

Doctoral Thesis

博士論文

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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## General Introduction

Seabirds are highly adapted ocean inhabitants, spending upward of 90% of their lives at sea (Balance et al., 2019). As such, they are well adapted to multiple media: land, oceans, and the air. Though seabirds travel through the air, they then feed on or in the oceans. This combination means seabird foraging behaviour is particularly unique. Foraging behaviour can be separated into two distinct phases, search and prey capture. Both of these components of foraging are important in reconstructing the ecology of a species and understanding how changes to its environment may affect the species' population. Foraging efficiency (the intake of energy – the cost of obtaining it) in seabirds is largely determined by their ability to travel to a prey patch due to the large distances they must often travel (Weimerskirch et al., 2003). How seabirds find and capture prey is a question that has formed much debate in the scientific literature. Seabirds have developed a number of foraging methods, both in prey capture techniques and search behaviours (Shealer, 2001). This variety in behaviours is reflected in the range of scientific literature available on the topic of seabird foraging. However, details on seabird foraging are as yet relatively scarce.

## 1.1 The senses of a seabird

Avian travel has long held interest concerning the ability of birds to correctly and efficiently decide on travel headings to reach intended destinations. Efficient foraging requires seabirds to identify productive areas across the featureless oceans they travel. Seabirds must travel long distances, both during migrations and foraging trips. Therefore, directing travel is vital in optimising foraging efficiency, and so understanding their means of navigation during foraging trips is paramount.

### 1.1.1 Visual senses

Visual cues are effective methods by which information of local conditions (prey presence) can be passed on between individuals. This 'local enhancement' exchanges information of successful foraging spots. The form of these visual cues are largely made up of conspecific or other seabirds rafting on the water surface (Weimerskirch et al., 2010a), or associations with marine predators that are well documented in the scientific literature (Nevitt and RR, 1999; Sakamoto et al., 2009a; Silverman et al., 2004; Thiebot and Weimerskirch, 2012). These associations indicate that the visual senses are important to these animals in choosing foraging spots, as presence of these visual cues indicate a high likelihood of prey, and so potential energy gain. Similarly, use of visual guides to direct birds to nesting grounds has been suggested in previous studies, using coastlines as visible markers to follow (Pollonara et al., 2015; Yamamoto et al., 2008).

### 1.1.2 Social transfer and memory

Visual cues and local enhancement are restricted by the visual range of the searching individual. At greater distances, it is unlikely that visual cues are sufficient to guide seabirds to prey

patches, especially when flying over a potentially hazy environment which may be concealed by cloud cover. The relatively direct tracks recorded of seabirds travelling to foraging spots or homing (Pollonara et al., 2015; Weimerskirch, 2007) indicate a strong navigation system involved in directing travel headings. Seabirds and large marine predators can associate known areas with persistent prey presence (Davoren, 2013), and so an initial heading may be garnered from past trips. However, following this initial heading, birds must rely on some means to navigate towards likely foraging spots, particularly as they come into closer proximity to prey patches. Sharing information across conspecifics would optimise foraging trips through directing travel to known productive foraging spots. The "information center hypothesis" (ICH) theorises that such information is spread at the returning site of central place foragers, i.e. nest colonies. Such transfer of information passes on knowledge of locations of previous foraging spots, beyond visual ranges of the colonies. However, little evidence of ICH as a mechanism for information transfer at scales greater than those of visual cues exists (Davoren et al., 2003).

### 1.1.3 Avian geomagnetism senses

Birds are reported to sense the Earth's geomagnetic field through receptors in their eyes and use it to orient and navigate over long distances, particularly during migration (Hiscock et al., 2016; Wiltschko et al., 2011). While this research has focussed on small, primarily terrestrial passerines, some experiments on seabirds have explored the relative use of geomagnetic senses in navigation. Magnets attached to Scopoli's shearwaters (*Calonectris diomedea*) performing foraging trips showed no difference in navigation ability in comparison to control birds, suggesting the role of geomagnetism during such trips is reduced in comparison to other sensory input.



### 1.1.4 Avian olfactory senses

Homing pigeons (*Columba livia*) have gained reputations as skilled navigators, capable of returning to a home site regardless of their release point. Debate about the means by which pigeons direct their travel began a line of avian research surrounding the use of atmospheric odours. Nerve sectioning to induce anosmia in pigeons was one of the initial indications of the reliance of birds on olfaction to navigate, as anosmic birds' orientations were greatly distributed (Papi et al., 1972). The concept of an 'odour map' was conceived and developed as a way for birds to orient themselves based on odour characteristics of their environment (Bonadonna et al., 2003; Papi et al., 1972). Such discussion has focussed on seabirds, wide-ranging animals that primarily travel over a featureless landscape. Tube-nosed seabirds (of the order Procellariiformes) in particular have received attention due to their enhanced olfactory apparatus (Bang, 1971, 1960; Jacobs, 2012). The development of theories regarding use of olfaction in seabirds began to spread across the scientific community following studies involving Procellariiform seabirds displaying attraction to artificial oil slicks (Dell'Arciccia et al., 2014; Grubb, 1972; Nevitt, 2000; Nevitt and RR, 1999; Nevitt et al., 1995). These studies showed attraction of Procellariiformes to artificial concentrations of cod liver oil and/or dimethyl sulphide (DMS). DMS is a naturally occurring by-product of decomposition of dimethylsulphoniopropionate, produced when zooplankton graze on phytoplankton. DMS is therefore an indicator of zooplankton presence, ergo indicative of high productivity (Cantin et al., 1996; Dacey and Wakeham, 1986; Jean et al., 2009; Simó, 2001). Abilities of Procellariiformes to detect DMS has similarly been shown through experimental testing. Blue petrel chicks (*Halobaena caerulea*) displayed sensitivity to picomolar concentrations of DMS in controlled experiments (Bonadonna et al., 2006).

## 1.2 Studying seabirds through biologging

Studying behaviours of marine species has inherent difficulties in observing these species both above and, more importantly, below the water surface. The field of biologging, where tags recording data attached to animals enable collection of information on their movements in their natural habitats, provided an innovative solution to this challenge. This information can then be used to infer behaviour or explore the effects of external factors of study species. Since the inception of biologging, using capillary tubes and ink to measure maximum pressures experienced by seals during dives (Kooyman, 1965), development of smaller and more sophisticated tags has expanded the possibilities of biologging studies through recording of novel data types and the use of innovative analytical methods (Hooker et al., 2007; Kooyman, 2004). In biologging studies, ensuring tagged individuals do not experience any reduction of fitness or ability to perform typical behaviours is paramount. This is a key factor when conceiving a biologging-based study and has proved to be a considerable challenge in previous research (Bowlin et al., 2010; Gessaman and Nagy, 1988). As flight and flight efficiency is of utmost importance to seabirds, tag mass is a key factor in ensuring this lack of unintended impact during tag deployments. As a result, tagging of seabirds is often limited by the relative mass of tags to the tagged individual's body mass.

### 1.2.1 Foraging behaviour

Seabirds are a group for which the development of miniaturised biologging tags has provided solutions to investigate a wide array of research questions, in particular relating to foraging behaviour. Foremost in the research of seabird ecology is a need to understand where these wide-ranging animals travel. Tags recording Global Positioning System (GPS) locations have

found wide utility in seabird study. GPS data allow not only an understanding of the precise movements of animals, but also uncover movement patterns. The seemingly patchy and unpredictable nature of the ocean environment in which seabirds thrive has led researchers to examine how exactly these animals overcome the challenges they face when foraging in this disparate and ever-changing habitat. Theoretical systems by which animals can optimise their search behaviours have continued to grow over the years, stemming from the concept of optimal foraging (Stephens and Krebs, 1987), whereby animals should search for prey as long as it remains energetically conducive to do so. Understanding animal movements with a behavioural context allows testing of these theories over time. The methods by which seabirds orient themselves and maintain flight paths to foraging spots should change across scales in response to the heterogeneity of spatial prey distribution (Russell et al., 1992). Such adaptations to movement at this finer scale is termed area-restricted search (ARS) (Fauchald and Tveraa, 2003; Kareiva and Odell, 1987), where predators, when in areas of high prey density, increase turning rates in response to encounters with prey and reduce speeds to maximise durations within profitable areas. Conversely, when in low prey-dense regions, predators will travel quickly and with few heading changes to leave the regions as quickly as possible. ARS provides an optimal search strategy to maximise profit during a foraging trip. ARS behaviour is observable in GPS recordings through a technique known as first-passage time (Fauchald and Tveraa, 2003) and has been observed in a number of studies on seabirds (Bastos et al., 2020; Nevitt, 2000; Opper et al., 2018; Yoda et al., 2014).

### **1.2.2 Recording acceleration and depth**

In the study of marine predators, pressure sensors generate vertical profiles of dives, elucidating descent, ascent, and bottom phases, and indicating V- or U-shaped dive profiles. This practice

has been successfully used in the study of seabirds across a number of species. However, seabirds as a whole provide an intriguing variety of dive behaviours, including depths. Some birds, particularly those specialised in long distance, high efficiency flight, have adapted means to forage near the water surface. These animals exhibit near- or at-surface behaviours, thus minimising the pressures they experience. This can render pressure sensors less able to decipher foraging behaviour, as little to no strong pressure signals are recorded. The resolution of pressure sensors available on most biologging tags prevents isolation of these specific and slight changes in pressure. Similarly, isolating water level altitudes is unlikely to correctly identify foraging in these animals due to the common propensity of seabirds to rest on the water surface. Use of acceleration recordings from animal-borne tags has increased in the scientific literature, with fine-scale recordings of animal movements providing a means to accurately reconstruct intricate and short-lasting behaviours (Hooker et al., 2007; Sato et al., 2009; Soto et al., 2008; Zimmer et al., 2003). Biologging can therefore describe behaviours (including foraging) of seabirds, while also revealing movement patterns.

### **1.3 Seabirds as ocean observers**

Seabirds provide a platform through which researchers wishing to understand the health of the oceans can sample the large spatial scales seabirds live in and that humans rarely access (Piatt and Sydeman, 2007). They are also, for portions of the year, tied to a specific terrestrial area, such as during breeding and chick rearing, and so sampling the oceans using these animals is more viable than permanently marine species. To best add context to any ecological findings of seabirds, information about their foraging habits, prey species, and behaviours are required. This information allows policymakers to take in findings from ecological research on seabirds in the proper context, and so understand their findings better. Currently, research questions on

the topic of the oceanic environment are largely focussed on the topic of climate change and effects of those changes on organisms across all trophic levels. As such, there is a need to add contextual foraging behaviour to better understand these changes and their effects.

## 1.4 Study species and area

Streaked shearwaters, (*Calonectris leucomelas*), are pelagic seabirds with nesting grounds in temperate and sub-tropical regions of Asia, including Japan, South Korea, China, and Russia (Oka, 2004) and migrate to the seas off northern New Guinea, the Arafura Sea, and the South China Sea to overwinter (Yamamoto et al., 2010). They are mid-sized seabirds ( $\sim 500\text{g}$ ) that, during the breeding season, have been recorded performing dual foraging, switching between short and long foraging trips to provision chicks or themselves, respectively. Streaked shearwaters are burrowing birds, nesting under the ground. Research on Japanese streaked shearwaters has been extensive and covers breeding birds in a number of nest sites (Oka, 2004; Sakao et al., 2018; Shirai et al., 2012; Yamamoto et al., 2012; Yoda et al., 2014). In this study, the Funakoshi-Ohshima island ( $39^{\circ}24'N, 141^{\circ}59'E$ ) colony was selected. Birds from this site are in close proximity to an interesting oceanographic region with two major currents, the Oyashio and Kuroshio current, producing complex and productive conditions. The Kuroshio current, part of the North Pacific subtropical gyre, typically runs from west to east along the southern edge of Honshu, where it is known as the Kuroshio extension. The Kuroshio current is comprised of warm, low-nutrient surface water that makes up the western boundary of the North Pacific subtropical gyre. The Kuroshio current separates from the eastern coast of Japan, becoming the Kuroshio extension, entering the North Pacific Ocean. This eastward movement and removal of coastal constraints prompts the generation of eddies. The Kuroshio Extension region has a substantially higher sea level height anomaly than surrounding waters, indicating high eddy

variability (Qiu, 2001). This variability is added to by large changes over interannual-timescales that have been the focus of prior oceanographic research. The Oyashio is a subarctic current found along the eastern edge of Hokkaido. The Oyashio is a cold subarctic current with nutrient rich surface waters and is the western boundary of the North Pacific sub-Arctic gyre (Qiu, 2001; Sakurai, 2007). The boundary layer between the Oyashio and Kuroshio current, the Kuroshio-Oyashio transition region (KO), causes formations of warm-core rings in both the Oyashio and KO, consistently causing massive phytoplanktonic blooms during the spring (Isada et al., 2009). This region is an important summer feeding ground for migrant species from subtropical regions, including Japanese anchovy (*Engraulis japonicus*), Pacific saury (*Calolabiss saira*), and Japanese common squid (*Todarodes pacificus*), all previously reported in streaked shearwater diet composition (Matsumoto et al., 2012; Yamamoto et al., 2008). Significant changes in abundance and distribution of regularly present species has shown accordance with changes in physical oceanography (Sakurai, 2007), and so streaked shearwaters must use some method of prey detection to orient themselves and reliably find prey patches to survive across years with differing prey abundance.

## 1.5 Objectives of this study

Understanding how seabirds forage and find prey adds context to any findings of their foraging trends. It also provides a means to better predict effects of changes to the ocean environment on seabird populations. Fine-scale examination of foraging behaviour in conjunction with external environmental conditions is needed to provide evidence of the search behaviours of these animals. The aims of this thesis are therefore to find evidence of how streaked shearwaters find and feed on prey. To achieve this, foraging behaviour must be identified then examined with the context of environmental conditions, in this case wind. This can be achieved through the

use of animal-borne tag data. Acceleration recordings contain fine-scale movements, and so can identify foraging behaviour, however, require a detection method. This is undertaken in Chapter 2 using tags recording a combination of video and acceleration, and GPS and acceleration. To understand wind conditions at similar scales to those of shearwater foraging trips, fine-scale wind recordings are needed. Methods of wind estimation from seabird GPS tracks are examined in Chapter 3. The shearwaters' interactions with wind as they approach foraging spots are then explored in Chapter 4. Finally, Chapter 5 summarises and discusses the results of the previous chapters.

# Foraging Detection Method

## 2.1 Background

Identifying and understanding foraging behaviour in animals details how and where they find prey. This information can be used to highlight areas of ecological importance, thereby informing conservation efforts (Einoder, 2009; Thaxter et al., 2012), indicate foraging strategies and prey species (Matsumoto et al., 2012; Ropert-Coudert et al., 2006), and show the relationship animals have with their environments (McConnell et al., 1992; Weimerskirch et al., 2010b). Detecting such behaviour can be logistically difficult through direct observation, however, animal-borne biologging devices provide a means to record animal movements in their natural habitat (Hooker et al., 2007). Biologging tags recording a variety of datatypes such as pressure (depth), GPS, and acceleration, have been applied to a wide range of species. All these data require interpreting to identify the behaviours involved.

In seabird species, biologging data used to detect foraging have previously focussed on depth recordings deciphered from pressure sensor and acceleration data (Chimienti et al., 2017; Linnebjerg et al., 2013; Ronconi et al., 2010). Birds diving to suitable depths provide a record of dive behaviour by recording the pressures the animal experiences. This method becomes less suitable for shallow dives as diving to shallower depths means the animals experience reduced pressure differences in short periods that are less detectable by sensors (Cianchetti-Benedetti



et al., 2017). However, acceleration signals are high frequency records of motion and contain details of the tagged animal's behaviours. These signals can be used to decipher behaviours but require a detection method to translate acceleration signals into specific behaviours. Such techniques require some form of explicit validation. Previously, studies using acceleration alone to identify foraging have used automated methods (Berlincourt et al., 2015; Sakamoto et al., 2009a) or concurrently recorded data (depth) (Cianchetti-Benedetti et al., 2017) as an indication of foraging behaviour. Use of the methods employed by these studies can be limited in specific circumstances. Short and shallow dive behaviours reduce the effectiveness of automated methods and concurrent pressure sensor data. Automated clustering of acceleration signals requires distinction in frequencies of acceleration to separate behaviours, for example using different rates of flapping to distinguish flight and take-off. However, behaviours lasting short durations can be missed using this method as the small sample size of acceleration signals reduces the ability to accurately identify and categorise behaviour frequencies. Similarly, shallow dives can be missed by pressure sensors through a lack of resolution. Sur et al. (2017) combined acceleration, GPS, and external video recordings to classify behaviours from acceleration recordings. Video recordings are an ideal method to identify behaviours, however, have inherent drawbacks in their deployment. Firstly, recording video is energetically costly and so long recordings lasting one or more foraging trips would require battery capacity greater than those of tags currently in use. Secondly, the need for sufficient battery capacity would increase the mass of the deployed tags. Tagging animals can itself cause those animals to vary in their behaviours, thus no longer reflecting their typical ecology (Arlt et al., 2013; Igual et al., 2004; Ludynia et al., 2012; Phillips et al., 2003). Tags are advised to fall under the limit of 5% of the subject's body mass, however, this value is not based on empirical study (Phillips et al., 2003). The limit of tag-to-body mass was suggested to decrease to  $< 3\%$  of body mass (Phillips et al., 2003), though this value, and

the effects of the tag can vary considerably across species (Gillies et al., 2020).

Continual advances in technology reduce size and mass of tag components, allowing application of tags to lighter and smaller species, including seabirds, without significantly affecting their locomotive or foraging abilities. Developments in animal-borne video camera loggers produced tags capable of visually recording bird behaviours while concurrently recording three-dimensional acceleration. Thus, seabird activities can be directly observed alongside an acceleration record of body movements. This provides a means to generate and validate a behaviour detection method using video recordings.

Shearwaters are seabirds in the order Procellariiformes that are globally distributed, and exhibit a similarly wide range of foraging behaviours. Shearwater species are known to dive in order to forage, however, the characteristics of foraging dives varies considerably across the *Puffinus*, *Procellaria*, and *Calonectris* genera, with *Calonectris* species typically the shallowest divers (Burger, 2001). Prior studies examining shearwater foraging in detail have described surface foraging in Scopoli's shearwaters (Cianchetti-Benedetti et al., 2017), streaked shearwaters (Matsumoto et al., 2012), and short-tailed shearwaters (*Puffinus tenuirostris*) (Berlincourt et al., 2015). Streaked shearwaters perform exceptionally short and shallow dives. Thus far, information about the foraging habits of these animals has been collated using GPS (Yoda et al., 2014), and acceleration and depth data (Matsumoto et al., 2012). However, development of new smaller and lighter video tags can provide greater detail on a species for whom this method was previously impractical. This study examines video footage collected by animal-borne tags alongside concurrent high-resolution acceleration data to generate a detection method to identify foraging behaviour. This detection method is then applied to longer term acceleration and GPS data (without associated video footage) to evaluate foraging characteristics of these animals.

## 2.2 Materials and methods

### 2.2.1 Field experiments

Experiments were carried out on breeding streaked shearwaters (*Calonectris leucomelas*, mean body mass  $\pm$  standard deviation,  $560 \pm 52$  g,  $n = 25$ ) at Funakoshi-Ohshima Island, Japan, during the chick-rearing periods of August-September 2018 and August 2019. A total of 27 birds were captured by hand at their burrows and one tag was attached to each bird. Five birds were tagged with combined video and acceleration (DVL) tags (DVL400-3DGT, Little Leonardo, Tokyo, Japan) in 2018, attached to the chest feathers using waterproof tape (Tesa, Hamburg, Germany) and instant glue (Loctite, Düsseldorf, Germany). DVL tags were attached to the chest to better observe foraging behaviours and subsurface prey or predators during landings. These loggers were used to derive the behaviour detection algorithm. Twelve other individuals were tagged with GPS and acceleration (AxyTrek) tags (Axy-Trek Marine, Technosmart, Guidonia Montecelio, Italy) to the back feathers in 2018 and ten in 2019. AxyTrek tags recorded for considerably longer durations than the DVL tags, and so the developed behaviour detection algorithm was applied to the AxyTrek data and details of foraging behaviours were examined. Five DVL tags (1 male, 4 female) and 11 AxyTrek tags (7 male, 4 female) were successfully recovered in 2018. Nine AxyTrek tags (7 male, 2 female) were successfully recovered in 2019. Field experiments were conducted under permission from the Ministry of the Environment and the Agency for Cultural Affairs, government of Japan, and the the Animal Ethics Committee of Atmosphere and Ocean Research Institute of the University of Tokyo (permission number P18-6, P19-13).

DVL tags were set to record acceleration in three axes (longitudinal  $x$ , dorsoventral  $z$ , and lateral  $y$ , Fig. 2.1) at a sample rate of 20 Hz and recorded 2 hours of continuous video at 30

fps. Acceleration was recorded from the moment the tags were attached, while video recordings were programmed to begin at 12:00, 10:00, 12:00, 12:00, and 11:00 of the attachment day of the 5 DVL tags, respectively. AxyTrek tags were set to record acceleration in three axes at 25 Hz. Ten AxyTrek tags in 2019 and two in 2018 recorded a positional fix every 5 seconds, while the other 10 AxyTrek tags in 2018 recorded a fix every 30 seconds. AxyTrek and DVL tags weigh 20g and 25g in air, respectively,  $< 5\%$  of the bird's body mass.

### **2.2.2 Video analysis**

Behaviours performed by tagged birds, and their start/end times, were determined from viewing DVL video recordings. Flight (made up of flapping and gliding) and non-flight behaviours (diving or landing) were identified by submergence of the video camera. Two types of foraging behaviour were observed, surface seizing and foraging dives. Surface seizing was characterised by frequent take-offs and landings, during which the bird could occasionally be seen submerging its head. Take-offs during surface seizing were separated from take-offs preceding flight by whether the bird subsequently performed another landing or a glide (when no flapping was observed). Foraging dives were distinguishable during video recordings by clear descent and ascent phases. The video cameras were occasionally obscured, making behaviours unable to be deciphered and birds also occasionally pecked tags during flight. Data from these periods (ranging from 19 – 28%) were not included in further analysis. Videos were viewed using VLC (VideoLAN).

