論 文 の 内 容 の 要 旨

論文題目　　Foraging behaviour of streaked shearwaters (*Calonectris leucomelas*) in relation to wind conditions
（海上風に関連したオオミズナギドリの採餌行動）

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Chapter 1: General Introduction

Foraging behaviour contains two distinct phases: search, and prey capture. The efficiency of foraging is important to animals that exist in patchy environments with prey patches found in heterogeneous concentrations. Seabirds are a group of animals for whom efficiency plays a major role in their adaptation. In the search for prey, seabirds have developed strategies to aid them, namely visual, social transfer, and olfactory. While evidence exists for all, the use of olfaction by birds in the order Procellariiformes has been investigated in the scientific literature. Dimethylsulphide (DMS), a by-product of the breakdown of zooplankton and found to be detectable and attractive to seabirds, has been touted as a viable method by which birds can navigate. However, little research has explored the role of DMS in directing birds to foraging spots.

Streaked shearwaters are mid-sized birds of the order Procellariiformes. These birds are highly adapted to efficient locomotion, travelling by using dynamic soaring to minimise energetic costs. To classify foraging behaviours, animal-borne data loggers recording GPS and video of the birds during foraging trips were used to generate a classification algorithm. To understand their relationship with winds during search, data loggers recording acceleration and GPS were attached to shearwaters. The GPS tracks were used to estimate wind vectors using two different estimation methods, which were compared and validated against an independent data source. Results from the better performing estimation method were combined with foraging detections from the acceleration records, and the relationship between winds and foraging was examined.

Chapter 2: Foraging Detection Method

The identification of foraging behaviour in animals is important to understand how and where they feed. In seabirds, techniques have been developed to derive foraging behaviours from animal-borne data recorded by pressure sensors, GPS, and acceleration. Streaked shearwaters are shallow diving birds, and so use of pressure sensors to estimate dive behaviour is not as feasible due to the reduced pressure experienced, and so reduced signals recorded by the sensor. To identify and categorise behaviours, the study of this chapter instead used acceleration data. This data is high in its sampling rate and can contain information about minute movements of an animal. Acceleration therefore provides an ideal alternative for the detection of foraging behaviours. Five recently developed combination video and acceleration recording tags light enough to be deployed on seabirds were used to record a total of 10 hours of footage and acceleration during foraging trips of shearwaters in 2018. The video recordings allowed the birds' behaviours to be estimated and provided context for the acceleration records.

Four distinct behaviours were observed during the video footage, flight, take-off, surface seizing (consisting of repeated landings with little/no submersion separated by short take-offs), and foraging dives (full submersion visible on the recording). Shearwaters were observed foraging in association with large marine predators including dolphins, large fish, and other seabirds. The video records were used to estimate behaviour performed, and a behaviour detection algorithm generated that could classify behaviours from acceleration data. Over 70% of video-recorded foraging behaviours were correctly identified by the algorithm, with a false positive rate (behaviour incorrectly classified as foraging) of less than 3%. The detection method was therefore a little conservative, however, produced very few false positive detections.

The generated algorithm was then applied to longer term acceleration data from combination GPS and acceleration tags attached to 20 birds, 11 in 2018 and 9 in 2019 and foraging locations were determined. Tags lasted from 4 to 11 days in duration and recorded multiple foraging trips between 1 and 8 days in length. Birds performed an average of 46 foraging dives and 17 surface seizes per day. Kernel density estimates of foraging locations separated by behaviour and sex largely overlapped, showed little difference between sexes and foraging behaviours. The generated detection method provides a means to investigate fine-scale foraging in this, and other, shallow-diving species. The video recordings also document two forms of foraging behaviour and the associations between streaked shearwaters and other marine predators when foraging.

Chapter 3: Wind Vector Estimation Method Comparison

Throughout their lifespans, seabirds must interact with winds near constantly. Winds are vital to the efficiency of travel and can be important in the dispersal of odours over the ocean. However, the scales at which ocean wind data is available differs greatly from most scales that seabird biologging studies utilise. Studies investigating the relationship birds have with ocean winds have typically used wind data aggregates for 3 to 6-hour periods spanning over largescale spatial grids (12.5 × 12.5 km for example). It is therefore difficult to compare fine-scale behavioural data with ocean winds due to this disparity in scales. However, methods to estimate wind vectors from seabird GPS tracks have been recently developed. Two such methods, known as the curve and distribution methods, are investigated in this chapter and their validations by an independent data source are compared. These methods use the relationships between speed and heading to estimate wind vectors.

