The Foraging Behaviour of Wandering Albatrosses

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Abstract:

Wandering albatrosses (*Diomedea exulans*) are amongst the largest seabirds in the world. They have a circumpolar distribution and mainly feed on pelagic squid, which are highly mobile, possess well-developed senses and mostly dwell at great depths where they are considered inaccessible to wandering albatrosses. How these birds find and capture these elusive, deep-sea squid has been extensively debated in the literature. This research aims to investigate the foraging behaviour of chick-brooding wandering albatrosses, with particular focus on the diel partitioning of foraging behaviours and to examine the extent of anecdotally reported 'circling behaviour', where they spin on the surface of the water, which may be linked to foraging. To do this, high-resolution (40 Hz) data was collected using tags recording tri-axial acceleration and magnetic field intensity sensors attached to 24 individual wandering albatrosses breeding on Marion Island between 2007 and 2018. Individual foraging trips were found to have lasted between one and seven days across all the birds. Sixty-two percent of this total duration consisted of flying and 38% consisted of sitting on the surface of the water. Of the flight time, 47% occurred during the day time and 53% during the night time while 54% of the total time sitting on the surface of the water occurred during the day time and 46% occurred at night. Over a 24-hour period, the birds took off from the water surface to engage in flight a mean of 8.4 times during daylight and 7.2 times at night, with no significant difference between day and night. This accords with conventional belief that these birds locate their sparsely-distributed prey by searching during their flights over large distances, pitching down on the water periodically to exploit surface-located food. Long periods on the water were evident, and circling behaviour at this time was observed seven times in four individuals (17%). The duration of these bouts ranged from 4-64 minutes (x=32, SD=24) with all birds commencing circling during periods believed to be darkness/semi darkness. I suggest that the circling creates bioluminescence that attracts squid. These findings contribute to future research by demonstrating a novel foraging strategy as a behavioural response to external environmental conditions. This knowledge is becoming increasingly important with the growing anthropogenic pressures, particularly in the Southern Ocean.

Declarations and Statements:

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed............[redacted] ....

Date....................27/06/2023..

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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I hereby give consent for my thesis, if accepted, to be available for electronic sharing

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The University’s ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

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Contents

Acknowledgements:

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Tables and figures:

Definitions and Abbreviations:

Abbreviation	Definition
Vu	Vulnerable
IUCN	International Union for Conservation of Nature
MPA	Marine Protected Area
VHF	Very High Frequency
IBA	Important Bird Area
RTC	Real Time Clock
DDMT	Daily Diary Multiple Trace
EAT	East Africa Time
GMT	Greenwich Mean Time
BST	British Summer Time
DVM	Diel Vertical Migration
SST	Sea Surface Temperature
Chl-a	chlorophyll
SWIR	Southwest Indian Ridge
ABFZ	Andrew Bain Fracture Zone
ACC	Antarctic Circumpolar Current
APF	Antarctic Polar Front
SSH	Sea Surface Height

Introduction:

In 1758, the wandering albatross (*Diomedea exulans*) was formally introduced to Western science when the Swedish taxonomist Carl Linnaeus gave the seabird its name. It is named for the Greek legend Diomedea, one of the leaders in the Trojan war whose companions were turned into birds by Aphrodite [1] while exulans is Latin for 'exile' or 'wanderer' [2]. It is one of the two members of the genus Diomedea (the great albatrosses) from the order Procellariiformes and it has a wide-ranging circumpolar distribution [3,4]. It is one of the largest (8-12 kg), and most studied seabirds in the world and it has the longest wingspan of any living bird, typically ranging from 2.5 to 3.5 m [5–7]. Like most procellariform species, wandering albatross are well known to fly over the ocean in long, low-energy, looping, gliding flights, mostly without flapping their wings [8] . This is known as dynamic soaring, which is a flying technique where energy from the wind gradient close to the surface of the water is utilised to sustain speed and height [9]. This is achieved when the albatross moves across the wind layer while heading upwind and then it turns to head downwind crossing the wind layer again, the crossing between the air masses of different velocity providing the energy for sustained soaring [9]. Wandering albatrosses travel on these long looping flights [10] over both neritic waters (depths of 2000 m or less) and oceanic waters (2000 m or more) [11,12] and throughout their approximate 50-year lifetime, an individual is estimated to travel 8.5 million km [13]. Wandering albatrosses have a long breeding season, they lay a single egg over a period of five weeks during December and January, which then typically hatches in March, with the young fledging the following December [14]. The entire period from the arrival of adults at the breeding colony to their last visit to their chick spans approximately 383 days, with the chick-rearing period alone taking approximately 278 days [15]. The slow growth rate of the chicks and long rearing time is reported to be linked with the rate at which adults can provision the chicks with food, primarily elusive and rare squid (see below). As a result of this, wandering albatrosses are considered to breed biannually and this, together with rising high mortality rates [16,17], has led to them being classified as 'Vulnerable' (Vu) by the IUCN Red List of Threatened Species: In 2018, the species was first classified as vulnerable with populations today continuing to decline [14] despite short periods of stability. It is estimated that their global populations will decline a further 30% over the next 70 years [14,18]. In 1998, the total annual breeding population was estimated at 8500 pairs, which is equivalent to 28000 adult individuals, with the current total annual breeding population estimated at 6000 pairs, equivalent to 20100 adult individuals [14]. In 2018, the largest breeding population, estimated at 1900 pairs, was found on Marion Island [14], part of the Prince Edwards Islands in South Africa.