### **2.2.3 Behaviour acceleration characteristics**

The behaviour detection method was derived from acceleration signals of DVL tags. Through visual inspection of the DVL acceleration recordings, a step-by-step process was generated to identify flight, rest, take-off, surface seizing, and foraging dives. This detection method was

validated against the video footage.

Acceleration is comprised of static (associated to posture) and dynamic (primarily caused by propulsion from the animal) components. Static acceleration ( $x_S$ ,  $z_S$ , and  $y_S$ ) was estimated by passing the raw signal through a low-pass filter (order 100) at 1.5 Hz (Sato et al., 2008). Dynamic acceleration ( $x_D$ ,  $z_D$ , and  $y_D$ ) was calculated by subtracting static acceleration from the raw acceleration signals. Static and dynamic components were used to categorise behaviours.

### Identifying flight

Streaked shearwater flight is made up of flapping and glides. Flapping motion is recorded in the dynamic dorsoventral acceleration ( $z_D$ ), which contains the oscillating motion of wingstrokes. These oscillations are estimated by the differences in local maxima and minima of the  $z_D$  signal (Fig. 2.1). This motion produces larger displacements in  $z_D$  than glides, which should produce little dynamic movement. Differences between local maxima and minima of  $z_D$  show a strong bi-modal distribution, and the inter-peak trough of this distribution can then be used to isolate flapping behaviour (Fig. 2.1). The inter-peak trough of the differences in  $z_D$  maxima/minima would be the threshold to identify flaps. However, though the behaviour detection method was generated using DVL tag data, I intended to apply the method to AxyTrek data. As DVL- and AxyTrek-bearing individuals were either tagged using chest- or back-mountings, respectively, the recorded acceleration signals would differ in their characteristics. Therefore, the same threshold values would not be suitable across tags and so I generated threshold values for each individual tag by estimating periods of flight from their acceleration recordings to act as reference periods to generate the thresholds.

Flight can be estimated by using *a priori* knowledge of flapping frequencies. A spectrogram of dorsoventral acceleration was generated using a Fast Fourier Transform with a 4 second

window and 85% overlap. Streaked shearwaters typically flap at rates around 4 Hz during flight (Sato et al., 2009), so spectrograms should show higher energy densities around 4 Hz than for higher frequency flight. To estimate periods of time with relatively high energy densities at the frequencies expected during flight, the energy densities within two bands, the flapping flight band (3.5 to 5 Hz), and the take-off band (5+ Hz), were summed and their difference calculated. The flapping flight band frequency range should contain the 4 Hz flapping signals typically performed during flight, while the 5+ Hz take-off band should contain higher rate flapping. Differences in energy densities between the flapping flight and take-off bands were summed in one minute moving windows. Minutes with the greatest positive difference in energy densities (where the flapping flight band energy was greater than the take-off band energy) were selected as predicted flight minutes (PFMs). Selected minutes were required to be at least 5 minutes apart to avoid selecting PFMs from the same short period of flight, generating threshold values from a wider range, and so a better encapsulation, of acceleration signals during flight. Ten PFMs were selected for each DVL tag recording and 20 for each day of AxyTrek tag recordings. Analysis was performed using custom scripts in MATLAB (MATLAB, 2019).

For each tag, differences in  $z_D$  maxima/minima in all PFMs were calculated and the median of the inter-peak troughs was set as the threshold to identify flaps. These flaps are then grouped into flapping bouts with no gaps less than 0.5 seconds. These flapping bouts are then further grouped to contain all flapping behaviour with no more than 30 seconds between them. Figure 2.1 shows an example of the bi-modal distribution in displacements between flaps and glides, and the resulting selected flapping bout.

### Identifying take-off

During take-offs and dives/landings, birds undergo large rotations in the longitudinal axis as they align themselves upward to gain altitude or downward to reach the water surface, respectively. During flight, these rotations are likely smaller as the bird maintains a steady course. These rotations are recorded in pitch angles, which were calculated using the equation 2.1 derived from a method using acceleration to identify body angle in diving seals (Sato et al., 2003). Similar signals were observed in the roll axis data, however, the signal was much less defined in comparison to the pitch axis. To identify take-offs, transitions to periods of flapping are tested for presence of a large upward pitch change. Large pitch changes were estimated as  $1.5\times$  the median of maximum differences in local pitch maxima and minima during PFMs. The large pitch change threshold for DVL tags was taken as the median of all DVL large pitch change thresholds to account for the relatively short duration (2 hours per tag) of DVL acceleration data.

$$Pitch = \arcsin x_S \tag{2.1}$$

### Identifying foraging behaviours

To identify foraging behaviours, large pitch changes were also used. Large pitch changes within 23.3 seconds (the mean foraging bout duration recorded on video) were grouped. Each of these large pitch change groups were then checked for foraging dives or surface seizing. Foraging dives required a pitch angle under the median of minimum PFM pitch angles  $-30$  degrees (representing the downward orientation), followed by a pitch angle exceeding the median of mean PFM pitches  $+2$  times the median PFM pitch variance (representing a return to the surface) within 10 seconds. Surface seizing required 3+ large pitch changes to occur within 2 seconds of one another. All

remaining periods were classed as unknown. When applying the detection algorithm to AxyTrek data, upward pitch changes originating above the median of minimum PFM pitch values were removed.

### Identifying rest

As no rest behaviour was observed during the video recordings, it was estimated from overall dynamic body acceleration (ODBA), the sum of the absolute dynamic acceleration in each axis. ODBA is commonly used as a representation of relative movement (Gleiss et al., 2010; Wilson et al., 2006). A 10 second moving average of ODBA ( $ODmn$ ) was calculated, and from visual inspection of a timeseries of  $ODmn$  and travel speeds of AxyTrek data  $0.2g$  ( $g = 9.8ms^{-2}$ ) was identified to be a suitable threshold under which rest behaviour was assigned.

### Validation of accelerometry behaviour detection with video recordings

The detection method was performed on each DVL tags' acceleration data. The detected behaviours were then validated by comparison to the behaviours observed on the concurrent video recordings. Validation rates (true and false positive rates) were calculated for each tag. A behaviour ethogram from video recordings sampled at the same rate as the acceleration data (behaviours assigned every 0.05 seconds) was generated. True and false positive rates (TPR and FPR, respectively) were calculated using Eq 2.2.

$$\begin{aligned} TPR &= \frac{PF_c}{V_F} \\ FPR &= \frac{PF_i}{V_O} \end{aligned} \tag{2.2}$$

where  $PF_c$  is the total duration of the correctly identified behaviour,  $PF_i$  is the total duration of the incorrectly labelled behaviour,  $V_F$  is the total duration of the video-recorded behaviour, and  $V_O$  is the total duration of other video recorded behaviours.



### 2.2.4 Application of behaviour detection algorithm to long duration acceleration

The behaviour detection method was applied to the long-term AxyTrek tag datasets, identifying flight, rest, take-off, surface seizing, and foraging dives. Behaviours were also grouped into three functional categories: resting, transit (flight and take-offs), and foraging (surface seizing and foraging dives). Analysis was performed on individual days of data for computing ease. Data collected while the birds were within 1.5 km from the nest colony were removed. Surface seizing or foraging dives were assigned to each GPS fix within 30 seconds of the behaviour. Speeds were calculated from Euclidean distances between GPS fixes. Due to small inaccuracies in GPS locations that caused incorrectly large displacements during rest, speeds were calculated between fixes using a 5-fix moving window. GPS fixes showing unrealistic speeds ( $>80$  kph) were removed. Trip durations were recorded from visual observation of the data, and foraging trips were assigned as long ( $> 2$  days) or short ( $\leq 2$  days), as per techniques in (Matsumoto et al., 2012). GPS fixes assigned with foraging behaviours with speeds greater than 15 kph (Shiomi et al., 2012) were reclassified as flight. Flight and unknown behaviours lasting less than 5 seconds were removed. Utilisation distributions of foraging behaviours and male/female foraging spots were generated for each year from grouped data of all individuals, ad hoc smoothing parameter, and  $1000 \times 1000$  grid (approximately  $400 \times 500$  m grid cells) with the kernelUD function (R package, *adehabitatHR*). Linear mixed effects models were used to test for differences in distance travelled or time spent foraging across sexes and if total daily durations of behaviour categories (foraging, transit, or rest) differed between long ( $> 2$  days) or short ( $\leq 2$  days) foraging trips. Individual and trip number were included as random effects. GPS data was analysed using the R statistical language (R Core Team, 2017).

## 2.3 Results

### 2.3.1 Video-recorded behaviours and presence of other predators

During video recordings, birds flew for 75.6 minutes on average ( $\pm 36$  standard deviation), spent 1.1 minutes taking off ( $\pm 0.9$ ), surface seized for 10 minutes ( $\pm 7$ ), performed foraging dives for 0.4 minutes ( $\pm 0.7$ ) out of the total 2 hour video durations. Video recordings contained two types of foraging behaviour: surface seizing, and foraging dives. Surface seizing consisted of landings and take-offs occurring in quick succession (Fig. 2.2). During foraging dives the water surface was visible on the video footage as the birds ascended, indicating the birds fully submerging (Fig. 2.3). Recordings of foraging behaviours in conspecifics showed that during surface seizing the shearwaters would submerge their heads under the water surface, as visible both from the tagged animal and in a recorded conspecific (Fig. 2.2). DVL-tagged individuals all performed surface seizing (mean landing duration  $\pm$  standard deviation  $1.5 \pm 1.4$ s, mean take-off duration  $0.6 \pm 1.6$ s, mean total duration including inter-landing take-offs  $23.1 \pm 40.4$ s). Foraging dives following a plunge from the air and after an initial landing were both recorded. Four DVL-tagged individuals performed foraging dives (mean dive duration  $3.2 \pm 1.2$ s). Pre-flight take-offs were considerably longer than those of surface seizing, lasting  $3.0 \pm 1.3$ s mean duration. During the recordings, four prey captures, both by the tagged individual and others, were observed (two examples in Fig. 2.4). The videos also showed large groups of conspecifics sitting on the water surface, and other marine predators, including common dolphinfish (*Coryphaena hippurus*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*).

### 2.3.2 Behaviour detection validation

Flight was correctly classified for 84 to 97% of tag durations (mean 90%) with no false positives, while surface seizing was correctly identified between 52 to 99% of observed surface seizing across all tags, with a mean of 79% (Table 2.1). False positive detections of surface seizing ranged from 1 to 7%. Most false positive detections of surface seizing events occurred from the detection method grouping surface seizing events separated by short flights. Foraging dives were correctly identified from 47 to 98% of observed foraging dive durations, and incorrectly detected for < 1% of video-recorded foraging dives across all tags. False positive foraging dive detections were caused by misclassifying surface seizing behaviour. Four surface seizing events were incorrectly classified as foraging dives. Video-recorded foraging behaviour was observed during all detected foraging bouts. The detection method was designed to minimise false positives (type 1 error) to ensure foraging detections were most likely to accurately detect foraging though this did reduce the true positive detection rates. No rest behaviour was observed during DVL recordings, and so neither were any take-offs from rest.

### 2.3.3 Foraging trips from long duration tags

Forty foraging trips were made over 99 total days of recording, lasting from 1 to 8 days (example track in Fig. 2.5). Individuals and their foraging trip durations are listed in full in Tables 2.2 and 2.3. Single day trips were the most common and were recorded in all but one individual. Shearwaters performed an average 39 foraging dives per day lasting a total of 72 seconds and 53 dives lasting 102 total seconds in 2018 and 2019, respectively. Surface seizing events occurred 15 and 18 times per day lasting 481 and 448 seconds in total during 2018 and 2019, respectively. Daily activity budgets of foraging trips (Fig. 2.6) showed that birds spent most their time in

transit (median 56% on long trips, 50% on short trips), followed by resting (37% on long trips, 45% on short trips). Foraging took up 0.6 and 0.8% of long and short trips, respectively. Over 90% of foraging detections occurred at speeds (calculated via a 5-minute moving window) less than 15kph.

On average, males travelled a greater maximum distance from the nest colony (466 km $\pm$ 85, mean  $\pm$  sd,  $n = 7$  in 2018, 321 km $\pm$ 160,  $n = 7$  in 2019) than females (385 km $\pm$ 150,  $n = 4$  in 2018, 163 km $\pm$ 75,  $n = 2$ ) though the trip reaching the furthest distance from the nest colony (610 km) was performed by a female. Distributions of foraging behaviours differed little (Fig. 2.7), with overlaps between utilisation distributions of foraging dives and surface seizures. In 2018, the proportion of foraging dive utilisation distributions within surface seizing distributions were 97, 83, 59, and 56% at 95, 75, 50, and 25% contours, respectively. In 2019, 70, 57, 42, and 36% of foraging dive utilisation distributions overlapped with those of surface seizing at 95, 75, 50, and 25% contours, respectively. Males showed similar foraging distributions in 2018 and 2019 (Fig. 2.8), while females foraged much more expansively in 2018 than 2019. Distance travelled from the nest colony did not differ between sexes ( $p > 0.05$ ) while males and females did not differ significantly in daily durations of surface seizing or foraging dives ( $p > 0.05$ , Fig. 2.9). Daily durations of either surface seizing or foraging dives did not differ significantly between short or long foraging trips ( $p > 0.05$ ). Percentage of foraging trips spent foraging did not differ significantly ( $p > 0.05$ ), however, birds flew more and rested less during long trip days ( $p < 0.05$ ). During long trips, foraging occurred most during the afternoon while flight occurred most during the early morning, showing an inverse relationship with rest (Fig. 2.10), while in short trips shearwaters flew and foraged in the early morning, also foraging throughout the afternoon, then rested in the evenings.

Behaviours that occurred most during the 5 minutes before dives were transit (66%), followed

by unknown (16%), rest (14%), and surface seizing (5%), and prior to surface seizing, transit occurred most (56%), followed by rest (27%), and unknown (10%). Seven percent of surface seizing events occurred following surface seizing separated by short changes in behaviour (short flights/rests between surface seizing events). The most detected behaviour in the 5 minutes following dives and surface seizing was also transit (51 and 68%, respectively). Surface seizing was the next most common behaviour after foraging dives (22%), followed by unknown (21%) and rest (7%). Unknown (9%) and rest (8%) were the next most common behaviours following surface seizing. The remaining 15% of surface seizing events were also followed by more surface seizing separated by short flights/rests.

## 2.4 Discussion

In this study, two types of foraging behaviour were found from streaked shearwaters recorded on video to validate the detection method developed and generate a detection method to estimate these behaviours from acceleration signals. Video recordings directly observing both styles of foraging are presented. Foraging behaviour of shallow-diving seabirds can be underrepresented in the scientific literature due to complexity in deriving those behaviours from on-board tag data. I provide a framework to estimate shallow-dive foraging behaviour which helps address this imbalance, and demonstrate the use of the detection method to gather information on the foraging habits of streaked shearwaters nesting in northeastern Japan.

### 2.4.1 Shallow foraging behaviours

This study is the first to the author's knowledge to describe foraging behaviours of streaked shearwaters in fine detail through video recordings. In this study, two distinct types of foraging were observed, surface seizing where birds do not fully submerge themselves under the water

surface, and foraging dives, where birds dive into the water from either air or from the surface. The two types of foraging behaviour identified may be deployed in different scenarios or for the capture of different prey. Drone footage recorded near the nest colony showed shearwaters surface seizing, landing repeatedly in the same fashion as the tag video recordings. During the footage, large fish, believed to be chub mackerel (*Scomber japonicus*) or blue mackerel (*Scomber australasicus*) can also be observed under the water, with birds appearing to fly between landings to maintain proximity with their prey. Surface seizing may therefore allow shearwaters to prey on near-surface moving schools of prey that are clearly visible from above the water surface.

Foraging dives usually occurred between or following surface seizing behaviours. The foraging dives were concentrated around periods when large marine predators were visible. The shearwaters may have used the visual cue of another predator to intensify foraging effort. Foraging dives may be used to forage on fish that are further from the water surface. Four successful prey captures which came as a result of rapid dives were recorded on video. Following prey capture, the birds ingested the fish when in flight. The short contact between the birds and the water surface when capturing prey indicates that the prey were very close to the water surface when captured.

Diving Procellariiformes can employ underwater flapping to propel themselves during dives. Indeed, this behaviour has been used in dive identification in the past (Berlincourt et al., 2015). This propulsion allows the birds to reach or maintain sufficient depths to forage. The acceleration signals of foraging dives in this study show no clear evidence of continual subsurface flapping, only initial flapping motion as the birds enter the water (Fig. 2.3). The short durations of foraging dives also suggest limited propulsion to reach or maintain greater depths. As dives were observed originating from both plunges from the air and diving after landing on the water surface, the birds are likely diving to very shallow depths. This is consistent with prior

literature showing shearwaters of the *Calonectris* genus diving to significantly shallower depths than *Puffinus* shearwater species (Burger, 2001). Reduced ability to reach greater depths limits prey availability as capture requires prey species to be found in the upper levels of the water column.

### **2.4.2 Marine predator association**

During video recordings, large marine predators can be seen both over (porpoising dolphins) and under the water surface. During these periods, the tagged individuals increased their foraging intensity, increasing the number of surface seizing and foraging dives, as well as foraging dive duration. Associations between seabirds and marine predators have been previously reported (Nevitt and RR, 1999; Sakamoto et al., 2009b; Silverman et al., 2004; Thiebot and Weimerskirch, 2012) and are due, in part, to the effect of marine predators on the accessibility of prey. Marine predators feeding from underneath force fish to the surface. This grants seabirds greater access to prey that, particularly for shallow-diving species, they may be less capable of reaching without the upward forcing of prey by marine predators. Foraging marine predators and/or conspecifics also act as visual cues for the presence of prey (Nevitt, 2008; Weimerskirch et al., 2010a). During video recordings, conspecifics and marine predators were visible from the air, resting and/or foraging. These visual cues can direct the shearwaters to intensify foraging effort in that area.

### **2.4.3 Acceleration behaviour detection**

Detection of shallow-dive foraging behaviour has proven difficult in the past as pressure sensors do not have the resolution required to detect the small signal changes produced during short dives or landings (Cianchetti-Benedetti et al., 2017). In this study, I used acceleration data with

a high resolution to estimate behaviours based on acceleration signals resulting from the tagged individuals' movements. The use of tags that record both video and acceleration allowed for validation of detected behaviours through recorded behavioural footage. This direct observation of seabirds' behaviours during acceleration recordings is rare in the scientific literature and only achievable due to advances in miniaturised video data loggers. The validations show that the behaviour detection method developed was capable of categorising flight (90% TPR, 0% FPR), surface seizing (79% TPR, 5% FPR), and foraging dives (66% TPR, < 1% FPR) in streaked shearwaters. Foraging behaviours detected in AxyTrek data were largely (> 90%) under speed thresholds for foraging in streaked shearwaters (Shiomi et al., 2012). Developing a successful behavioural detection method is important for future ecological studies regarding this or similar species. Accurately quantifying foraging behaviour is necessary to not misrepresent findings of ecological studies, and the potential to underestimate foraging behaviour in shallow-diving birds is greater when using methods previously developed for deeper diving birds. This study's detection method provides an alternate that should reduce this risk of underestimation.

#### **2.4.4 Detection method characteristics**

The low false positive rates of the detection method reflect the reliability of detected foraging behaviours. Reducing type 1 error (false positives) was a primary focus, and therefore the detection method was strict enough to ensure a high likelihood of correctly identified foraging. The results suggest the detection method indicates foraging behaviour with few false positive detections, and the results from analysing AxyTrek data should suitably reflect the shearwaters' foraging spots. Although foraging may have been underestimated, it is unlikely, given the relatively high true positive rates of this study, that inclusion of all foraging behaviours would significantly change the activity budget values. The method provides understanding of how and



where these birds are focussing their foraging efforts.

True positive rates of both surface seizing and foraging dives varied considerably across the DVL tags. The variability in true positive rates of surface seize detection was caused by presence of foraging dives in the midst of surface seizing bouts. The detection method initially identified the foraging dives first. The surface seizing behaviours that remained were therefore cut into shorter periods. Detection of surface seizing bouts required presence of 3+ large pitch changes within 2 seconds, so shorter surface seizing bouts were more likely to be misclassified. Similarly, large variability in foraging dive detection rates were due to the low total number of observed foraging dives (min 0, max 11) which caused relative true positive rates to fluctuate greatly. Despite these fluctuations, visual inspection of the acceleration signals of AxyTrek foraging detections, as well as the speeds the birds were travelling at when foraging was indicated, suggested the detection method performed well when applied over longer recording durations.

Behaviour estimation using acceleration data is relatively common in biologging studies. Accelerometers are becoming more ubiquitous across tags through miniaturisation and increased efficiency of battery capacity and writing to memory. Similarly, automated methods to analyse these data have become common in the scientific literature (Bom et al., 2014; Patterson et al., 2019; Sakamoto et al., 2009a). Use of these unsupervised methods allows acceleration data to be easily analysed without time-consuming examination of the data by hand. However, these methods require clear distinction in acceleration signals between behaviours. Application of k-means clustering as per (Sakamoto et al., 2009a) to the DVL dataset was unsuccessful due to the extremely short duration of foraging behaviours and relative similarity in their signals to those of flight. A previous study (Cianchetti-Benedetti et al., 2017) reported issues identifying foraging in shallow-diving Scopoli's shearwaters due to pressure sensors being unable to accurately detect dives lasting <2 seconds, but were successful in their detection by using acceleration data. The

method they report was also unsuccessful in detecting streaked shearwater foraging, due to the thresholds not being applicable to the data. The method identifies dives using a threshold of -1 g in the longitudinal acceleration. The recordings rarely passed this threshold, with most surface seizing behaviour being missed, and so a custom detection method was generated.

