2c).

4. Discussion

Theoretical studies predict how animals should adjust their movements in response to prey-encounter events [2]. Foraging decisions in macaroni penguins, Eudyptes chrysolophus, which
forage in similar pelagic domains to fur seals, have been shown to be influenced by prey encounters but only during the immediately preceding dive [21]. However, this study did not analyse the effect of previous experience over longer periods of diving. We investigated the effect of foraging experiences during the preceding 1–1500 s (about 1–10 dives) on successive horizontal movements. This study is the first report (to the best of our knowledge), for any diving animal, that foraging decisions are influenced by prey encounters experienced during the past two to three dives (244 s). For Antartic fur seals, the linear horizontal distance travelled between feeding phases was affected by the mouth-opening rate in the past 244 s, which is longer than the sum of the average durations of a feeding phase (62 s) and a dive cycle (150 s; figure 1). Assuming that mouth-opening events can be used as a prey-encounter index, our study shows that Antarctic fur seals stayed in the same area when they experienced high rates of prey-encounter events. AIC values fluctuated with a cycle of 145 s, and the cycle was similar to the average duration of a dive cycle. This result suggests that the horizontal movements of fur seals were influenced by prey-encounter rates during each feeding phase of the previous dives.

Terrestrial animals such as intermediate egrets, *Egretta intermedia*, show decision-making processes based on their foraging experiences at more than one temporal scale [4]. Terrestrial animals can usually maintain foraging effort, including prey search and capture, and they do not need to cease feeding for breathing. However, air-breathing diving animals need to commute between the prey patch and the water surface to breathe. Therefore, foraging in air-breathing diving animals has to be intermittent because of the alternating foraging and non-foraging periods. This limitation imposes additional constraints on diving animals—not only do they make trade-offs about continuing to forage in the present locality or moving to a new site, but they must also determine how prey patches might change during the period when they are unobserved.

Data accessibility. Raw data deposited at: http://dx.doi.org/10.5061/dryad.pk368.

Authors’ contributions. T.I., I.J.S., P.N.T., Y.N. and A.T. designed the research. T.I., K.Q.S., E.W.J.E. and T.A. performed the research. T.I., K.Q.S., Y.G., K.S. and T.A. analysed the data. T.I. and K.S. wrote the first draft. All authors finalized the manuscript. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. This study was supported by the Japanese Antarctic Research programme and the programme Bio-logging Science of the University of Tokyo (UTBLS).

Acknowledgements. We thank the field staff at Bird Island Research Station, British Antarctic Survey, in the 2008/2009 season for assistance with fieldwork; T. Akamatsu, Y. Mori and Y. Y. Watanabe for help with data analysis; I. Suzuki, C. Rutz and two anonymous referees for reviewing the manuscript and providing helpful suggestions. The work was approved by the British Antarctic Survey and the University of Cambridge Animal Welfare Review Committee.

Figure 2. (a) AIC values from generalized linear-mixed models for linear horizontal distance travelled after feeding phase of Antarctic fur seals, with each explanatory variable based on the mouth-opening rate in the past 1 to 1500 s, respectively. AIC values were lowest when the explanatory variable was the mouth-opening rate in the previous 244 s. (b) The autocorrelation coefficient of AIC value with slide time. The arrow indicates the peak of the autocorrelation coefficient. The peak was calculated when slide time was 145 s. (c) Relationship between the mouth-opening rate (number per second) in the previous 244 s and the linear horizontal distance travelled after a feeding phase during diving bouts. When the mouth-opening rate was high, the linear horizontal distance travelled was short (n = 1026 dives from three seals).
References