The sampling rate of the data used for the original curve method study and the recordings from streaked shearwater records in 2019 as described in Chapter 2 differed. The curve method was therefore tested for sensitivity to data sampling rates by subsampling the GPS tracks used in the method then comparing the results. Results from the application of the curve and distribution methods were then compared with wind vectors from the Japanese Meteorological Agency's reanalysis mesoscale model. Subsampling the data did not appear to have a large effect on the outcome of the curve method, with high correlation in both the estimated wind speeds and directions. However, the curve method estimates did not correlate well with the reanalysis model in either speed or direction, typically underestimating wind speeds. The distribution method, however, produced wind estimates that correlated well with the mesoscale model, although wind speeds were still underestimated. This may be due to differences in the altitude of the model (10m) vs. where the birds typically fly (~5m). As it performed better than the curve method, the distribution method was adopted for use in Chapter 4,

Chapter 4: Use of Wind in Prey Search

During the search phase, seabirds are travelling over an environment with no clear cues as to where prey are available. Though visual cues may be important in identifying prey patches (as indicated by the recording of associations with marine predators in Chapter 2), these cues cannot be used over larger distances outside of a seabird's visual range. Therefore, shearwaters must use some other cue to maintain a constant heading whilst travelling to foraging spots. Olfaction has been widely discussed as a viable method for seabirds to identify productive regions, and evidence exists to suggest birds can navigate via olfaction. However, no studies have directly tested the movement of seabirds in winds as they approach foraging spots. Through a combination of the foraging detections from Chapter 2 and the wind vector estimates from Chapter 3 (using the distribution method), this relationship is analysed.

Calculated winds were grouped by distance to the next foraging spot. The relative wind headings (the bird's heading minus the wind heading) were calculated and tested for uniformity. As shearwaters approached foraging spots, their use of winds changed from sidewinds to near-headwind conditions. From 50 to 30 km to the next foraging spot, birds' use of winds showed a bimodal distribution with peaks at sidewinds. From 30 km to the foraging spot, birds mostly flew in headwind conditions, which were significantly non-normally distributed (Hermans-Rasson test, $p < 0.01$). At closer proximity, the relative wind conditions began to be more normally distributed when birds were <2 km from the next foraging spot. When travelling upwind, birds may encounter scents such as DMS, carried from foraging spots that provide a means to maintain their heading. The dispersals of relative wind headings (the variation of the wind conditions the birds are travelling in) increased when birds were <10 km from the next foraging spot. This could represent a transition to a less wind-directed travel method, with the dispersals of relative wind headings increasing and birds flying less consistently into the wind. To check how birds would fly when travelling and not approaching prey, the relative wind headings were also grouped by distance from the nest colony to test for changes in the birds' wind strategies when leaving or returning to the colony. During this travel phase, birds used sidewind conditions regardless of trip length. Sidewinds are efficient for flight in shearwaters as they can perform dynamic soaring. As expected, birds moved slower in headwinds, and avoided flying in headwinds during high wind speed conditions. Therefore, the shearwaters chose to fly under inefficient conditions as they neared foraging spots. It appears likely they do so to take advantage of the scents carried by the wind to locate prey.

Chapter 5: General Discussion

In the above studies, streaked shearwater foraging is examined in a fine scale, from detecting foraging through high-sampled acceleration data, to examining the wind conditions the birds use during search. Animal-borne recordings of seabird foraging behaviour are currently rare in the scientific literature and uncover detail about the behaviours themselves and seabird ecology, with direct evidence of association with other predators, the first such study regarding streaked shearwaters. The detailed information provided by the foraging detection method can improve researchers' understanding about the daily activities of seabirds and how they manage to survive in the ocean environment. These details could be vital to understanding the effects of changes to the environment on seabird populations. Examination and comparison of wind estimation methods is vital to the development of this field, and its use in examining wind strategies of foraging seabirds provides evidence for the use of olfactory senses as a tool to facilitate intermediate search. Most olfactory-based seabird research has taken place in the southern oceans, therefore providing evidence of olfactory-reliance in the northern hemisphere is important to better our understanding of seabird foraging strategies in dynamic ocean environment. Seabirds provide researchers with a unique tool for sampling the environment they live in, a large environment that is often difficult to sample. This information includes sampling of ocean productivity via foraging to gathering data about the atmosphere through wind estimation. To this end, adding the context of seabird foraging through detailed analysis of their foraging ecology is crucial. Seabirds can therefore provide vital information regarding the state of the oceanic environment.