It is worth noting that the sample size in this study was low, and also particularly skewed in sex, with considerably fewer females tagged than males, particularly in 2019. As such, the ecological findings of this study may be limited due to their low sample size. Additional data to complement that collected for this study would allow for a deeper investigation into the foraging ecology of these animals.

### **2.4.5 Foraging trip characteristics**

The disparity in trip durations across 2018 and 2019 is clearly reflected in the foraging spot concentrations (Figures 2.7 and 2.8), and may be due to the tagging experiments in 2019 occurring earlier in the breeding season than 2018. Streaked shearwaters, like many pelagic seabirds, perform a dual foraging strategy, using short foraging trips to provision the chick, and longer trips to self-provision (Chaurand and Weimerskirch, 1994; DeBose and Nevitt, 2003; Ochi et al., 2016; Weimerskirch and Cherel, 1998). As chicks grow through the breeding season, parents are able to perform longer foraging trips, with chicks able to withstand longer periods between feedings. This is reflected in the greater distribution of foraging behaviour further from the nest colony in 2018 and the use of near-colony foraging grounds in 2019.

The activity time budget generated by the behaviour prediction assigns a small proportion of time to foraging, with most time during foraging trips devoted to flight or rest. The results show agreement of the proportion of daily rest behaviour in agreement with those of shearwaters from the same nest site in 2010 (Yoda et al., 2014). During longer trips, birds flew more

and rested less, however, there was no change in proportion of daily foraging. This is also consistent with the overlaps between both surface seizing and foraging dives in their spatial distributions. Shearwaters foraging in the same region as those of this study showed a change in diet composition in response to length of foraging trip (Matsumoto et al., 2012). No significant change in daily durations of surface seizing or foraging dives between short and long trips suggests shearwaters use both behaviours to forage for a variety of prey species. The few prey captures recorded by camera footage prevent much insight to be made into the depths at which shearwaters captured prey, however, from visual inspection of video recordings, depths did not seem to exceed three to four meters, differing little if dives originated from the water surface or air.

Prey captures occurred close to the water surface which may relate to the prey individual being at a shallow enough depth to ease capture, suggesting shearwaters would preferentially predate species in closer proximity to the water surface. However, given the shallow nature of the shearwaters' diving, it is likely that external factors such as marine predators causing upward forcing of prey species or physical changes to sea surface heights (Yoda et al., 2014) are the determining factors in predation.

Both foraging behaviours were followed and preceded most by flight in the surrounding 5 minutes. This reflects travel to or from the foraging area, or the birds' continued search while foraging. However, rest was the second most common behaviour prior to foraging. This suggests the shearwaters performed 'sit-and-wait' foraging, where birds sit on the water surface waiting for prey to become available for capture (Miramontes et al., 2012; Weimerskirch et al., 2007; Wilson et al., 1995).

In all shearwaters, some foraging occurred around 04:00 close to the nest site (< 10 km from the colony, small peaks visible in Fig. 2.10). Foraging at this location was typically made up

of surface foraging with few dives occurring. This time and location aligns with the presence of set nets and Pacific saury fishing vessels. These vessels are equipped with lighting rigs that are visible from the nest colony and would provide a stable foraging ground for streaked shearwaters. Surface seizing near fishing vessels, where the birds capture remnants of vessel catches, can be seen in their high spatial concentration near the nest colony in both years (Fig. 2.7).

Through calculation of foraging behaviours by acceleration, greater detail of foraging characteristics can be unveiled, especially in conjunction with other forms of research on shearwater foraging. For example, Shirai et al. (2012) estimated that mean streaked shearwater metabolic rate during foraging trips amounted to  $759.2 \pm 362.8$  kJ per day (recorded from 3 individuals on Awa Island, Japan). Estimating the number of prey required to be captured to fulfil this energetic requirement however, is difficult as shearwaters forage on multiple species of which energy densities vary considerably (Yamamoto et al., 2011). However, Japanese anchovy that take up 50% of streaked shearwater stomach contents following foraging trips (Matsumoto et al., 2012) have an energy density of  $7 \text{ kJ g}^{-1}$  (Ochi et al., 2016). Therefore, a rough estimate of how many fish a shearwater would need to capture to supply this energy is 57-160 anchovies per day. Given the short proportion of daily foraging activity ( $< 1\%$  of foraging trip durations) and that only 4 fish were captured during 10 hours of DVL video recording, it is unlikely that these numbers are realistic. Additionally, streaked shearwaters are also known to forage Pacific saury, which are more than doubly energy dense than Japanese anchovy ( $14.6 \text{ kJ g}^{-1}$ ), and so their varied diet likely reduces this number. However, the estimation could be more detailed using analysis of acceleration records to estimate pursuit diving events and estimated shearwater mass during before and after flights using methods described in Sato et al. (2008).

### 2.4.6 Effects of tag mass

Biologging studies can suffer from unintended effects of tag attachments altering behaviour of individuals (Gómez et al., 2013; Igual et al., 2004; Ludynia et al., 2012; Phillips et al., 2003). Impacts of tags vary both across taxa and individuals (Gillies et al., 2020). The effect of tags increase with mass and at 5% can have significant effects on lengths of foraging trips, though not the proportion of time spent foraging or resting (Gillies et al., 2020). This study may therefore be subject to differences in foraging trip characteristics, however, the foraging behaviours I report are likely to reflect those performed by unencumbered individuals.

### 2.4.7 Future steps

The detection method generated in this study would benefit from a greater pool of video recordings. The relatively short duration of the video tags reduced the number of observable behaviours, with little rest behaviour detected throughout their deployment. This study therefore makes the assumption that rest behaviour would likely be observable through reduced acceleration magnitudes. A larger dataset of video and acceleration recordings would increase the accuracy and reliability of the derived detection method. Similarly, the small sample size, both in number of individuals and duration, of longer term acceleration and GPS data obtained during this study curtails findings on trends in male/female foraging and use of foraging behaviours. However, it does provide viable paths for future studies looking specifically at foraging or search behaviour. At present, the foraging detection method does not allow for precise quantification of foraging events and should be an additional aim for future study to add greater detail to streaked shearwater foraging.

This study was carried out during the breeding season to optimise tag retrieval. The findings

I make on the foraging characteristics and distributions of these animals are therefore limited to the breeding seasons only. Development of miniature satellite-relaying loggers for seabirds would allow in-depth research into foraging behaviour during non-breeding seasons and testing of changes to foraging strategy when the birds are not limited by proximity to a nest colony, and are only self-provisioning.

With increasing tag capabilities and memory and battery capacities, combining fine-scale behaviour classifications with alternate analysis methods could provide novel insights into the foraging and energetic ecology of seabirds. Custom video and GPS tags (Korpela et al., 2020) attached to streaked shearwaters, where video recordings were turned on when on-board processing estimated area-restricted search behaviour occurred, focussed the video recordings to periods related to foraging. Developing the method presented in this paper could allow a similar application of on-board processing of acceleration data to record foraging behaviour, increasing the sample size of recorded foraging behaviours in streaked shearwaters and other shallow-diving seabirds.

Table 2.1: True positive and false positive rates of behaviour estimation of video-acceleration tags

Tag	Flight		Surface seizing		Foraging dive	
	TPR (%)	FPR (%)	TPR (%)	FPR (%)	TPR (%)	FPR (%)
<b>17008</b>	91	0	80	6	61	< 1
<b>18012</b>	85	0	52	6	47	< 1
<b>18014</b>	84	0	68	7	98	< 1
<b>18017</b>	93	0	95	6	57	< 1
<b>18018</b>	97	0	99	1	NA	NA
<b>Mean</b>	90	0	79	5	66	< 1

Validation rates (true positive rate, TPR; false positive rate FPR) of estimated behaviours across all video and acceleration tags.

Table 2.2: Tag deployment and foraging trip durations

Tag	Deployment duration (days)	Trip duration (days)						
2017-9-S1	5	1	4					
1-S2	11	2	4	1	4			
3-S2	12	3	1	4	1	1	1	1
4-S1	10	3	1	6				
5-S1	9	8	1					
6-S1	9	4	5					
7-S1	11	2	5	1	1	2		
8-S1	10	3	1	5	1			
9-S1	9	2	1	4	2			
10-S1	6	1	4	1				
11-S1	6	1	3	1	1			

Total duration of tag deployments from the start of the first foraging trip to the end of the last recorded in 2018. Individual foraging trip durations in days are listed.



Table 2.3: Tag deployment and foraging trip durations

Tag	Deployment duration (days)	Trip duration (days)						
1-S1	4	1	1	1	1+			
2-S1	4	1	3					
2018-01-S1	5	1	1	1	1	1+		
2018-03-S1	5	1	4					
2018-04-S1	5	1	2	1	NA			
2018-05-S1	5	1	4					
3-S1	5	1	1	1	1	1+		
4-S1	4	1	1	1	2			
5-S1	5	1	1	3				

Total duration of tag deployments from the start of the first foraging trip to the end of the last recorded in 2019. Individual foraging trip durations in days are listed. Foraging trips that stopped recording prior to the bird returning to the nest site by the end of the day are labelled with a "+" to indicate that the bird likely remained at sea for at least another day. Tag 2018-04-S1 ended recording in the morning of the fifth day, and so the foraging trip duration is labelled NA.

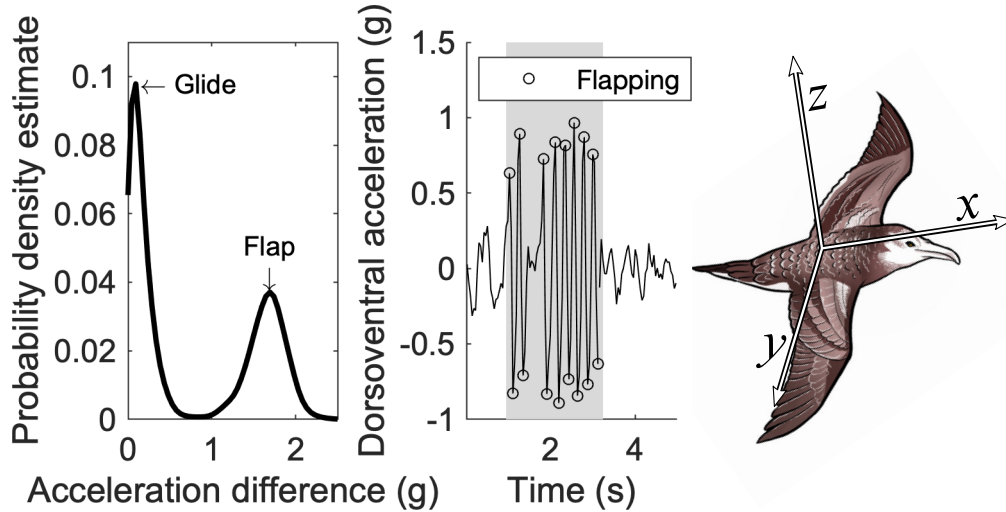


Figure 2.1: **Flapping detection.** An example of the flapping detection method for one AxyTrek tagged individual. The example bird (right) has three arrows showing the acceleration signals recorded and their orientation.  $x$  represents the longitudinal axis,  $z$  the dorsoventral, and  $y$  the lateral. The probability density estimate calculated by a kernel smoothing function of the difference in dynamic dorsoventral acceleration during estimated flight periods (left) showing flapping (smaller peak) and gliding (larger peak). Removing peaks and troughs with a difference less than the inter-peak trough isolates flapping behaviour (middle). Selected peaks and troughs (circled) separated by a duration of less than 0.5 seconds are grouped into flapping bouts (grey region).

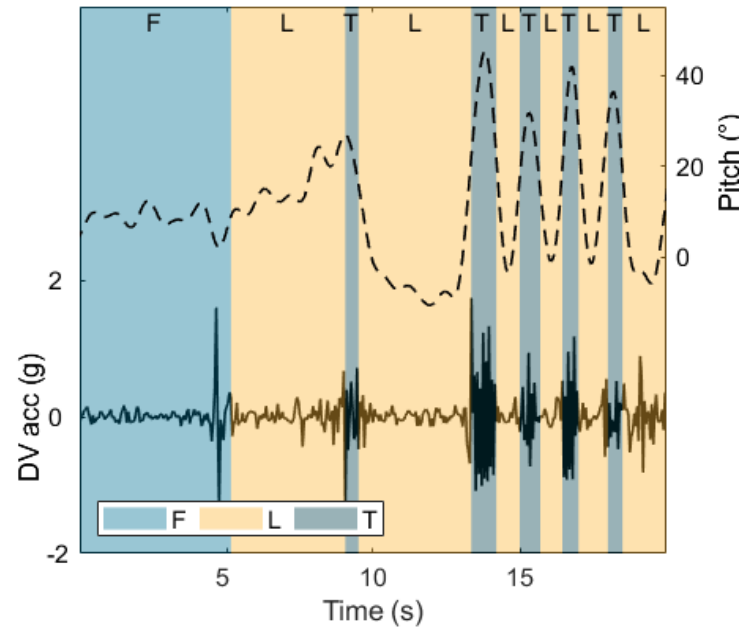


Figure 2.2: **Surface seizing example.** Dynamic dorsoventral acceleration (DV acc; solid line) and pitch (dashed line) during a transition from flight to surface seizing event, as recorded by video (top). The background is colour-coded depending on behaviour, flight (F), landing (L), and take-off (T), and each behaviour is labelled above. This foraging consisted of a series of short landings during which the tag was submerged separated by even shorter take-offs. The video-recordings captured some non-tagged birds performing foraging behaviours (bottom). In this example, a non-tagged conspecific clearly has its head submerged while sat on the water surface.

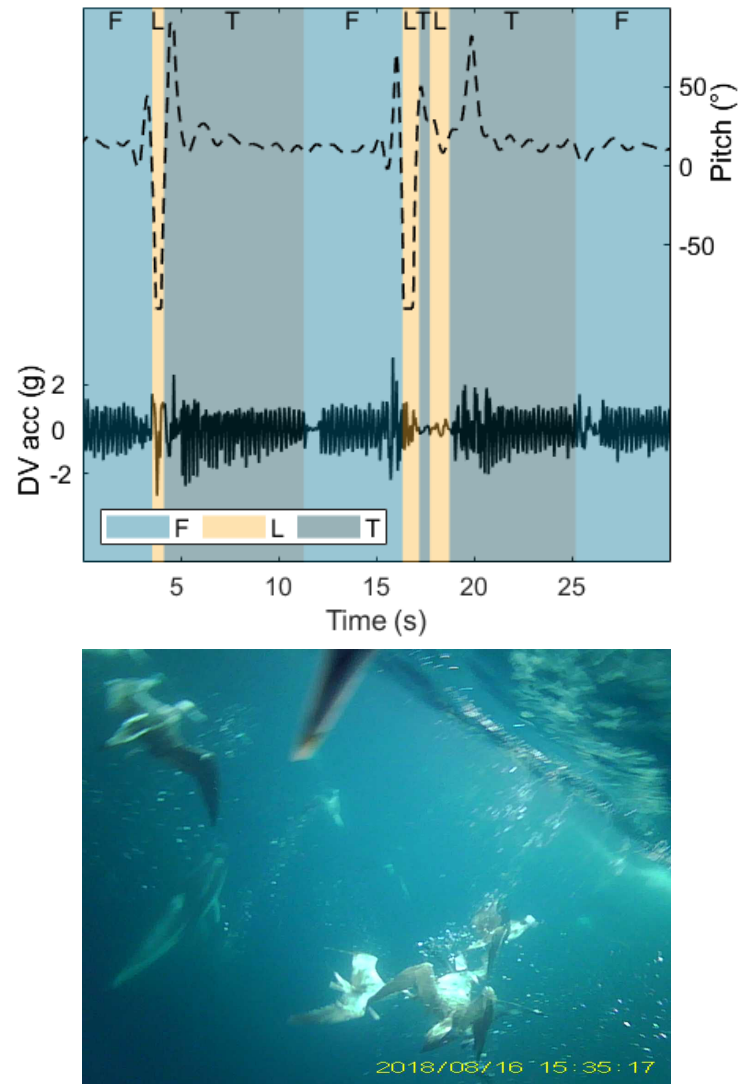


Figure 2.3: **Foraging dive example.** The dynamic dorsoventral acceleration (DV acc; solid line) and pitch (dashed line) during two foraging dives between periods of flight (top). The colour of the background refers to the behaviour observed, flight (F), landing (L), and take-off (T), and each behaviour is labelled above. During these landings, the water surface can be observed from underneath during the video recording, suggesting full submersion of the bird. Birds are assumed to be searching for or pursuing prey during these submersions. Below is a screenshot from a video-recording showing another shearwater completely submerged during a foraging dive.



Figure 2.4: **Screenshots of prey captures.** A number of prey captures were observed in the DVL recordings. These examples show an unknown species capture by a conspecific which is then competed for by other shearwaters following take-off (left), and a Pacific saury caught by the tagged individual during a surface seizing event (right). This footage suggests that shearwaters capture prey then feed whilst in flight.

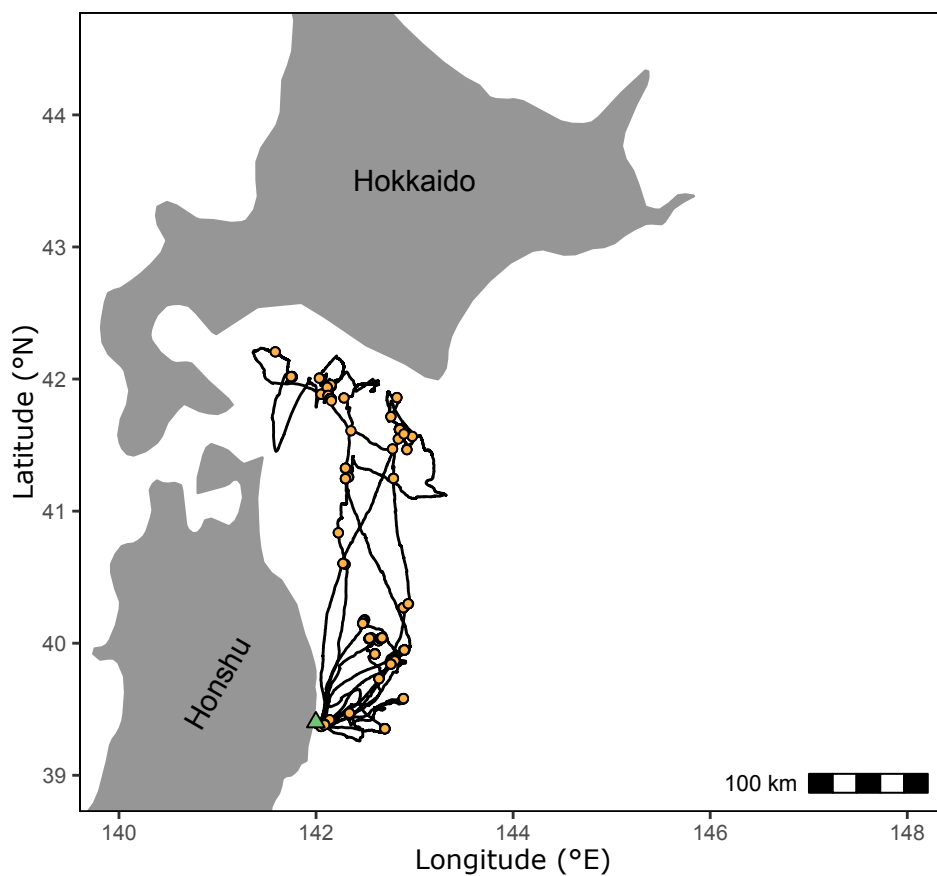


Figure 2.5: **Example track and foraging locations of single individual.** GPS track and foraging points (orange dots) of a single bird tracked over 12 days, 7 foraging trips. The nesting site is indicated by a green triangle.

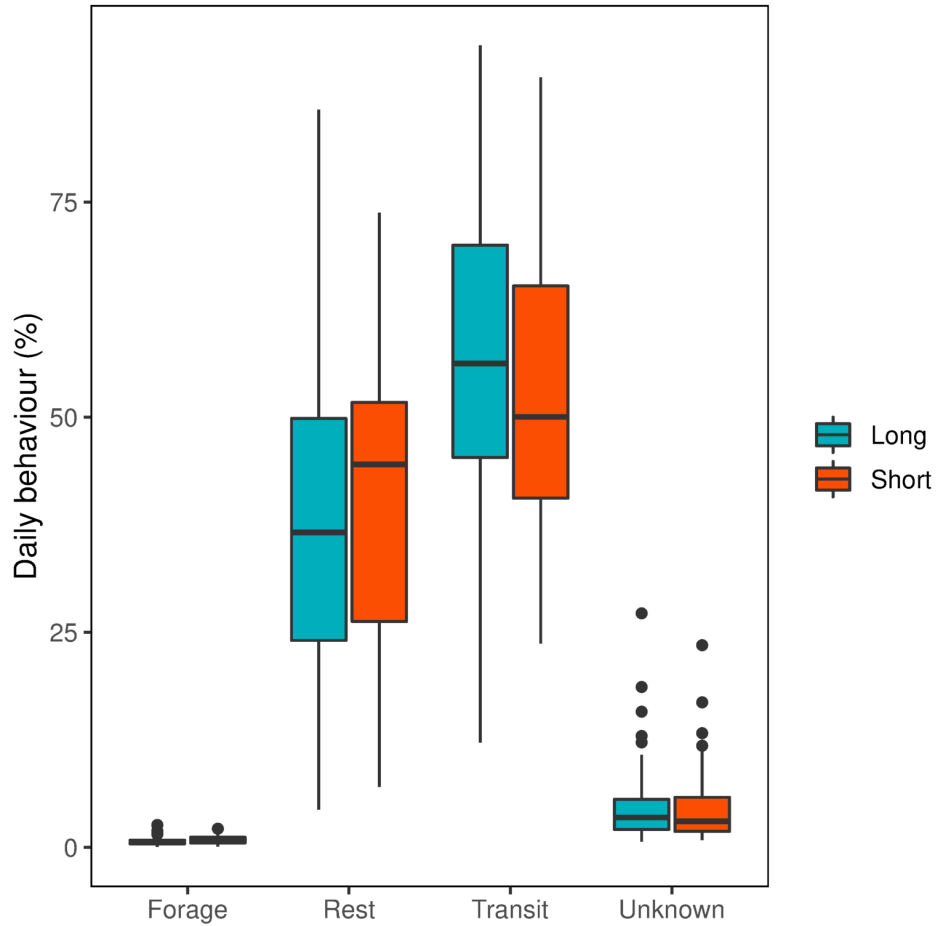


Figure 2.6: **Daily proportions of behaviours detected by foraging algorithm.**

Proportions of 24-hour period the foraging algorithm assigned to each behaviour classification: forage, rest, transit, and unknown. Behaviour proportions are split into long (2+ days) and short (<2 days) trips. Data are presented as the median with the surrounding box edges being the 25th and 75th percentiles and the whiskers  $1.5 \times$  the interquartile range.

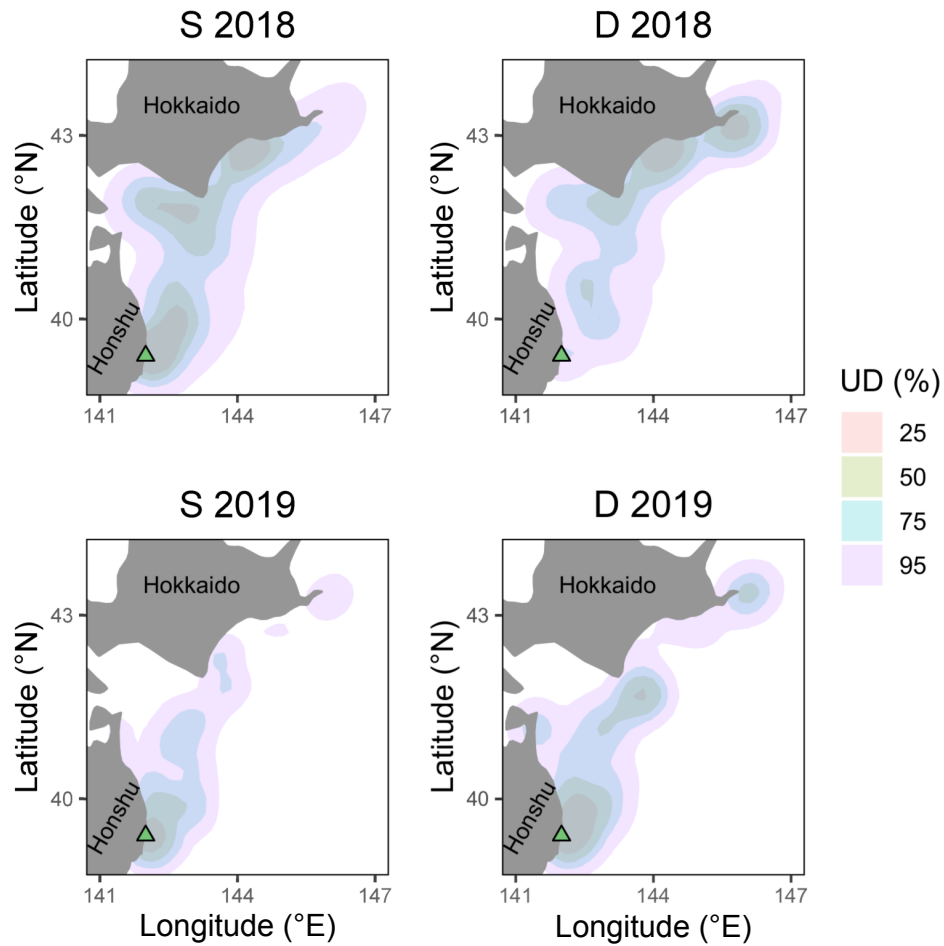


Figure 2.7: **Utilisation distributions of foraging locations by behaviour.** Distribution of GPS fixes with a foraging behaviour occurring within 30 seconds. Distributions are split into dives (D) and surface seizing (S). Rows are split by year, 2018 on the top, 2019 on the bottom. The nesting site is indicated by a green triangle.



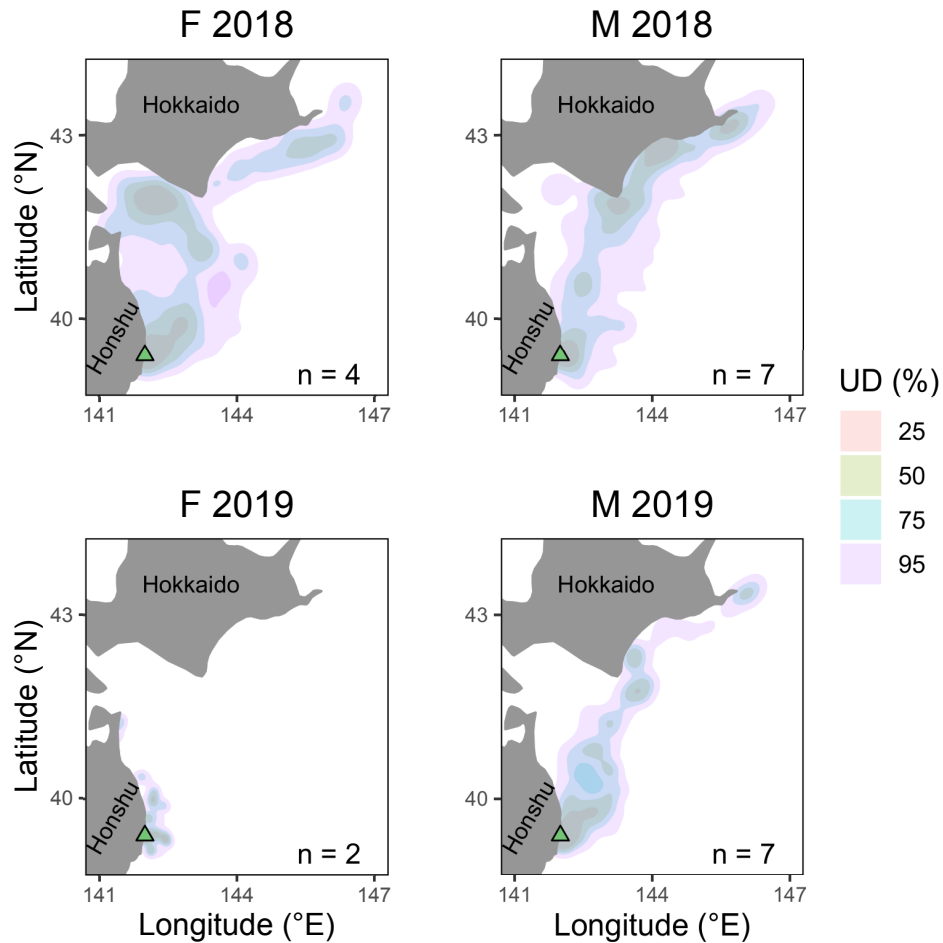


Figure 2.8: **Utilisation distributions of foraging locations by sex.** Distribution of GPS fixes with a foraging behaviour occurring within 30 seconds. Distributions are split by sex (female:F, male:M). Rows are split by year, 2018 on the top, 2019 on the bottom. The nesting site is indicated by a green triangle. The number of tagged individuals (n) is shown within the plot.

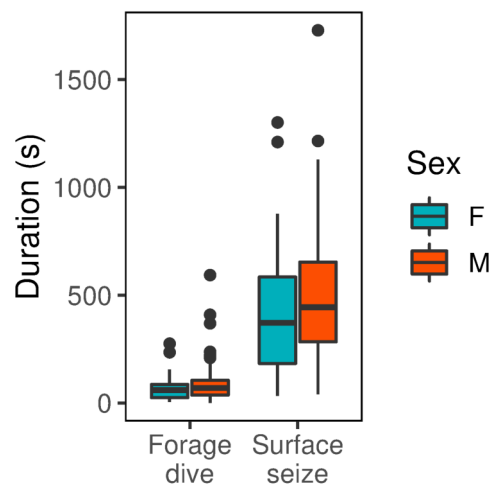


Figure 2.9: **Daily foraging durations of males and females.** Daily durations of diving (D) or surface seizing (S) between males and females. Males tended to forage for longer than females, however, this difference was not significant ( $p > 0.05$ , linear mixed model with ID and trip number as mixed effects).

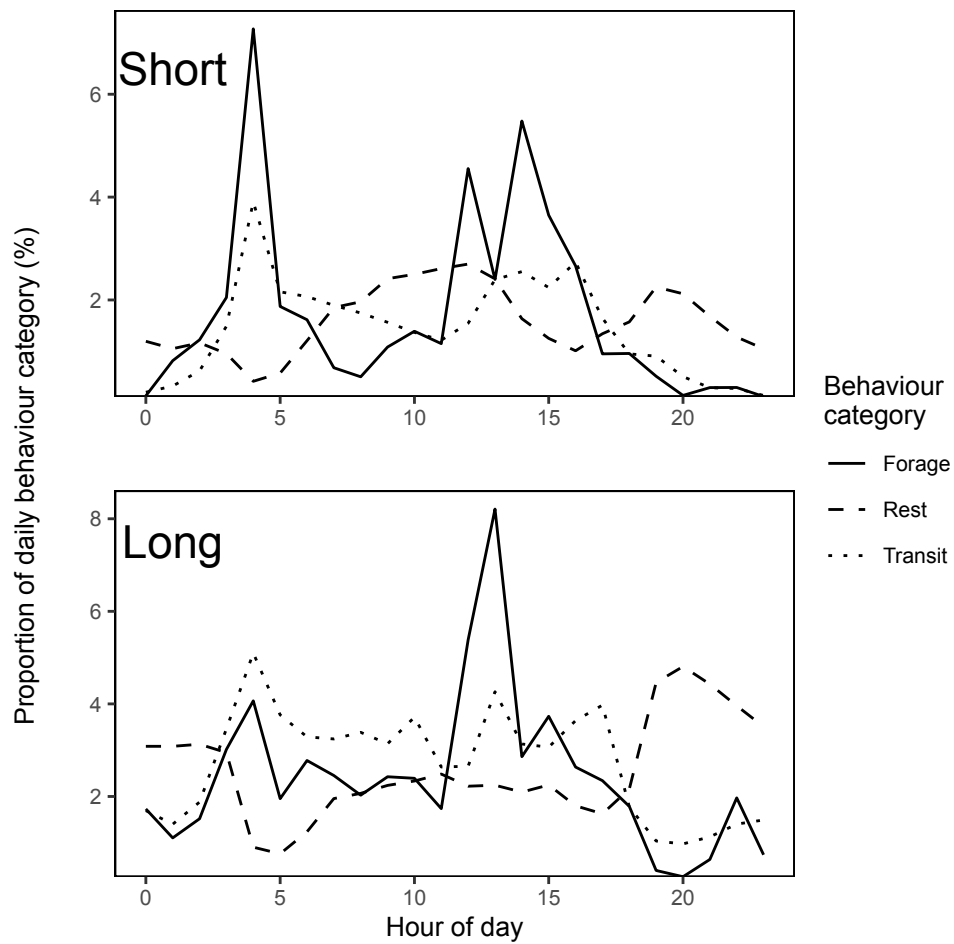


Figure 2.10: **Hourly proportions of behaviour categories during foraging trips.** Hourly proportions of daily categories across short (top) and long (bottom) foraging trips. Solid lines show foraging behaviour, dashed show rest, and dotted show transit.

# Wind Vector Estimation Method Comparison

## 3.1 Background

Seabirds have an intrinsic relationship with winds as they travel large distances across open oceans. Flight is among the most energetically costly locomotive behaviours (Elliott et al., 2013; Pennycuick, 1975; Tucker and Schmidt-Koenig, 1971), and, outside of behaviour (flapping rates and/or gliding), the efficiency of flight is largely governed by wind conditions. Typical avian flight speeds are in the same order of magnitude as wind speeds and so the cost of flight can be halved or doubled depending on the winds in which birds are flying (Liechti, 2006). Winds are also vital for the dispersion of odours from productive regions, which will be considered in greater detail in Chapter 4. Therefore, winds play a large role in the life of birds foraging at sea. Following the results of Chapter 2, the impact of wind on foraging strategies is considered further below.

Fine-scale wind recordings are not currently available from oceanographic data repositories. Understanding the interaction between seabirds and their local environment, specifically atmospheric conditions, is often limited by spatial and temporal scales. For example, the blended sea wind dataset from the National Oceanic and Atmospheric Administration (NOAA) provides sea winds within a  $0.25^\circ$  grid with temporal resolutions of 6 hours at minimum. The Japanese Meteorological Agency (JMA) record sea winds with an output every

3 hours from a mesoscale model reanalysis data set. Studies directly investigating relationships between seabird flight patterns and wind themselves utilise winds with spatial resolution  $0.5^\circ$  and time resolution of 6 hours (Abolaffio et al., 2018; Reynolds et al., 2015). Given the relatively large offset between the spatial and temporal characteristics of these data and the scales at which seabirds travel during foraging trips, testing for relationships at the finer scale of movement is not possible. However, recent studies have developed means to estimate wind conditions from seabird GPS tracks, using the relationship between ground speeds and heading (Yonehara et al., 2016), and the relationship of the bird headings to the mean track vector (Goto et al., 2017).

### 3.1.1 The curve method

The original method presented by Yonehara et al. (2016) assumes that the primary force affecting the speed of a flying bird should be wind. Therefore, when flying windward, the speed of the bird should increase just as it should decrease when moving leeward. Under sidewind conditions, travel speeds should increase the more the bird moves with the wind, and similarly decrease the more the bird moves into the wind. The relationship between flight direction and heading should reflect this. Using a 5-minute window of known flight tracks (decided via a speed threshold of  $5 \text{ ms}^{-1}$ ), ground speeds are plotted against track headings on Cartesian coordinates. A sine curve is fitted to the ground speeds using the relationship of ground speed  $V$  against the track direction  $\theta$  in equation 3.1, where  $\theta$  refers to the clockwise angle from north.

$$V = V_a + a \sin \theta + b \cos \theta \quad (3.1)$$

where  $V$ ,  $a$ , and  $b$  are coefficients,  $V_a$  represents air speed. The coefficients and air speed are estimated by least squares, and the wind direction and speed are then estimated. An adaptation

of this method (hereby known as the curve method) where the track vectors are plotted on polar coordinates instead fits a circle to the data, again using least squares (Fig. 3.1). The wind vector, made up of the wind's speed ( $w_v$ ) and direction ( $w_d$  in degrees clockwise from north), can be converted into their  $x$  and  $y$  components (wind components in the longitudinal and latitudinal directions) via equations Equations (3.2) and (3.3)

$$x = w_v \times \cos(w_d) \quad (3.2)$$

$$y = w_v \times \sin(w_d) \quad (3.3)$$

A circle is then fitted using the relationship of ground speed ( $v_d$ ) as a function of track direction ( $g_d$ ) using equation 3.4

$$f(w_d, w_v, a_v) = y \sin(g_d) + x \cos(g_d) + \sqrt{(y \sin(g_d) + x \cos(g_d))^2 - y^2 - x^2} - v_g \quad (3.4)$$

The offset of the centre of the circle from the origin (0,0) then represents the wind vector. GPS recordings used in the original study of the curve method were sampled at 1 fix per second.

### 3.1.2 The distribution method

The alternate method (hereby known as the distribution method), presented by Goto et al. (2017), uses the distribution of vectors of the GPS track to estimate wind conditions. A GPS track of a bird's movement represents the position of the bird relative to the Earth. This position is a result of the movement of the animal within a flow. For example, as a bird flies in a wind, its position is determined by a combination of the bird's flight and the wind. In vector notation, the track vector  $\mathbf{v}_T$  (from GPS recordings) is the sum of the heading vector  $\mathbf{v}_H$  and the wind vector  $\mathbf{w}$ :

$$\mathbf{v}_T = \mathbf{v}_H + \mathbf{w} \quad (3.5)$$

To estimate  $\mathbf{v}_H$  and  $\mathbf{w}$ , a movement model with a number of assumptions is used. The biased random walk (BRW) (Codling et al., 2010) is a commonly applied movement model capable of describing animal movement toward a particular goal destination using probability distributions. The BRW uses mutually independent probability distributions to describe the length and direction of a movement vector, and so assumes symmetry of direction about the mean. In other words, as a bird heads towards a destination, the BRW assumes there will be some fluctuation in the bird's heading during travel, but this fluctuation will be equal to either side of the destination. However, when the bird moves in a flow such as wind, this symmetrical assumption may not be true as the wind may move the bird more to one side. The bird's vector relative to the flow, the heading vector, however, will still be symmetrical, and so the BRW applies. The heading vector is therefore estimated using the BRW, with the vector length and direction (the bird's air speed and heading, respectively), estimated using the Weibull ( $f(s_{H,k}|\gamma, \rho)$ , where  $\gamma$  represents the heading speed) and von Mises ( $g(\theta_{H,k}|\phi, \kappa)$  where  $\phi$  represents the mean heading direction and  $\kappa$  is the concentration parameter, a characterisation of the distribution's variance) distributions, respectively.

The estimated heading vector is translated by the wind vector to equal the track vector as per Eq. 3.5. Figure 3.2 shows an example of the methodology applied to a 2018 streaked shearwater recording. The GPS tracks are split into 51-minute windows (Fig. 3.2a). As GPS fixes can occasionally be missed or alter their inter-fix intervals, over 45 GPS fixes (of an expected 51) were required within each window. The  $x$  and  $y$  components (longitudinal and latitudinal components, respectively) of the tracks are extracted (Fig. 3.2b) and the Weibull and von Mises distributions are fitted (Fig. 3.2b). The fitted distribution is symmetrical about the heading

vector, but, in the case of Fig. 3.2, not the track vector. The wind vector, assumed to be constant for the 51-minute fitting window, is then derived from Eq. 3.5, which translates the heading vector to the track vector (Fig. 3.2d). GPS recordings used in the original study of the distribution method were sampled at 1 fix per minute.

### 3.1.3 Method suitabilities

The primary difference between the two methodologies described above is the rate of sampling of the GPS data used in their original studies. The curve method used data sampled at 1 fix per second, while the distribution method used data sampled at 1 fix per minute. GPS tracks recorded during the breeding seasons of 2018 and 2019 recorded GPS at 1 fix every 5 or 30 seconds. Recordings with GPS sampling rates of 1 fix every 30 seconds were assumed to only be suitable for the distribution method.

The size of the windows across which the two methods operate (5 minutes for the curve method, 51 minutes for the distribution method) means that often the distribution method has reduced coverage of a foraging trip as birds are required to be flying for a considerably longer duration for the method to be applicable. To maximise the coverage of wind conditions estimated during a foraging trip, it is desirable to use the curve method estimates if the method proves to be reliable in comparison to validation data. In this chapter, the effect of applying the curve method to subsampled data is investigated by comparing curve method wind estimates using GPS recordings from streaked shearwaters sampled at 1 fix per second and 1 fix per 5 seconds. The accuracy of the curve and distribution methods are also tested by validating wind estimates from both methods against an independent source of wind vectors, the JMA reanalysis mesoscale model.



## 3.2 Materials and methods

The data used in this methodology analysis include the GPS recordings from AxyTrek tags in 2018 and 2019 as reported in Chapter 2. These tags were configured to record 1 GPS fix either every 5 or 30 seconds. These recordings were supplemented with data recordings of streaked shearwaters in Funakoshi-Ohshima island during the breeding seasons of 2014, 2016, and 2017, sampled at 1 fix every second.

### 3.2.1 Curve method sampling rate sensitivity

The curve method was applied twice to the 1 Hz sampled data (from 2014, 2016, and 2017, collectively), once using the original recordings, then again to the same data subsampled to 1 fix per 5 seconds to test the sensitivity of the method. The method was applied using the same length window size (5 minutes) across both sampling frequency recordings. Resultant wind direction and speed estimates for the original 1 Hz data within 10 seconds (within 2 inter-sample intervals) of an estimate from the subsampled data were compared and tested for correlation. Wind directions were tested using the Jammalamadaka-Sarma correlation coefficient via the "circular" package of R (Agostinelli and Lund, 2017) and wind speeds using Pearson's correlation coefficient.

### 3.2.2 Wind estimate validation

The curve method was applied to recordings from 2019 using a 5-minute window. The distribution method was applied to recordings from 2018 and 2019 subsampled to a sampling frequency of 1 fix per minute as per the sampling rate of the original study. All wind estimates were validated against wind vectors from the JMA mesoscale model reanalysis data (at 10m

altitude, the minimum altitude of available data, slightly above the typical flight altitudes of streaked shearwaters). These data were used for the original study of the distribution method (Goto et al., 2017). In the original study of the curve method (Yonehara et al., 2016), the validation data used were from SeaWinds microwave scatterometers, however, this data was not available for dates following the year 2014. Therefore, the same validation data is used for both the curve and distribution methods. Where available, the mean of distribution method wind vectors within 25 minutes of JMA wind vectors at time  $t$  were compared to the average of JMA wind vectors within 5 km of bird GPS tracks used in the wind estimation within  $t \pm 50$  minutes. For the curve method, wind estimates within 5 minutes of JMA wind vectors at time  $t$  were compared to JMA wind vectors averaged over 5 km of bird GPS tracks used in the wind estimation within  $t \pm 5$  minutes. The reduced search time and distance for the curve method was due to the shorter time window across which the method estimates wind vectors. The correlation between estimated and reanalysis model wind speeds and directions were calculated as described for the wind estimate comparisons, using the Pearson's correlation and Jammalamadaka-Sarma correlation coefficients, respectively. Analysis was performed using a combination of custom scripts in MATLAB (MATLAB, 2019), the R statistical language (R Core Team, 2017), and Julia (Bezanson et al., 2017).

### 3.3 Results

The relationship between the estimated wind directions from original and subsampled data from 2014, 2016, and 2017 were significantly correlated (correlation = 0.94, p-value < 0.0001,  $n = 8081$ , Fig. 3.3) with relatively little deviation between wind estimates if 1 Hz or 0.2 Hz data were used. Similarly, wind speeds showed high correlation ( $y = 0.94x + 0.3$ , p-value <  $2.2 \times 10^{-16}$ ,  $R^2 = 0.91$ ). The results are consistent with the method being robust to this decrease in the

number of data points required to estimate winds. This in turn indicates the suitability for this method when applied to data from 2019 recorded at 1 fix per 5 seconds.

Curve method wind estimates from 2019 were poorly correlated with JMA reanalysis data (wind direction: correlation 0.19, p-value  $< 0.01$ ; wind speed:  $y = 0.05x + 2$ , p-value = 0.4,  $R^2 = 0.003$ ,  $n = 208$  Fig. 3.4). Estimated wind vectors generated using the distribution method, however, correlated more favourably with JMA wind vectors at similar times and locations in both heading (corr = 0.417, p-value  $< 9 \times 10^{-7}$ ) and speed ( $y = 0.52x + 0.65$ , p-value  $< 3 \times 10^{-16}$ ,  $R^2 = 0.38$ ,  $n = 152$  Fig. 3.5), though speeds tended to be underestimated.

### 3.4 Discussion

In this chapter, two wind vector estimation methods using GPS tracks from streaked shearwaters along the eastern coast of Japan were examined. Effects of subsampled data on the curve method were investigated, and both methods were validated against modelled wind vectors produced by the JMA. However, the relatively poor relationship between curve method results and the JMA reanalysis wind vectors poses questions as to the accuracy of the method when compared to the same validation for the distribution method, which showed a stronger correlation to both the JMA wind directions and speeds. Through comparison of the wind vector estimation methods and validation against independent reanalysis model data, the distribution method appears most suitable for the purpose of identifying if birds are flying in tail, side, or headwind conditions.

The two methods tested in this chapter are important given the temporal scale at which they estimate wind vectors. Generating values across time windows of 5 and 51 minutes for the curve and distribution methods, respectively, produces wind vector data at much greater temporal and spatial resolution than currently available datasets using more traditional means. This is reflected in the temporal scale of the JMA model data selected for validation in this study. The

reanalysis wind vectors record 1 value per grid square every 3 hours. This is currently the finest temporal frequency of data available in the same region as the shearwaters' foraging grounds. Given this disparity in the timescales of the datasets being compared, we may therefore expect wind vectors to differ somewhat. To improve the validation testing of wind vector estimates, comparison of data from similar scales would be optimal. One possible method to do so would require deploying oceanographic buoys alongside translocated tagged shearwaters. This could provide wind data recorded at similar locations and times and at a finer scales than those available from satellite or large-scale model sources.

The curve method appeared to consistently underestimate wind speeds in comparison to both the distribution method and JMA wind vectors. Discussion of the effectiveness of the original method presented by Yonehara et al. (2016) has focussed on the differences in altitude between the JMA model and the seabirds used in this study. Streaked shearwaters typically fly low to the water surface, and so comparison of this data with the JMA model (calculated at 10m above sea level) may account for those differences in wind speeds. Differences between the curve and distribution method estimates for 2019 may arise from the difference in sampling window used between each method (5 minutes and 51 minutes, respectively). At longer timescales, the effects of wind gusts would be lessened, whereas should the shearwaters experience wind gusts, they are likely to have a greater effect on the wind estimates generated by the shorter curve method. Comparison of the acceleration recordings and flapping frequencies occurring in each segment used for the curve method may reveal some characteristics of shearwater flight. While these birds do perform efficient dynamic soaring, their reliance on flapping varies from larger, more glide-focussed Procellariiformes. Variation in the effect of flapping on wind speed in typical wind conditions occurs across species that differ in their proclivity for flapping vs. gliding (Spear and Ainley, 2008). Exploration of this phenomenon across Procellariiformes using

detailed biologging data may add considerations required for improved wind estimation.

Due to the range of available wind data, testing of wind estimates requires consideration of the comparison dataset used. In the original studies for the curve and distribution methods, data from a microwave scatterometer and a reanalysis mesoscale model, respectively, were used for testing estimation accuracy. To maintain consistency in comparison of the two methods, the JMA data were used for comparison in this study. However, the methods used to generate the JMA model results may cause some discrepancy with the curve method leading to poor validation performance. For future study, comparison with a larger number of validation datasets is required to test the efficacy of the curve and distribution methods, including the supplementary higher sampled data from 2014, 2016, and 2017. Consideration, too, must be given to the flight style of streaked shearwaters in the calculation of wind vectors using the curve method. The basis of the method assumes that the ground speed of soaring seabirds are mainly affected by winds. This assumption fits well for albatross species, that rarely flap during flight, and for streaked shearwaters during periods of dynamic soaring. However, shearwaters are more reliant on flapping during flight, and may flap more in response to wind to manually increase flight speed, which would therefore have adverse effect on the calculation of wind vectors using the curve method. Calculation of flapping behaviour in Chapter 2 can calculate the ratio of flapping and gliding. Future research could examine this ratio in comparison with the wind vectors generated, perhaps assigning a limit to the ratio to ensure better fit and more accurate wind vector estimation. Similarly, estimating the accuracy of GPS data used in both curve and distribution method calculations would be necessary to prune incorrect locations.

The curve and distribution methods differ in their effectiveness depending on the characteristics of the track segment used. As the curve method fits a circle to the vector data, a better fit is achieved if the track segment contains a wider range of headings to best fit a

circle to the east-west (x) and north-south (y) components. Indeed, should the track headings be concentrated in a single direction, the air speed (the radius of the fitted circle) may be overestimated, though this can be countered by setting an estimated value (15 metres per second) when running the fit estimation. The distribution method, conversely, produces a better fit when the track segment has little deviation from a single average heading, when the bird is consistently moving in the same direction. Periods of flight with little deviation indicate the birds are using some form of directional indicator. In the following Chapter, wind estimates prior to foraging events are examined to test for evidence of an olfactory-based search strategy. The distribution method is therefore best designed for this purpose and performed better in the validation testing, so was selected for use in the following chapter.

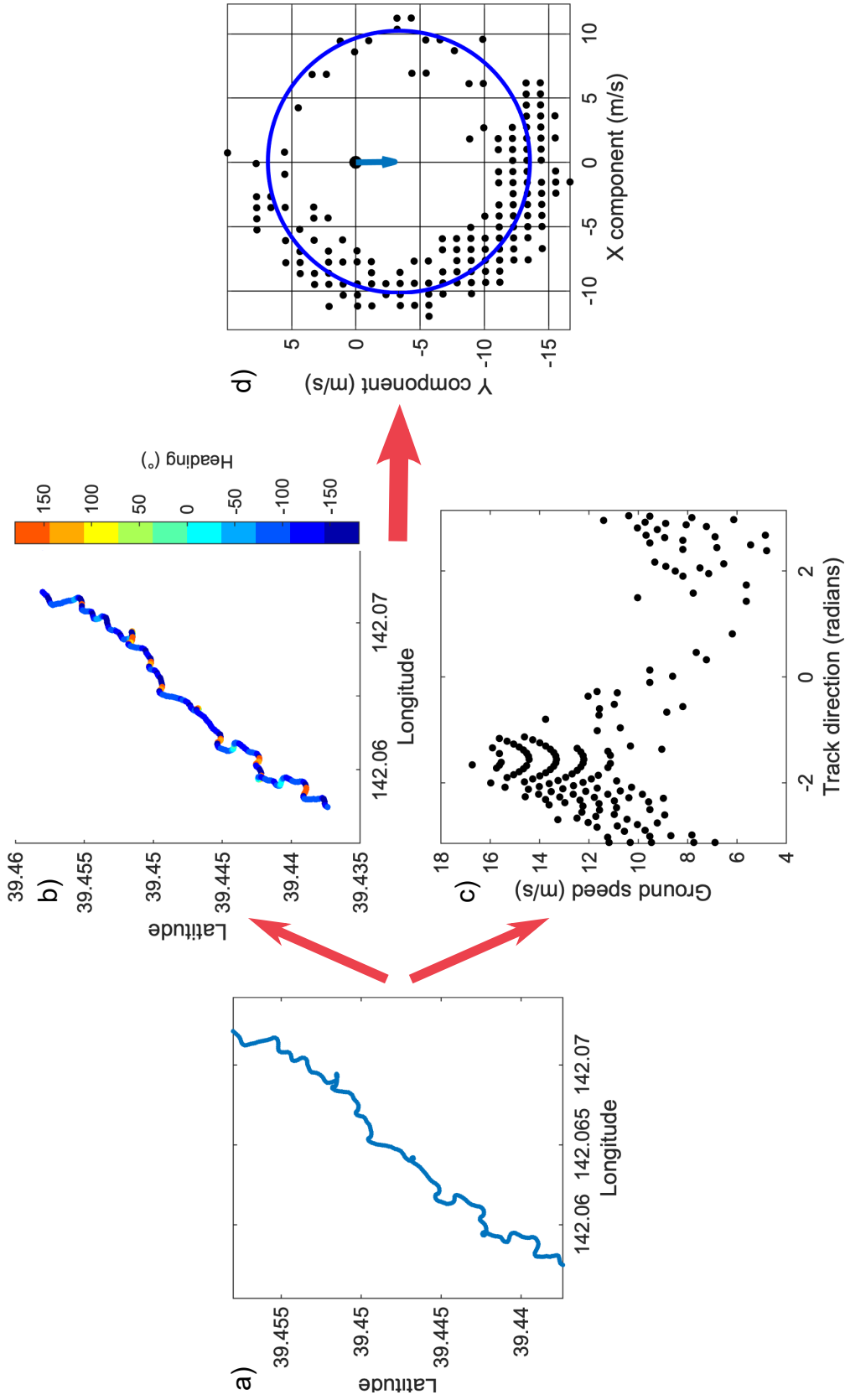


Figure 3.1: **Diagram of the curve method** An example of the curve method applied to a 5-minute 1 Hz sampled GPS track segment (a). The headings and speeds are extracted through the segment, and the  $x$  and  $y$  vector components (longitudinal and latitudinal components, respectively) calculated (b - c). A circle is fitted (d) using least squares means (blue circle) and the offset of the centre of the circle from  $(0, 0)$ , represented by the blue arrow, represents the wind vector.

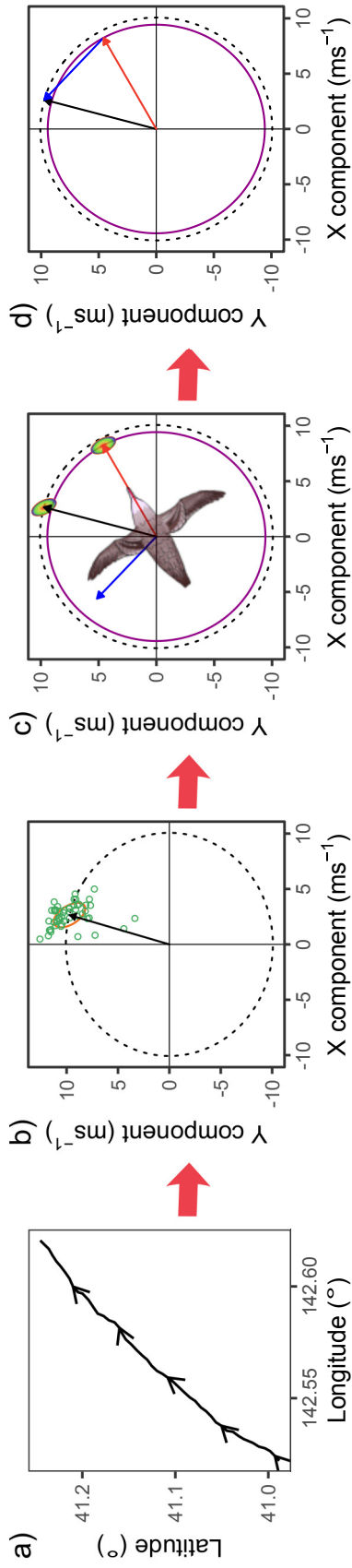


Figure 3.2: **Diagram of the distribution method** **a)** An example of the distribution method applied to a 51-minute GPS track segment. **b)** Track vectors (green circles) are extracted and the mean track vector (black arrow) calculated. The dotted black circle represents the mean track speed. **c)** Weibull and von Mises distributions are fitted to track speeds and headings, respectively. The mean heading vector (red arrow) shows symmetry with these distributions, while the track vector does not. The transformation of the heading vector to the track vector is achieved by the wind vector (blue arrow). The purple circle represents the mean air speed. **d)** The transformation of the heading vector to the track vector via the wind vector.



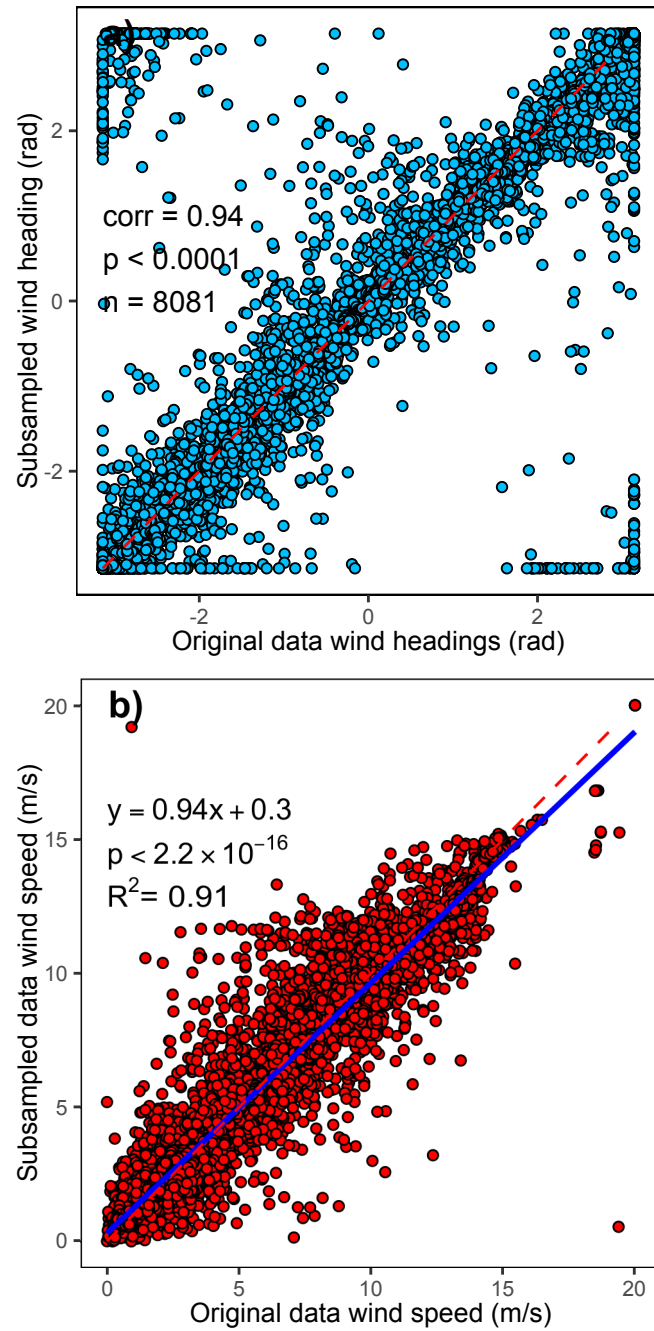


Figure 3.3: **Comparison of curve method wind estimations** Wind estimations from the curve method using original data sampled at one fix per second and subsampled data at one fix every five seconds ( $n = 7612$ ). The estimated wind headings (a) and speeds (b) are displayed with their correlation coefficients and p-values.

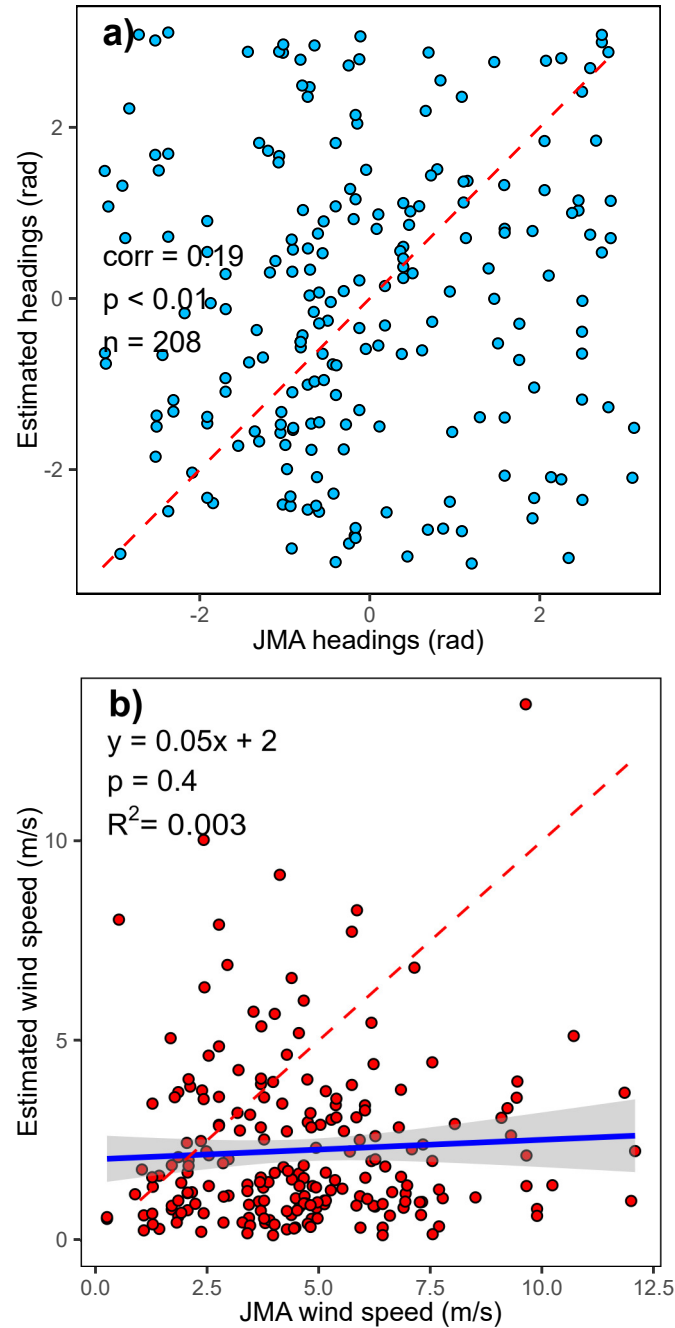


Figure 3.4: **Curve method estimated wind validation 2019** curve method estimated and Japanese Meteorological Agency (JMA) wind headings (a) and speeds (b) for the same times and locations ( $n = 208$ ). The dotted red line shows a 1:1 ratio in both plots. The Jammalamadaka-Sarma correlation coefficient between vector headings is shown within plot (a) and a linear regression and its equation is shown with the p-value from a Pearson's correlation coefficient within plot (b).

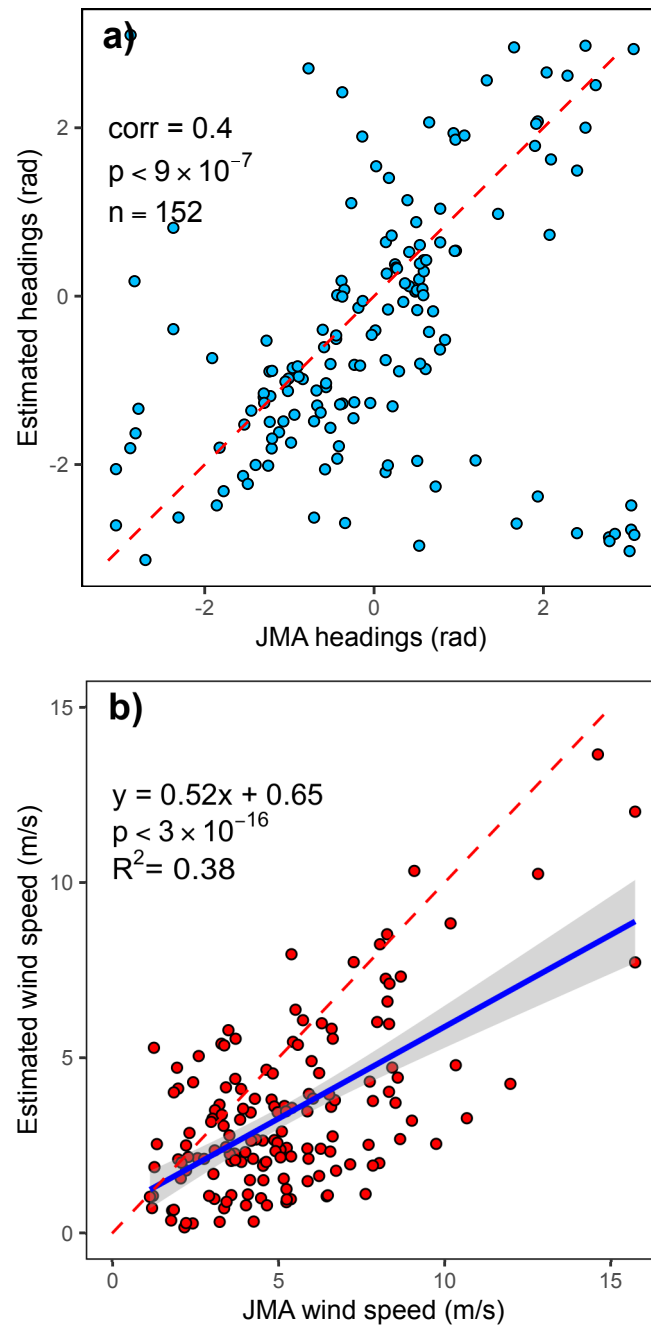


Figure 3.5: **Distribution method estimated wind vector validation** Estimated and Japanese Meteorological Agency (JMA) wind headings (a) and speeds (b) for the same times and locations. The dotted red line shows a 1:1 ratio in both plots. The Jammalamadaka-Sarma correlation coefficient between vector headings is shown within plot (a) and a linear regression and its equation is shown with the p-value from a Pearson's correlation coefficient within plot (b).

## Use of Winds in Prey Patch Search

### 4.1 Background

The marine environment inhabited by seabirds is patchy in its presence of viable prey. The distribution of plankton and large marine fauna which seabirds prey on vary both spatially and temporally, typically with smaller high density patches found within larger and less dense prey concentrations. As such, a vital aspect of seabird foraging behaviour is search, during which birds must use information gathered from their external environments to best identify where they are most likely to find food. Given the particularly large distances across which seabirds travel to foraging sites, the accuracy of their headings is hugely important. Maintenance of travel headings is important for the same reason, and provides an interesting question as to how seabirds keep a constant bearing while travelling over featureless ocean. A plausible answer lies in their olfactory capabilities.

#### 4.1.1 Evidence for olfactory navigation

Development of the theory of olfactory navigating in seabirds has been built around the initial evidence of enlarged olfactory bulbs, particularly in Procellariiformes (Bang, 1971, 1960). This theory was furthered through experimental testing in controlled conditions. Tests designed to stimulate some response indicating attraction, whereby subjects could choose a path or

simply respond to an artificial stimulus, usually dimethyl sulphide (DMS) or some other biogenic odourant, largely showed support for the theory of seabirds not only being capable of detecting DMS and/or other biogenic odours, but being actively attracted to them (Bonadonna et al., 2006; Dell’Ariccia et al., 2014; Nevitt, 2008; Nevitt and Bonadonna, 2005).

### 4.1.2 Evidence of olfaction in free-ranging birds

Testing for seabird olfactory reliance whilst in their natural environment is difficult without the inclusion of an artificial lure. Non-invasive methods to study seabird olfaction have thus far tested the movement patterns of seabirds for evidence of olfactory reliance. Birds travelling with little deviation in their heading (a uni-directional track) are assumed to travel via some directional cue. In the case of olfactory navigation, these cues, present in a fluctuating atmosphere, are expected to vary in their concentration such that pockets of concentrated odours, detectable by birds are distributed across the atmosphere. GPS tracks of tagged birds split into segments of uni-directional travel should therefore represent periods during which birds are within one of these odour concentrations, and so capable of detecting them and generating an odour map to orient themselves (Reynolds et al., 2015). In a naturally fluctuating environment, concentrated odours, and so lengths of uni-directional flight, are predicted to follow an exponentially truncated power law characterised by an exponent value of  $3/2$ .

This theory was tested in shearwater species from colonies in the North Atlantic Ocean, central Atlantic Ocean, and Mediterranean Sea (Reynolds et al., 2015). The exponent values of these distributions were later shown to be significantly correlated with local wind characteristics (Abolaffio et al., 2018). There is, therefore, compelling evidence for an olfactory reliance in several species of Procellariiformes. However, these studies have primarily focussed on homing

behaviour or navigation in general and so do not provide much evidence for the use of olfaction in the specific context of foraging behaviour. To do so, a fine-scale knowledge of when and where birds are foraging is required.

### 4.1.3 Evidence for olfactory reliance in search behaviour

Far-ranging Procellariiformes can use wind conditions to improve their travel efficiency (Sachs et al., 2013, 2012; Spivey et al., 2014; Weimerskirch et al., 2000). These birds therefore are capable of optimising their surrounding conditions to best suit their travel needs. Dynamic soaring is a method by which albatrosses and shearwaters can optimise their flight behaviour to expend as little energy as possible, thereby increasing potential travel distance (Sachs et al., 2013, 2012; Spivey et al., 2014). Dynamic soaring is described as a series of cyclical interactions with wind, where birds head windward and gain altitude. The bird then changes direction to a leeward heading and drops in altitude, picking up speed. The bird then curves back to a windward direction, gains altitude, and starts the procedure over again. This therefore generates a preference of wind condition for the birds to fly in, where efficiency can be maximised. Namely, birds flying in sidewind conditions can optimise their flight efficiency through dynamic soaring and effective use of wind conditions during flapping flight (Spivey et al., 2014). However, how birds interact with their conditions during search has not as yet been tested.

Assuming a constant production of odour at a prey patch, if using olfactory senses to orient themselves towards foraging spots, birds should fly windward, up an odour concentration gradient, towards the prey patch. As flight efficiency would drop during these headwind conditions, birds should also travel in sidewinds over longer distances to perform dynamic soaring and fly efficiently, using headwinds only as they approach a foraging spot. This theory is tested using a combination of the distribution wind estimation method defined in Chapter 3 with the

application of the foraging detection method from Chapter 2 to the long duration AxyTrek data. A behavioural context can be applied to winds the birds experience during a foraging trip and wind strategy as birds approach foraging spots are examined.

## 4.2 Materials and methods

### 4.2.1 Field experiments

Data were gathered as per in Chapter 2, with 11 chick-rearing streaked shearwaters tagged with GPS and acceleration tags (AxyTrek) in 2018, and nine in 2019. AxyTrek tags recorded 40 foraging trips over 99 days. Foraging behaviours was determined using the same acceleration-based foraging method. Foraging behaviours at time  $t$  were assigned to GPS positions within  $t \pm 30$  seconds.

### 4.2.2 Wind heading and speed calculation

The distribution method described in Chapter 3 was applied to streaked shearwater GPS tracks collected in 2018 and 2019. GPS tracks were converted into UTM values, and the resultant headings calculated through trigonometric means. The wind estimation method runs across 51-minute windows and examines the seabird's headings with the average GPS track heading across the window. For each window, average bird heading (calculated by  $\tan \Sigma y / \Sigma x$ , where  $y$  are the vertical (latitudinal) changes in position, and  $x$  are the horizontal (longitudinal) changes in position),  $x$  and  $y$  components of wind vectors, and distance to the next foraging spot as calculated by the method from Chapter 2 were calculated. An example of wind vectors calculated for a GPS track is shown in Fig. 4.1, and a closer focus on the winds a shearwater experiences as it approaches a foraging spot is shown in Fig. 4.2.

### 4.2.3 Relative wind headings and statistical analysis

As birds approach foraging spots, if these birds use olfaction to navigate to foraging spots, they should travel into the wind, encountering wind-transported DMS signals from a productive zone where plankton and other prey are present. To test this, the wind headings the birds are experiencing are required. These wind headings relative to the birds' movement were calculated by subtracting the wind headings from the average bird headings (averaged across the 51-minute wind estimation method). The relative wind headings are the angles of the wind on the bird, with 0 radians meaning a full tailwind, and  $\pi$  or  $-\pi$  meaning a direct headwind. Distances to next foraging spot were binned in kilometre bins from 10 to 1 km away, and in 10 kilometre bins from 50 to 10 km away. The relative wind headings within these bins were tested for uniformity in their distribution using the Hermans-Rasson test of uniformity. This test is preferred to the Rayleigh's test of uniformity (Jammalamadaka, 2001) as the Hermans-Rasson test has been shown to outperform the Rayleigh's test in cases with multimodal distributions (Landler et al., 2019). The Hermans-Rasson tests evaluates if distributions of circular data are uniform, i.e. showing no clear mean heading. If relative headings are not uniformly distributed, the mean heading is calculated with the corresponding  $\bar{r}$  value, a measure of the data concentration (the length of the mean vector/number of samples). To check for differences in the distribution of relative wind headings as birds approach foraging spots, the Watson-Wheeler two-sample test, a non-parametric test to check if sample headings come from the same population (Batschelet, 1981), was used on 1 and 10 km binned data for distances of  $< 10$  and  $< 50$  km from the next foraging point, respectively. The dispersals of relative wind headings within 5 km bins from 97.5 to 2.5 km to the next foraging spot were calculated to test how heavily birds relied on wind vectors for orientation.

Seabirds have been shown to alter travel behaviour as they approach foraging grounds,



switching from transit to search behaviours. This change in behaviour may be reflected in their use of wind conditions. To test for this change the relative wind headings of birds leaving the nest colony were examined for correlation with distance from the colony. Each GPS fix was assigned as outgoing or incoming as per the methods of (Shiomi et al., 2012), where the bird's speed relative to the nest colony was calculated for the proceeding hour. As birds leave the colony, their relative speed will be negative and as they approach it will be positive. Relative wind headings were binned into 5 km bins by distance from the nest colony and where bins contained more than 20 values, the Hermans-Rasson test determined the non-uniformity of the headings. Where non-uniform, mean headings and dispersals of relative wind headings were calculated. Analysis was performed using custom scripts in the R statistical language (R Core Team, 2017), and Julia (Bezanson et al., 2017).

The wind estimation method was applied to GPS recordings from 20 individuals in 2018 and 2019 (one example Fig. 4.1), generating wind vectors for portions of all individuals' tracks. The wind estimation maximum likelihood was required to pass two conditions about the estimations: anisotropic heading vector probability distribution and angle between mean heading and mean track vector is less than  $90^\circ$ . The goodness of fit was then verified by checking that the bird's heading and heading speed were distributed according to the Weibull and von Mises distribution, respectively, using a Kolmogorov-Smirnov test, and that the heading and heading speed were uncorrelated using a Pearson's correlation test. Wind estimates were only accepted once all these tests were passed. GPS data for the model were filtered to remove speeds under 15 kph (derived from (Shiomi et al., 2012)), and the 51-minute model windows were required to contain at least 45 data points. Wind vectors were calculated within 10 km of the next foraging spot in 19 individuals, in 15 individuals within 5 km, and in 11 individuals within 1 km. Foraging trip durations of wind vectors calculated within 10 km of the next foraging spot ranged from 1 to 8

days.

## 4.3 Results

### 4.3.1 Wind conditions across foraging trips

Wind vectors were calculated for  $7 \pm 3\%$  (mean  $\pm$  standard deviation) and  $5 \pm 3\%$  of tag recording minutes in 2018 and 2019, respectively. As shearwaters approached foraging spots, their use of wind conditions shifted from sidewind focussed distributions to near headwind conditions (Figures 4.3 and 4.4). At 50-40 and 40-30 from the next foraging spot, birds showed a bimodal distribution of side-to-head winds. All 1 and 10 km binned relative wind heading distributions less than 10 km from the next foraging spot were found to be non-uniformly distributed ( $p < 0.01$ , Hermans-Rasson test) and mean headings indicated birds flew in headwind conditions when approaching foraging spots (Fig. 4.5). Of the 1 km binned distributions, the only two that were significantly different in their distribution ( $p < 0.05$ , Watson-Wheeler test) were those from 2-1 and 1-0 km from the next foraging spot (Table 4.1).

$\bar{r}$  values of mean relative wind headings (the amount of the birds deviated from a steady course relative to wind headings) increased with proximity to foraging, particularly from 15 to 10 km (Fig. 4.6a). Once closer than 10 km from the next foraging spots themselves, their relative wind heading dispersals increased, suggesting they no longer travelled according to wind headings as diligently. From 40 km to the next foraging spot, wind speeds remained relatively stable, ranging between 1 and 5  $\text{ms}^{-1}$ , averaging at approximately 3  $\text{ms}^{-1}$  (Fig. 4.6b).

Within 200 km of the nest colony, birds on outward foraging trips used sidewind conditions during both long and short foraging trips, with a greater spread of wind conditions once at greater distances. These averaged relative wind headings at 200+km from the nest colony (only

recorded for birds on long duration trips) were dispersed in head/sidewind conditions, with winds moving against the birds' direction of movement (Fig. 4.7). Intuitively, shearwaters should avoid straight headwinds during high wind speeds, and this is reflected in birds flying in tail or sidewinds during high wind speed conditions (Fig. 4.8). Shearwaters flew in straight head and tailwinds when the wind speeds were slowest, and little difference was observed in this trend across long and short duration foraging trips (Fig. 4.8), suggesting this strategy was consistent even if birds were flying over short distances. As expected, resulting ground speeds of shearwaters were highest in tailwind conditions and slowest in headwind conditions (Fig. 4.9). Shearwaters appeared capable of flying at similar with birds flying at similar speeds during tail and sidewind conditions, particularly during high wind speeds (Fig. 4.9).

## 4.4 Discussion

Non-invasive direct testing the use of olfactory signals by seabirds during typical foraging flights is difficult due to logistic issues in observing seabirds across the ranges they travel during foraging trips. Similarly, the fine spatial and temporal scales of those trips compared to those of available meteorological and oceanographic data, and the complexities of the environments the birds interact with add challenges to this goal. However, through a combination of innovative analyses of biologging data, fine-scale behavioural patterns can be examined and so build evidence to support ecological theories. In this study, estimations of wind vectors from GPS recordings of streaked shearwaters in combination with acceleration-derived foraging behaviours can be used to investigate the role of wind in shearwater foraging. The results obtained show that when leaving the nest colony, birds use sidewind conditions to travel to offshore foraging zones and transition to using headwind conditions as they approach foraging spots (within 20 km). The results are consistent with the theory that streaked shearwaters can strategically use wind

conditions during foraging trips. These strategies are split into two main phases, transit and search, with birds transitioning between the two as they approach foraging spots.

#### **4.4.1 Wind estimation considerations**

The distribution method used to estimate wind vectors in this study uses windowed data 51 minutes in length. Previous recordings of streaked shearwaters foraging trips showed an average flight speed of 15 kph. Therefore, 51 minutes of flight recordings are likely to contain over 12.75 km, therefore analysing relative wind headings across 1 or even 10 km bins may not be possible to accurately indicate the wind usage of birds during a foraging trip. However, these results are more accurate to both the spatial and temporal scales of the birds' positions during foraging trips than other available data sources. The distribution method also generates wind estimates every minute, and so changes in relative wind usage may be visible when comparing across multiple bins. The findings of this study can therefore be used to indicate the trends of wind usage of seabirds, as well as provide a framework for more detailed analyses as wind estimation methods improve and are applied over finer scales. This study is therefore positioned as a starting point to more detailed research on seabird search behaviour as relates to wind usage.

#### **4.4.2 Transitional wind strategy**

The transit strategy involves the use of winds to most efficiently travel from the nest colony to foraging zones. The long distances travelled by seabirds during foraging trips maximises their requirement for flight efficiency. During foraging trips recorded by AxyTrek tags, streaked shearwaters predominantly used sidewinds within the first 200 km from the nest colony, within both short and long foraging trips. This indicates a highly efficient transit phase, with birds

optimising the wind strategy they use as they travel out to foraging grounds, using sidewind conditions to perform dynamic soaring flight. When experiencing the highest winds speeds, the birds flew in sidewinds (Fig. 4.8), perhaps adjusting their flight strategies to avoid flying in headwinds during high wind speeds where possible.

The greater concentration of headwind conditions used by shearwaters as they approach foraging spots (Fig. 4.4) suggests a transition from the initial high-efficiency transit phase from energetic efficiency to olfaction-based search. The change in relative wind headings is indicative of a move away from efficiency, with birds flying upwind, and so slowing their ground speeds (Fig. 4.9). The decreased dispersal of relative wind headings (Fig. 4.6a), meaning the birds deviated less from their relative wind headings (in this case headwinds), shows that not only do birds fly in less efficient conditions, but they also concentrated their headings into the wind. As birds were more capable of maintaining their heading relative to the wind, they likely required some indicator in the wind vector to do so. Odour signals carried by these winds may be sufficient to attract shearwaters such that they follow odour sources (i.e. travel upwind) towards a foraging spot. The point of transition around 20 km from the next foraging point is in good agreement with previous research intimating the use of olfaction to direct travel towards foraging spots in wandering (*Diomedea exulans*) (Nevitt, 2008). Birds moved upwind towards foraging spots from distances of approximately 20 km. This study therefore adds to this evidence for olfactory usage in seabirds, with increased resolution in the wind data used.

Odour signals in wind vectors require some level of turbulence to be transported through the atmosphere. However, signals that are detectable by seabirds are likely to be lost in highly turbulent environments (Abolaffio et al., 2018). Exceedingly high wind speeds can cause odour concentrations to fall as odour particles are spread over too wide an area, and reduce the effective concentration gradient of odour particles, becoming too disparate to aid in navigation. The lower

wind speeds shearwaters experienced when travelling into straight headwinds seem suitable for both downwind odour transport and maintenance of sufficiently high odour concentrations that are detectable by seabirds. As the wind estimation model could not consistently produce wind estimates through all GPS tracks, the data are not sufficient to characterise all wind speeds birds flew in on approach to a foraging spot. However, the present data are consistent with the theory of local wind conditions the birds use prior to foraging behaviour being conducive to olfactory navigation.

The final approach to a foraging spot is likely to include a behavioural transition in reliance from olfactory to visual senses as birds narrow in on precise foraging locations. The increase in relative wind heading dispersals as the shearwaters neared their next foraging spot may indicate this transition. Additionally, the gradual offset of relative wind headings as the birds approach foraging spots (Fig. 4.5) from headwind to sidewinds may reflect the birds adjust trajectories against the wind in response to visual cues, with less emphasis placed on flight according to wind-based scents.

The 1 km binned distributions were largely concentrated as winds heading southeast, relative to the birds' headings 4.5. This may be due to similar movement trends across all individuals heading in similar directions from the nest colony to foraging spots. Wind recordings from a previous study using streaked shearwater GPS recordings showed consistent north-westerly winds (Yonehara et al., 2016). With consistent wind conditions, shearwaters recording foraging trips over the same days are likely to produce a trend in the relative wind headings experienced, resulting in a mono- or bimodally concentrated relative wind heading distribution, as in this study.

### 4.4.3 Evidenciary support for olfactory usage

The theory of this study relies on the concept of an odour signal, such as DMS, carried by wind vectors, being detectable and so usable as a homing beacon for seabirds to locate their origin points. Seabirds, including shearwater species, when attracted to artificial oil slicks within a natural context, were observed flying upwind toward DMS-scented slicks (Dell'Aricecia et al., 2014). This study is consistent with these observations, namely the reduction in relative wind dispersals as birds approach foraging spots along with average relative wind headings. Combined with results of prior studies showing attraction in Procellariiformes to odours, this indicates streaked shearwaters may use odour-based signals to direct travel towards foraging spots. However, like-for-like comparisons may not be suitable across all Procellariiform species. While experiments on the effect of artificial DMS plumes on Procellariiform species showed attraction responses from many species (Nevitt et al., 1995), attraction to odours has not been found consistent across species, or indeed across odourants (Cunningham et al., 2003; Dell'Aricecia et al., 2014; Nevitt et al., 2004, 1995). One theory for the cause of this variation involves the phylogenetic history and evolution of Procellariiformes (Buskirk and Nevitt, 2007; Nevitt, 2008). Birds in this order can be largely classified into burrow or surface nesting species. The posited theory argues that chicks growing in burrows, such as streaked shearwaters, are deprived of light and instead focus on the odours brought in by the parents, particularly during feeding (Dell'Aricecia and Bonadonna, 2013; Nevitt, 2008).

A common thread among experimental study of seabird olfaction is the use of Y-mazes to quantify attraction to scents. The findings of this study would benefit from testing streaked shearwaters at Funakoshi-Ohshima island with Y-mazes. This would add evidence of these birds' attraction or lack thereof to DMS or other biogenic scents. Through personal communication, the author has learned of previous Y-maze tests with streaked shearwaters from other Japanese

colonies that did not show a significant response to DMS. However, it should be noted that the variety of attractant odours across Procellariiformes is wide and can vary across species, and so further testing may be necessary in the case of streaked shearwaters. Intriguingly, burrowing species have reacted less strongly to krill-originated odours than surface nesting counterparts in prior studies, though both groups were strongly attracted to fish-based scents (Nevitt, 1999; Nevitt et al., 2004; Nevitt, 2008; Nevitt et al., 1995). This supports the concept of seabirds utilising a variety of odours transferred over the oceanic landscape, generating odour maps by combined gradients of biological scents (Wallraff, 2004). In blue petrels (*Halobaena caerulea*), another burrow-nesting species, as parents feed their young, the chick begins to relate odours carried by the parent to feedings, and so builds an attraction (Nevitt, 2008). Parents continue to feed the chick and provide positive reinforcement of the odours they carry until fledging. Procellariiforms are adapted to be self-sufficient from fledging, and so this scent may be the method by which these birds initially isolate foraging spots. Therefore, if possible, samples of the parents' stomach contents and/or odours taken during the breeding season could uncover the biological odours streaked shearwater chicks may be attracted to.

This study provides an innovative method of observing seabird interaction with wind conditions in the context of foraging behaviour. While prior studies on search behaviours in seabirds have examined homing behaviour and/or general navigation, this more foraging-oriented study provides a framework for fine-scale study of seabird-wind interaction. In combination with experimental testing of shearwater olfactory sensitivity, the importance of olfactory cues could be explained with greater certainty.



Table 4.1: Watson-Wheeler tests for 1 kilometre binned data

Bin 1 (km)	Bin 2 (km)	Watson-Wheeler test result
0 - 1	1 - 2	$p < 0.01$
1 - 2	2 - 3	$p > 0.05$
2 - 3	3 - 4	$p > 0.05$
3 - 4	4 - 5	$p > 0.05$
4 - 5	5 - 6	$p > 0.05$
5 - 6	6 - 7	$p > 0.05$
6 - 7	7 - 8	$p > 0.05$
7 - 8	8 - 9	$p > 0.05$
8 - 9	9 - 10	$p > 0.05$
0 - 10	10 - 20	$p < 0.01$
10 - 20	20 - 30	$p < 0.01$
20 - 30	30 - 40	$p < 0.01$
30 - 40	40 - 50	$p > 0.05$

Results of Watson-Wheeler tests for homogeneity between 1 kilometre binned distributions of relative headings. The null hypothesis of no difference between distributions is rejected between 0-1 km and 1-2 km, and between all 10 km bins except 30-40 km and 40-50 km.

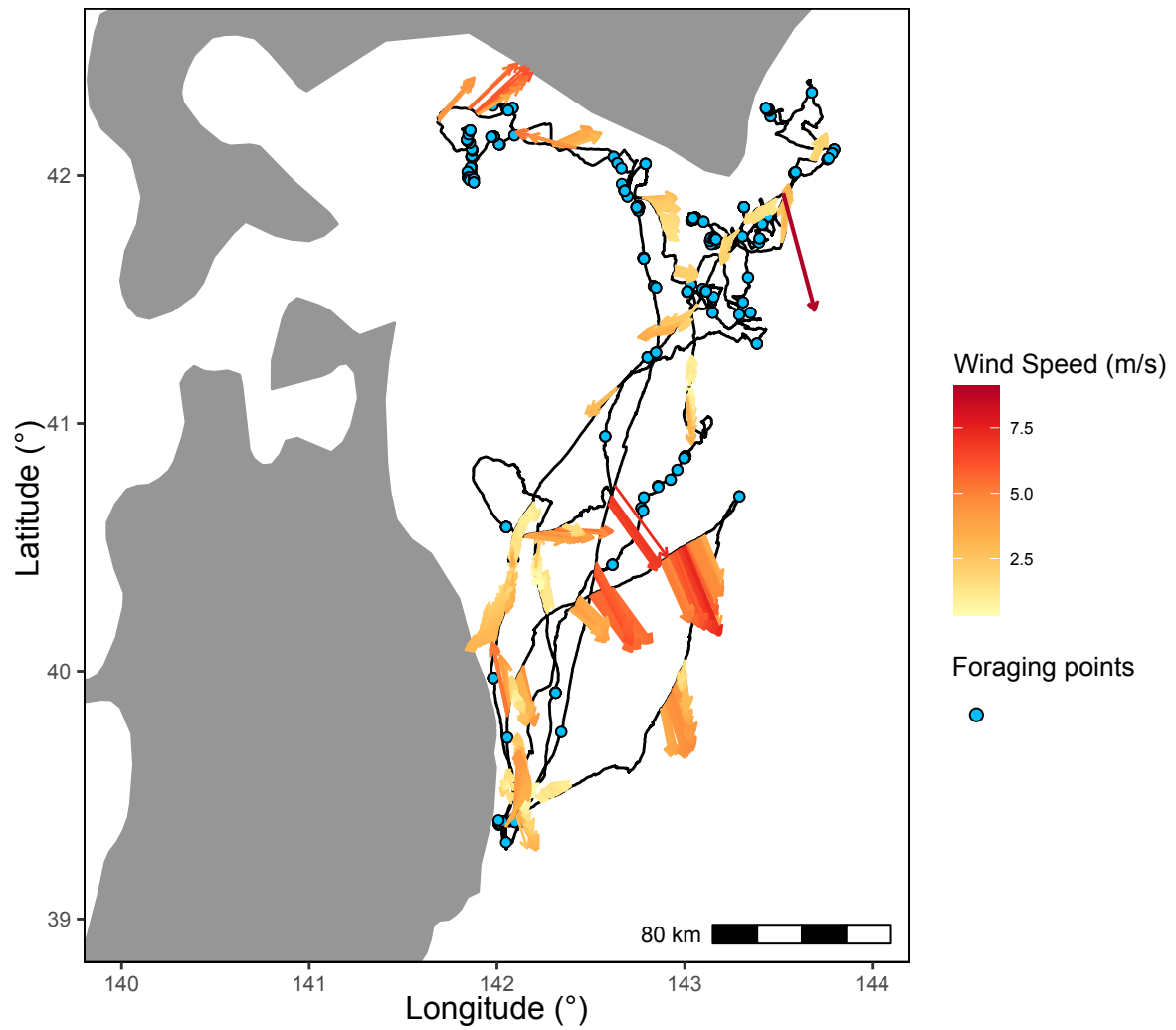


Figure 4.1: **Example of wind estimation applied to GPS track** Estimated wind vectors calculated for GPS tracks (black line) of one individual over 10 days which encompassed 3 foraging trips.

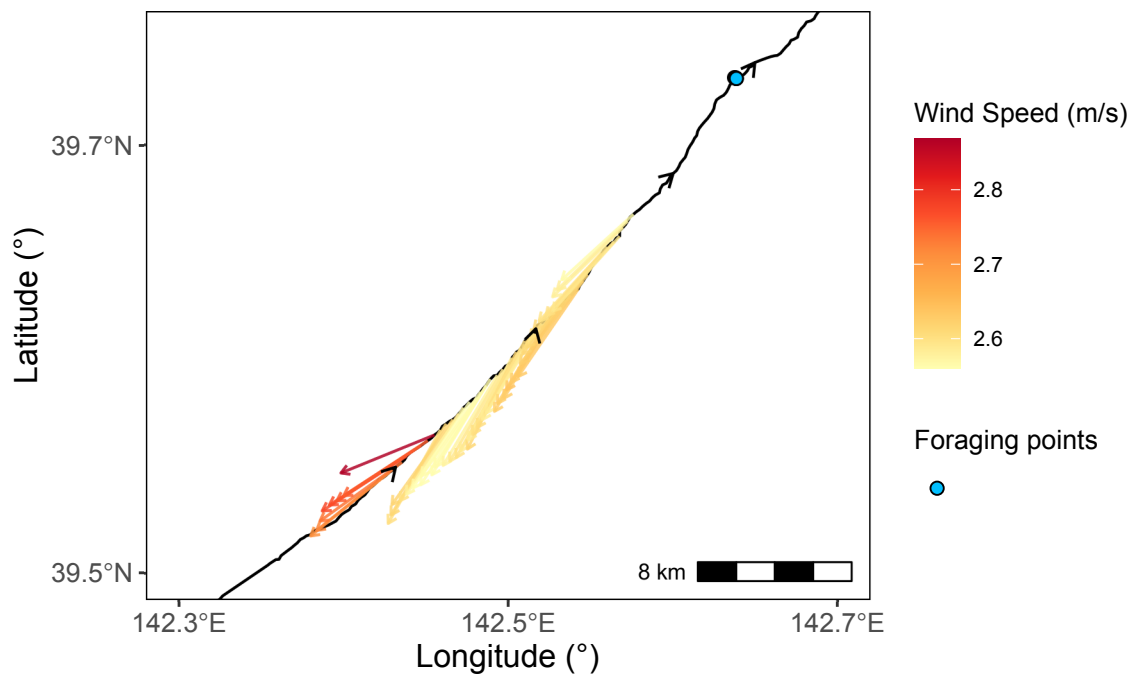


Figure 4.2: **Example of wind vectors as a bird approaches a foraging spot** Estimated wind vectors along a GPS track (black line) as the tagged individual approaches a foraging spot (blue circle). The bird's direction is indicated by black arrows along the track.

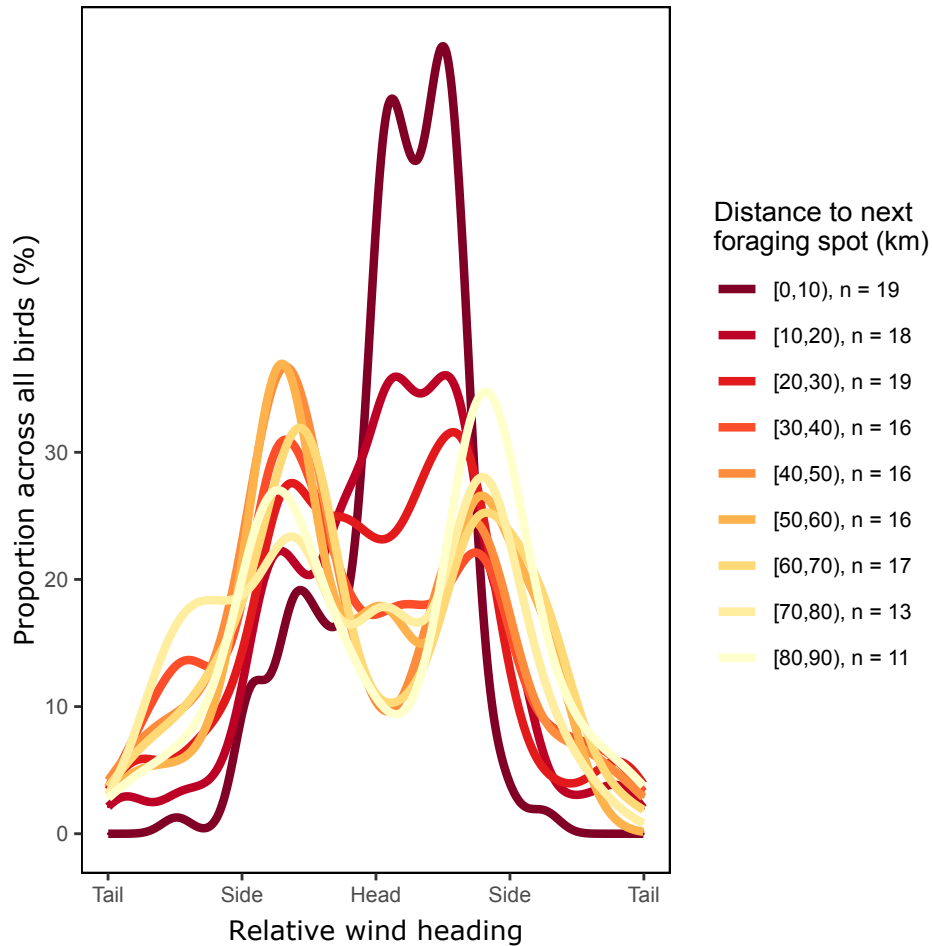


Figure 4.3: **Relative wind headings as birds approach foraging destinations** Densities of relative wind headings binned into 10 km bins of shearwaters as they approach foraging spots. Line colours range from light yellow (further) to dark red (closer) in correspondence to proximity to the next foraging spot. Birds showed a transition as they neared the next foraging site from flight-efficient in sidewinds to less efficient headwinds which can carry odour signals used in olfactory search.

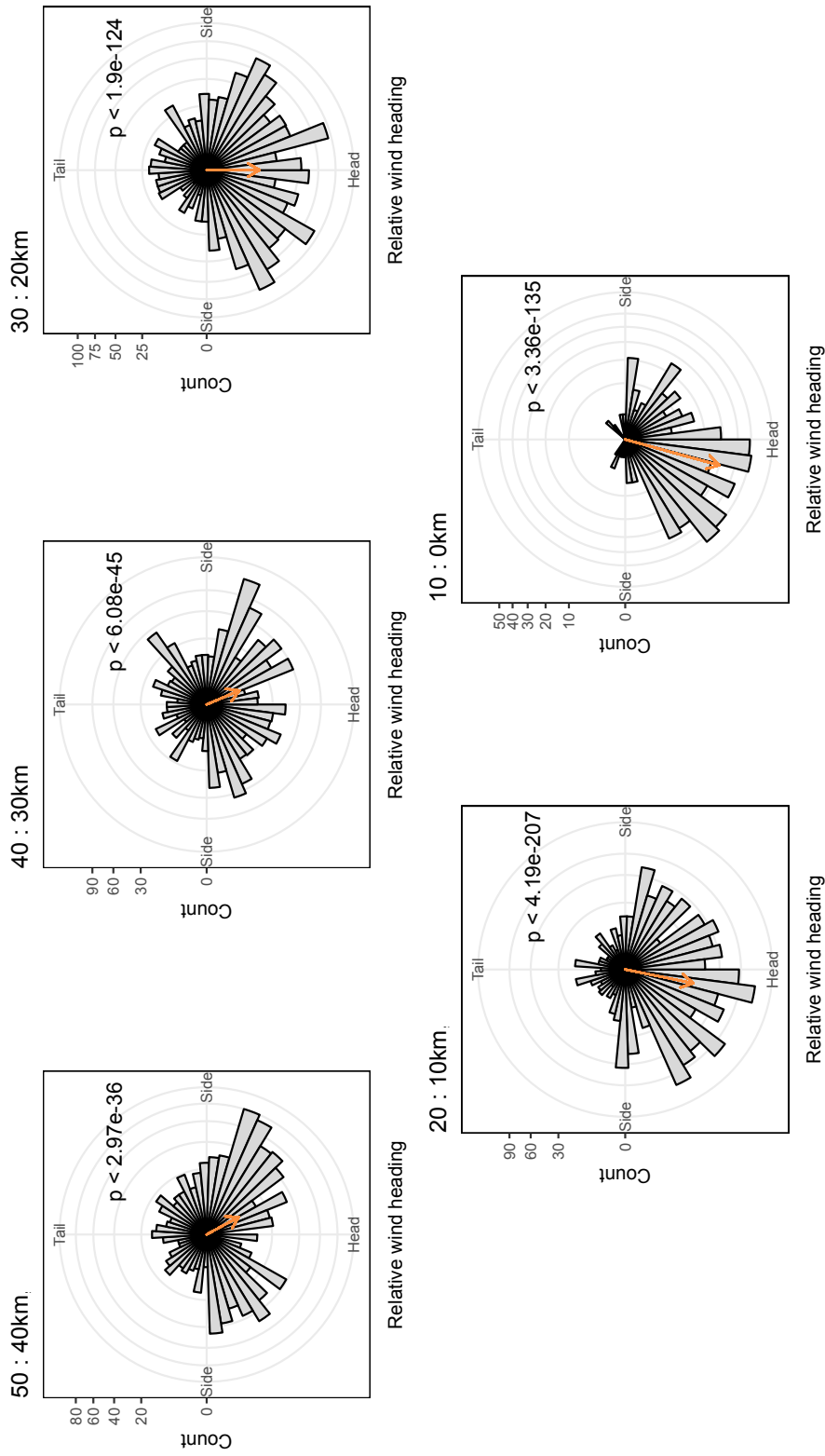
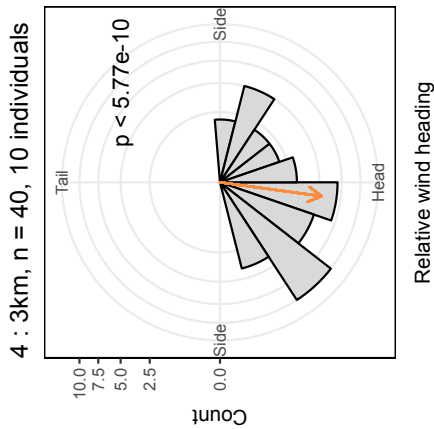
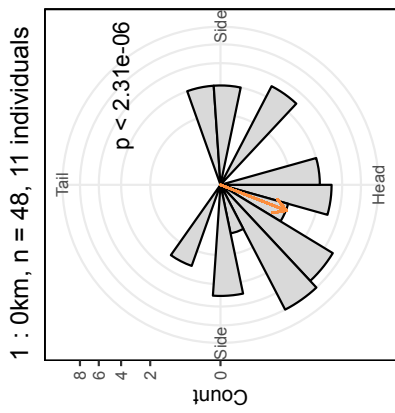
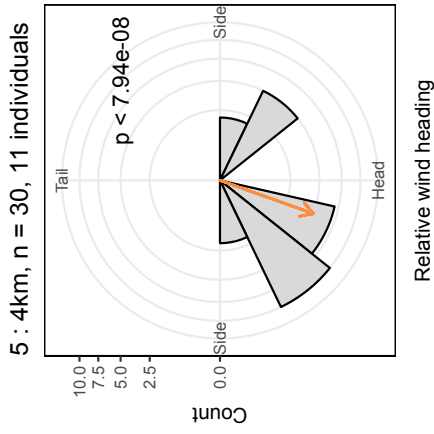
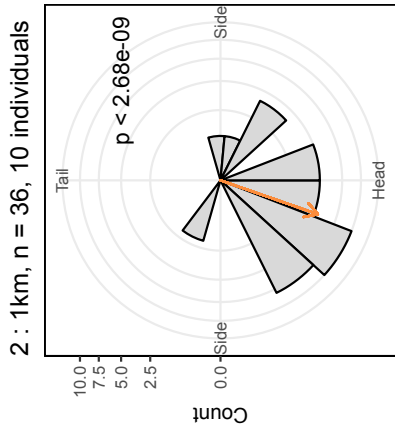
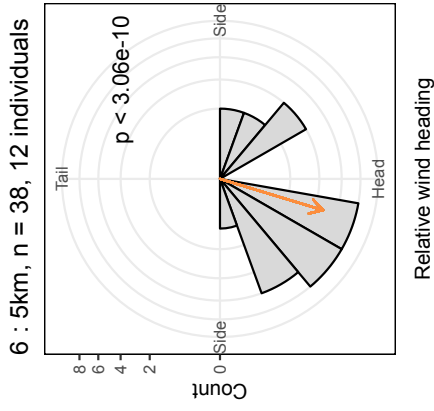
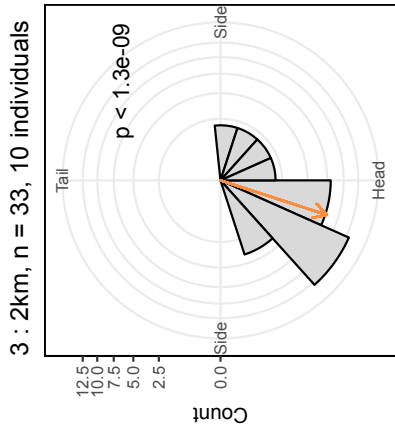


Figure 4.4: **Relative wind headings of 10 kilometre binned distances from next foraging spot.** Radii represent the square root of counts. The mean heading is represented by an orange arrow with radius equal to  $\bar{r} \times$  the square root of the maximum count.



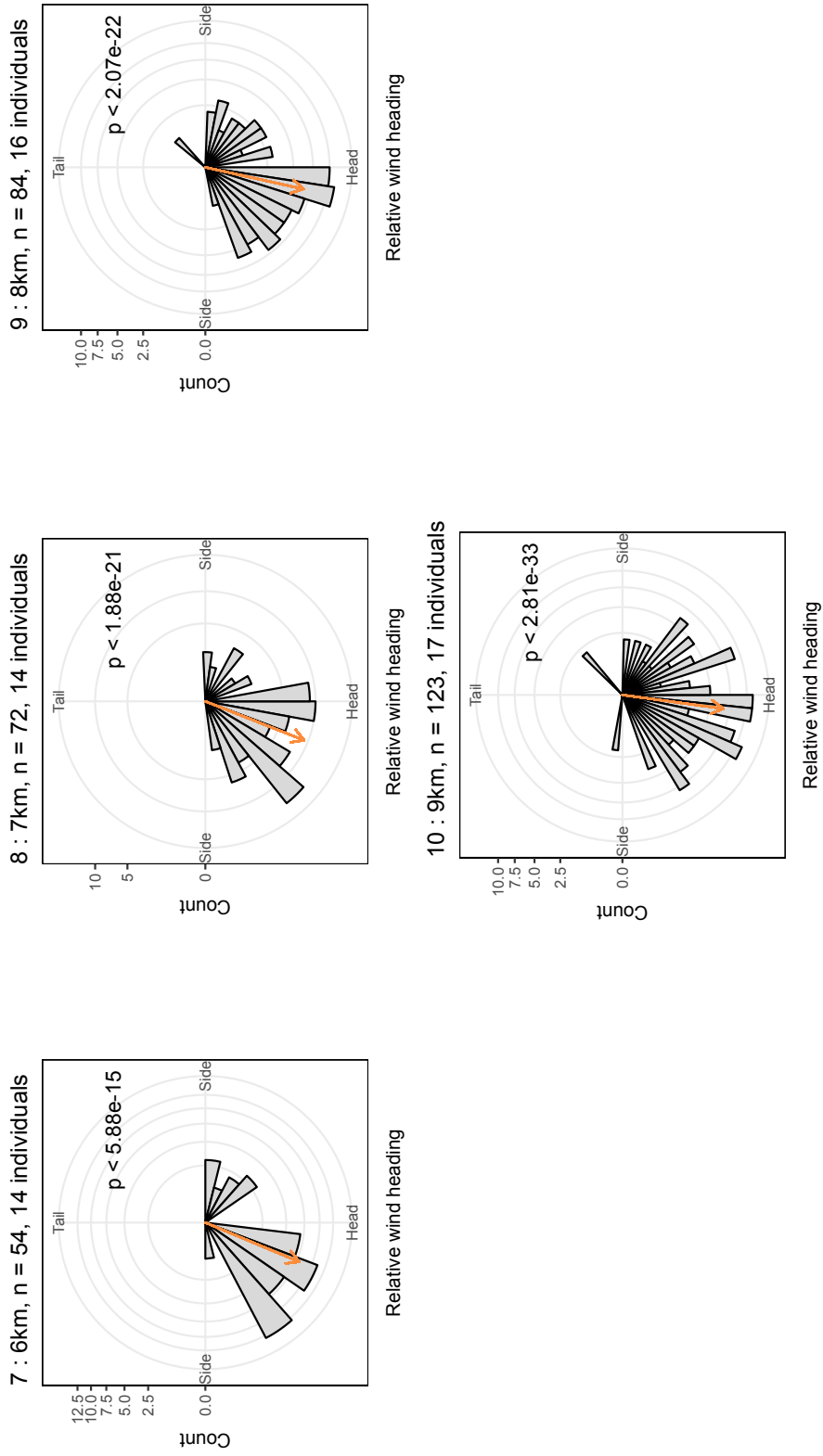
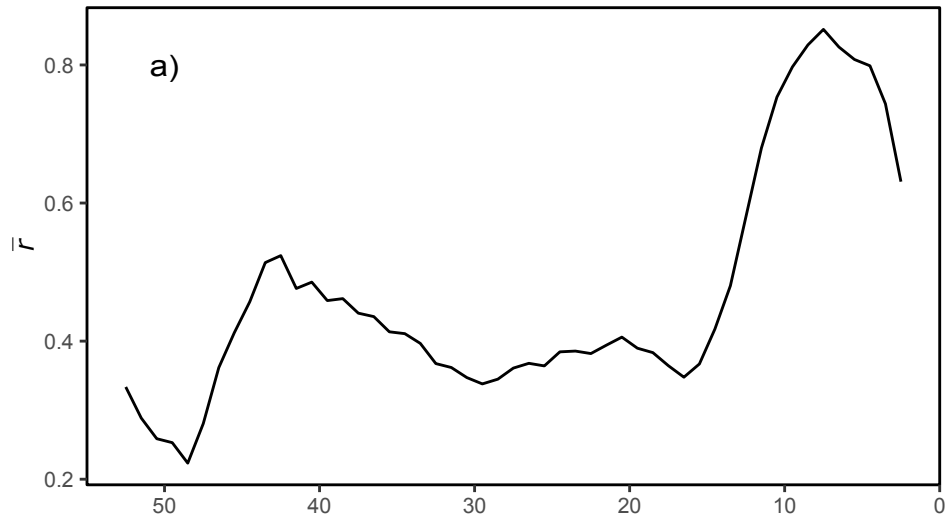
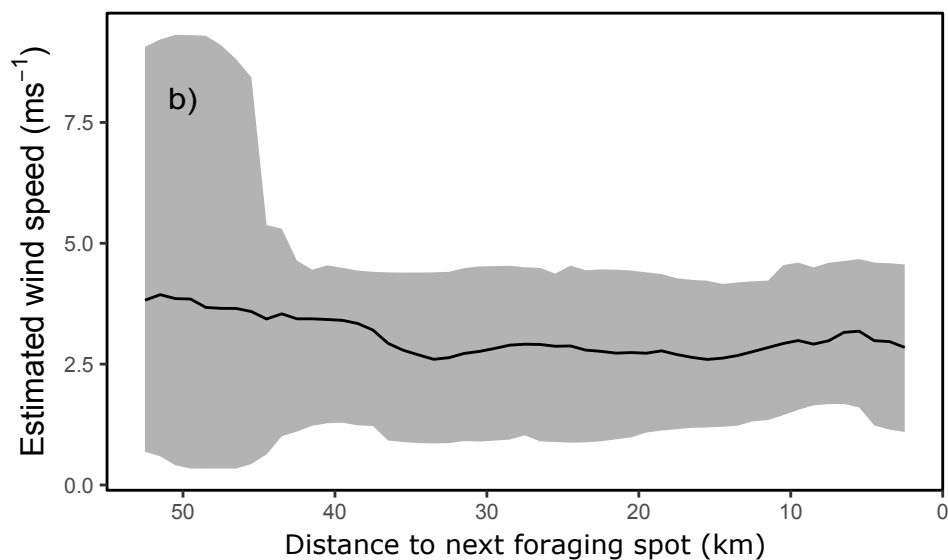


Figure 4.5 (*previous page*): **Relative wind headings of 1 kilometre binned distances from next foraging spot.** Radii represent the square root of counts. Where headings are not uniformly distributed (Hermans-Rasson test, p-value indicated on each plot), the mean heading is represented by an orange arrow with radius equal to  $\bar{r} \times$  the square root of the maximum count.



(a) Dispersals of relative wind headings calculated in 1 km moving windows as birds approach foraging spots.



(b) Mean estimated wind speeds with 10th and 90th percentile boundaries as birds approach foraging spots.

Figure 4.6: **Angular dispersal of relative wind and bird headings and estimated wind speeds as birds approach foraging spots.** The dispersal of relative wind headings (a) and wind speeds (b) of all birds as they approach foraging spots calculated in 1 km moving windows. The closer to 1  $\bar{r}$  is, the less dispersal. The grey area bounds are the 10th and 90th percentiles around the mean wind speed (solid line). Distance to the next foraging spot decreases from left to right.



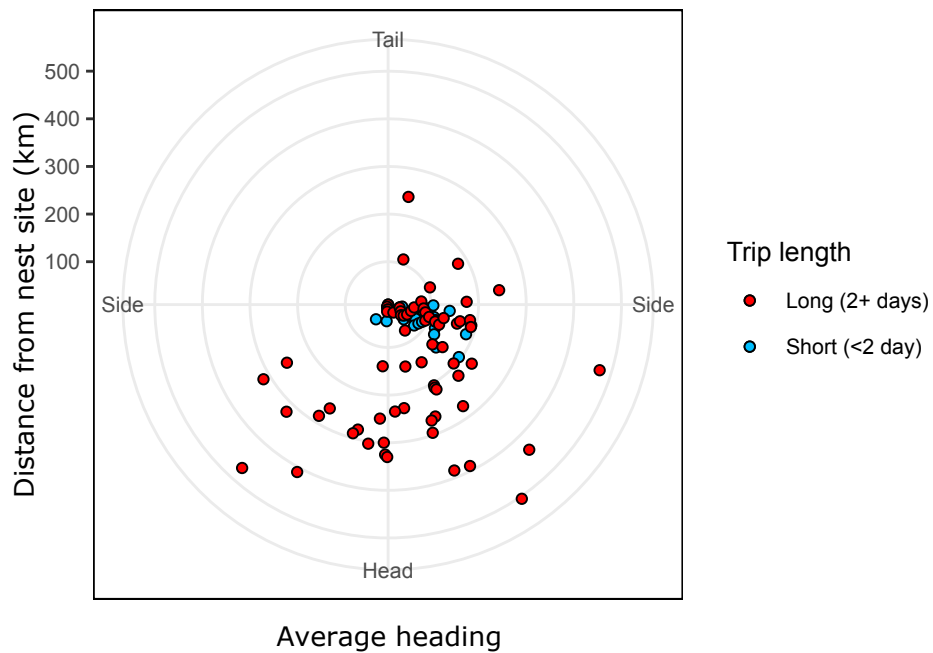


Figure 4.7: **Relative wind headings of shearwaters leaving the nest colony.** Mean relative wind headings for all shearwaters ( $n = 20$ ) leaving the nest colony on long (2+ days, red) or short ( $\leq 2$  days, blue) foraging trips. Radius records the distance from the nest colony. Data were tested for uniformity using the Hermans-Rasson test, and only those with significantly non-uniform ( $p < 0.01$ ) distributions are shown.

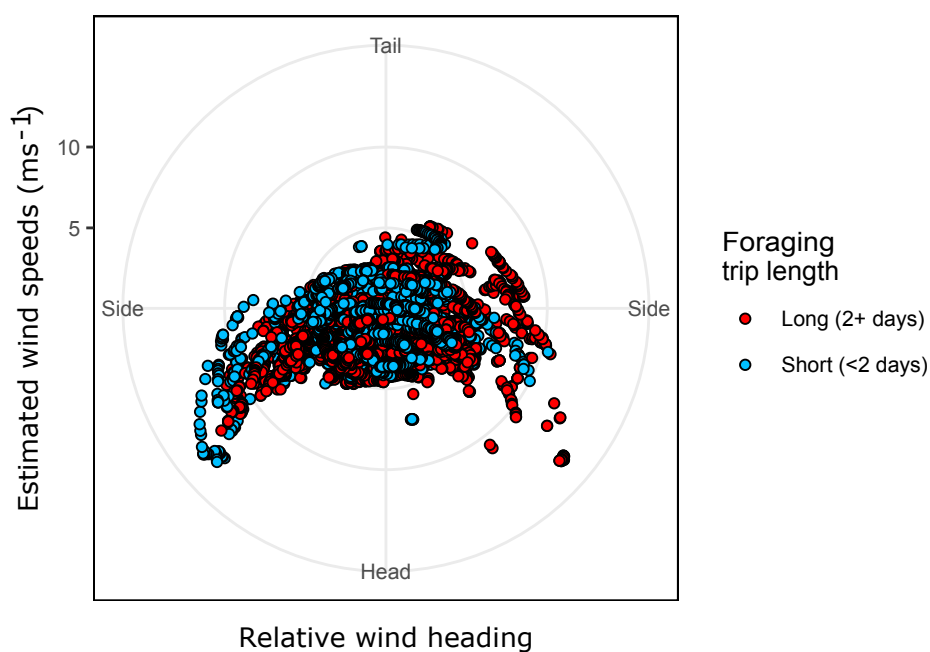


Figure 4.8: **Estimated wind speeds for relative wind headings.** Estimated wind speeds ( $\text{ms}^{-1}$ ) for relative wind headings calculated by subtracting estimated wind headings from average bird headings (averaged across a 1-minute moving window) across all individuals during long trips (2+ days duration) and within 100 km of the nest colony. At higher wind speeds, birds mostly flew in tail/sidewind conditions. The data shown is gathered from 17 individuals, 10 from 2018, 7 from 2019.

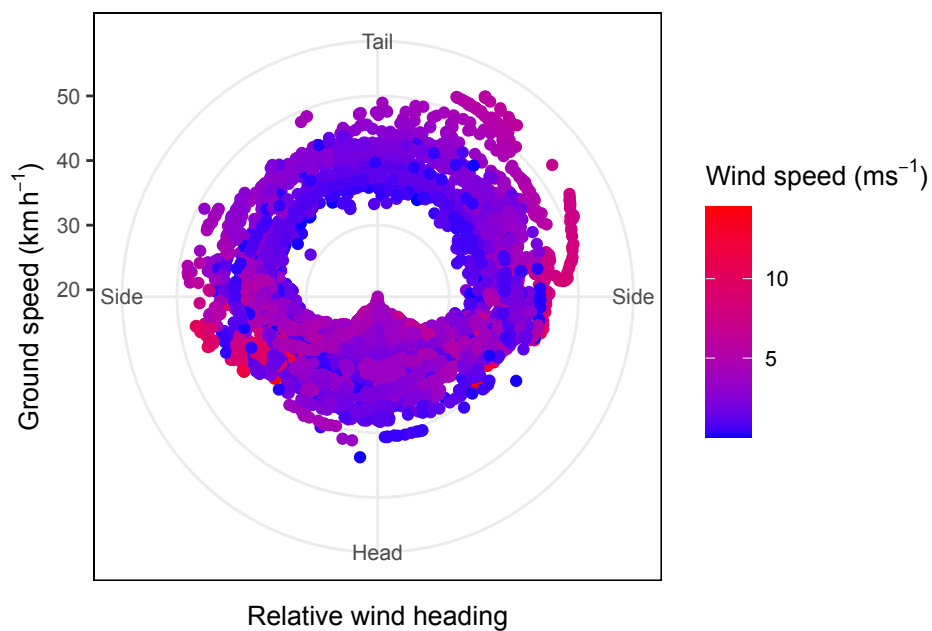


Figure 4.9: **Ground speeds across relative wind headings.** Travel speeds (km h<sup>-1</sup>) of winds shearwaters ( $n = 20$ ) experienced within 20 km to the next foraging spot. Estimated wind speeds (ms<sup>-1</sup>) are represented by colour. When experiencing higher wind speeds, birds flew in sidewinds. Birds flying in headwinds showed the lowest and widest range of travel speeds.

## General Discussion

The overall scope of this thesis was to examine foraging behaviour in streaked shearwaters, both the fine-scale details of foraging behaviours, and the search processes by which these birds locate foraging spots. In the previous chapters, fine-scale details of foraging behaviours of streaked shearwaters are described, and a behaviour detection method to classify behaviours from acceleration data was generated. The relationship between shearwaters and winds as they approach foraging spots was then investigated. This study combines new and previously developed techniques to make new inferences about the foraging ecology of streaked shearwaters. This work recorded and described two types of foraging behaviour by streaked shearwaters, along with a reliable detection method capable of identifying these behaviours and flight from acceleration signals. Using this method and a GPS-based wind estimation method, the transitional use of winds by streaked shearwaters along foraging trips is examined. Birds used sidewind conditions to efficiently travel from the nesting site to foraging grounds, then, while approaching a future foraging spot, shearwaters transitioned to less efficient headwinds that can carry odour signals from areas of high productivity to the bird, providing a likely foraging spot to direct the birds. This study adds details about streaked shearwater foraging, an analysis of wind vector calculation from seabird GPS records, and evidence supporting olfactory-based search behaviour during foraging trips.

## 5.1 Non-olfactory sources of navigation cues

Seabirds like streaked shearwaters living in ever-changing environments must use whatever tools are at their disposal to optimise their foraging strategies and increase their fitness. While much discussion has taken place regarding the role olfaction plays in streaked shearwater navigation and identification of profitable prey patch locations, there are considerations to make regarding other facets of shearwater ecology and how they inform navigation during foraging trips.

### 5.1.1 Oceanographic association

At large scales when searching for prey, seabirds should head towards more productive zones often associated with oceanographic or bathymetric features such as eddy formations or shelf breaks. Such associations have been well documented in multiple seabird species (Piatt et al., 2006; Weimerskirch, 2007; Yen et al., 2004). Prior studies on streaked shearwaters have shown similar associations with oceanographic features. Namely, shearwaters used eddy boundaries for foraging (Yoda et al., 2014), and showed a use of different sea surface temperatures (SSTs) depending on trip length (Matsumoto et al., 2012). This difference in SST was believed to be caused by the temperature preference of the Japanese anchovy, the main prey species of the shearwaters (Yamamoto et al., 2011). Association with sea surface height anomalies were also recorded in foraging streaked shearwaters (Yoda et al., 2014), as the birds foraged close to boundaries of anticyclonic eddies. The elevated water masses at these boundaries mean prey are more accessible at shallower depths, optimal for streaked shearwater foraging behaviour. Evidence, therefore, of these seabirds associating with oceanographic variables exists, however, birds detecting and using these conditions to direct travel remains difficult to prove.

### 5.1.2 Memory and social transfer

All experiments for this thesis took place during the breeding season, when shearwaters return to the nest colony. Annually returning to the same location, the seabirds may have built up knowledge of productive zones from previous years. The nest colony is in proximity to the highly productive Kuroshio-Oyashio system, which generates eddies streaked shearwaters have associated with (Yoda et al., 2014). It is therefore feasible that birds with experience of multiple breeding seasons retain memories of previously profitable regions, and so would have initial outward trajectories towards likely profitable zones without the need for real-time indication. Theoretical testing of memory effects on animal foraging behaviour have demonstrated the influence of memory on movement headings (Bracis et al., 2015), and indeed some seabirds have shown a greater reliance on memory cues when foraging, albeit either in contrast to expected Lévy search patterns or dependent on if the species is a specialist forager (Goyert, 2015; Regular et al., 2013). Memory can therefore provide a suitable starting point for navigation, and as all tagged individuals at Funakoshi-Ohshima island were veteran breeders, chosen for their likelihood to return to the nest to improve chances of tag recovery, these individuals may have memory banks that can determine initial flight headings from the island during foraging trips. Similarly, the transfer of information at the colony, such as following other conspecifics when leaving on foraging trips, shearwaters may decide their initial foraging headings by virtue of a visual cue to follow. Behaviour analysis in Chapter 2 revealed the shearwaters consistently foraged <10 km from the nest colony, typically early in the morning. This behaviour is explained as the birds foraging at nearby saury fisheries. Birds may have followed other shearwaters towards the fishing vessels, or relied on previous knowledge of this consistently available food source. However, feasible these social and memory cues are though, at closer proximities to prey, birds should navigate using more detailed real-time cues, such as vision.

Visual senses are of great importance to seabirds. Their visual capabilities have been long documented (Bang, 1971, 1960). Variability in optical designs is observed across species from different niches (terrestrial vs. marine, diurnal vs. nocturnal). Comparisons between common pigeon and Manx shearwater (*Puffinus puffinus*) eyes showed reduced visual acuity in the shearwater (Martin and de L. Brooke, 1991). These differences gave the indication of greater nocturnal behaviour in the shearwaters, though their semi-aquatic nature was also suggested as a source for these changes. Nocturnal foraging trends are also an indication of greater reliance on olfactory signals as birds must navigate using non-visual senses (Benvenuti et al., 1993; Buskirk and Nevitt, 2007). While nocturnal water landings have been recorded in streaked shearwaters (Matsumoto et al., 2012; Yamamoto et al., 2008), non-breeding streaked shearwaters recorded greater numbers of nocturnal water landings in concurrence with lunar cycles (Yamamoto et al., 2008), suggesting a reliance on this light source to allow use of visual cues. In Chapter 2, foraging behaviour of AxyTrek-tagged individuals was concentrated in the afternoons during long foraging trips and afternoons and mornings during short foraging trips with little to no nocturnal foraging recorded (Fig. 2.10). The short trips are intended for provisioning the chick, and so are time-constrained, which can explain the lack of nocturnal foraging, however, longer duration self-provisioning trips do not have this requirement, so nocturnal foraging is feasible within these trips. Additionally, the previously mentioned fishing vessel-associated foraging in the early mornings before sunrise may well have been prompted by visual cues, either from the presence of seabirds rafting or the light of the fishing vessel which is easily visible from the nest colony. Therefore, it seems shearwaters preferentially foraged during daylight hours both during self- and chick-provisioning foraging trips, indicative of greater visual reliance. Evidence is therefore present for reliance on visual and memory-based navigation, however, across an entire foraging trip, both these sensory functions would be defunct at either the largest (initially

leaving the colony) and smallest (identification and capture of prey) spatial scales.

## 5.2 Odours as an intermediate scale search tool

Search behaviour in animals is often considered on a multitude of scales, from navigation covering the largest distances animals travel, to the minute turns and pursuits when chasing prey. Olfactory navigation has proven a difficult concept to explain as, unlike visual stimuli or memories of known foraging grounds, odour can be ephemeral and heavily reliant on atmospheric conditions. Within the concept of an odour map, fluctuations in concentrations of composing odours must be considered. It is unrealistic that a sufficient odour concentration detectable by birds will be maintained during the course of a foraging trip, and so seabirds must constantly adapt in response to the changing sensory inputs they receive. Significant evidence exists that supports birds using a multitude of olfactory signals to build an odour map to aid in navigation, particularly in open oceans (Wallraff, 2004; Wallraff and Andreae, 2000). This concept was explored in Scopoli's, Cory's (*Calonectris borealis*), and Cape Verde (*Calonectris edwardsii*) shearwaters (Reynolds et al., 2015), with the concept of an intermittent odour map caused by these variations in odour concentrations. This study, and its successor (Abolaffio et al., 2018) were concerned with the oceanic navigation of seabirds by olfactory means throughout entire foraging trips. In relation to precise foraging behaviour (i.e. homing in on a foraging spot within some tens of kilometres), studies have provided evidence of the capability of Procellariiformes to detect small concentrations of odours in the atmosphere and demonstrated their attraction to an array of smells that occur naturally in the oceans. However, as yet, little direct evidence of birds using their capabilities to home in on foraging spots occurs in the scientific literature. The study in Chapter 4 is focussed specifically on smaller scale search behaviour, specifically those beyond visual range and smaller than overall navigation. The combination of Chapters 2



and 4 provides a means to do so, building on preceding study of seabird sensory ecology and navigation, along with the estimation of local conditions described in Chapter 3. These studies therefore sit as an intermediary between the direct evidence of seabirds attracted to odour slicks and evidence of their flight patterns exhibiting olfactory-navigation characteristics. Olfactory search behaviour can also act as an intermediate state prior to transitioning to the use of visual cues.

The concept built from results of the studies in Chapters 2 and 4 is one of streaked shearwaters transitioning to an olfactory-based navigation system following initial travel using optimal sidewinds. Previous evidence suggests visual effects are important to streaked shearwaters when capturing prey (Yamamoto et al., 2008), as do the hourly activity proportions in Chapter 2. However, association with oceanographic conditions suggests birds are capable of detecting or predicting foraging likelihood through some non-visual and non-memory based means. Streaked shearwaters from two nesting sites were observed associating with shifts in sea surface temperatures and overlap in foraging areas between both nesting sites was small (Yamamoto et al., 2011), suggesting both the capability to detect foraging through non-visual means, and avoidance of intraspecies conflicts at foraging grounds. This strategy suggests reliance on olfaction-based navigation as shearwaters could find foraging spots without other shearwaters being present, meaning both greater potential to find prey in changing conditions and less potential competition from conspecifics.

### **5.3 Study considerations**

Commonplace with most biologging studies is the restriction of a small sample size. This certainly is the case within this study, with relatively few tagging opportunities and a sample made up of unequal numbers of males and females. Sex-specific foraging differences have been

observed in streaked shearwaters (Yamamoto et al., 2011), however, this difference has been attributed to the pre-laying period, not chick-rearing, and so may not be of so great a concern for this work. The estimation of wind vectors is conditional on the original distribution method study's methodology, and the proportion of GPS tracks for which vectors were calculable was small. Collection of more data and application of an updated wind estimation method could both improve the reliability of the wind estimation method and allow more comparison of near-foraging wind usage. Understanding the cause for the underperformance of the curve method may allow shearwaters' relative wind conditions to be understood for a far greater proportion of foraging trips, and so testing for presence of behavioural transitions relating to olfactory vs. visual reliance may be possible.

### **5.3.1 Contributions of this study and further study**

The need for the development of a new behaviour detection algorithm in Chapter 2 was due to limited capabilities of traditional detection methods to determine foraging behaviours in the shallow-diving streaked shearwaters. This limitation reduces the scope for ecological studies involving streaked shearwater foraging behaviours, and with the developed algorithm, detailed analyses of how shearwaters search for and capture prey was possible, leading to the olfaction-based study from Chapter 4. Olfactory studies have thus far largely focussed on southern oceans (Dell'Araccia et al., 2014; Nevitt, 2000; Nevitt and RR, 1999; Nevitt and Bonadonna, 2005). These Southern Ocean studies, primarily Antarctic, took place in waters with the highest primary production and DMS emissions. Rates of DMS emissions decrease with latitude, particularly so in the Northern Hemisphere (Belviso et al., 2003; Kettle and Andreae, 2000) so birds living further from the poles may rely less on olfactory senses to navigate. Similarly, with more complex conditions around sea basins and closed seas, localised variation in responses

to odourants occurs across species with large geographic variation. Recent studies have similarly focussed on Atlantic and/or Mediterranean species (Bastos et al., 2020; Gagliardo et al., 2013; Padget et al., 2019). Within the context of other studies examining olfaction in Procellariiformes, this study adds a novel species and environment, namely streaked shearwaters and the Oyashio-Kurashio region. Given the variety of foraging behaviours and strategies in Procellariiformes (Burger, 2001), it is important to add details of foraging strategies in other species found across the globe. Seabirds adapted to their local environments may show differences in their behaviours while still reliant on the same underlying basis (for example, using memorised maps to determine initial travel headings). Collection of evidence for or against olfactory navigation is necessary to better understand how seabirds across the globe navigate in different conditions.

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