Marion Island.

Marion island (46°54'S,37°45'E) is an important breeding ground for millions of seabirds including the four other species of Procellariforms; the grey-headed albatross (*Thalassarche chrysostoma*), the northern giant petrel (*Macronectes halli*), the southern giant petrel (*Macronectes giganteus*) and the white-chinned petrel (*Procellaria aequinoctialis*) [19,20]. The volcanic island is thought to be less than one million years old [21] and has never been connected to a continent which gives it its own unique biota and bathymetry [20]. It is located in the Southern Ocean and regularly experiences strong westerly winds, nicknamed by sailors the roaring forties with an average velocity of 32 km [22]. The island has an oceanic climate with temperatures between 5° C and 10.5° C in summer and between 1° C and 6° C during the winter [22]. This isolation, variable bathymetry, low seasonal fluctuations and strong winds make it an ideal place to raise chicks for a wind-exploiting seabird like the wandering albatross [23]. However, the energetic cost of reproduction is considered high in most pelagic seabirds due to the separation of their breeding colonies and their foraging grounds which, in the case of wandering albatrosses, can be many hundreds of kilometres across the open ocean [24,25] to find their sparse and patchy prey resources [26]. Wandering albatrosses are well adapted to exploit the regions frequently occurring strong westerly winds: The birds use these in their energetically low-cost dynamic soaring flight, where they optimize their movements with wind direction to search for prey on the sea surface [27–29].

The Diet of Wandering Albatross and why it is important.

Studies have shown that wandering albatrosses mainly feed on pelagic squid (*Teuthida*), which are highly mobile animals with well-developed senses and dwell deep (as much as 6212 m) within the depths of the ocean [30–32]. Despite being well adapted for long-ranging flights, wandering albatrosses are generally considered physically unsuited for diving to depths >1 m [33] and so are considered to be a surface-seizing species [34]. How they find and capture these elusive, deep-sea squid is a conundrum over which multiple authors have debated over the years, not least because the knowledge is becoming increasingly important with growing anthropogenic pressures. One of the biggest threats comes from the interactions of wandering albatrosses with long-line fishing vessels in the sub-Antarctic waters as well as in areas further north because the prime long-line fishing areas for bluefin tuna (*Thunnus maccoyii)* and

Patagonian toothfish (*Dissostichus eleginoides*) overlap substantially with wandering albatross foraging grounds [35]. As these pressures increase, the need to understand the daily movements, behaviours, motivations and the distribution of both albatrosses and their prey also increases. This knowledge is particularly important when developing and maintaining effective conservation and management strategies such as Marine Protected Areas (MPAs), which will not only protect wandering albatrosses but aid in rebuilding the local fish stocks [36,37].

Monitoring foraging behaviours.

Accurate data on the foraging behaviour of wandering albatrosses requires long-term monitoring of their movements during the full extent of their foraging trips. Direct observation is not possible due to the remoteness of their foraging grounds so a method often used to study and quantify their behaviour uses 'bio-loggers'. These are sophisticated tags that can be attached to wild animals to record and store data pertaining to the animals' behaviour, physiology and ecology [38,39]. Gerald Kooyman attached the first biologging tag to a free-living weddell seal (*Leptonychotes weddelli*) in 1965, and since then biologging technology and use has advanced dramatically [40]. Before 1990, conventional Very-High Frequency (VHF) radio tags, where data were transmitted, were the norm. However, this came with many limitations in location precision which affected the quality and accuracy of the data collected [41]. The creation of a tag called the "Daily Diary", which incorporated a tri-axial accelerometer, magnetometer, thermometer and a pressure gauge together in one device, all of which recorded at rates of 8-40 Hz helped in overcoming the previous limitations [41]. These devices are now becoming smaller, more powerful, affordable and battery-efficient, and they are currently being used tag animals as small as bats and it is even thought that sometime in the future it will even be possible to tag even the smallest of mammals or birds [7,27,40,42].

Daily diary tags.

The particular value of 'Daily Diary-type' tags is that they provide detailed information on animal behaviour. The majority of behaviours can be defined *via* movement and posture patterns using the tri-axial accelerometers [43] while magnetometers provide data on animal heading and body rotations [44]. Indeed, consideration of the data from Daily Diary tags allows researchers to determine the timings, extent, intensity and energetic costs of defined behaviours [45]. To date, these tags have been used to get movement data on a wide range of species [46] such as the domestic cat (*Felis catus*) [47], domestic dogs (*Canis familiaris)* [48], Andean condors (*Vultur gryphus)* and humans *(Homo sapiens)*[48] as well as marine animals such as tiger sharks (*Galeocerdo cuvier*) [44] and whitetip reef sharks (*Triaenodon obesus*) [49]. Wandering albatrosses are an excellent candidate for biologging investigations as they are long-lived, far-ranging, large-sized, have high site fidelity and do not show much fear towards humans [7,27]. Indeed, many researchers have taken advantage of this and used wandering albatross movement data as a proxy for other far-ranging seabirds [50]. According to previous studies, most wandering albatrosses engage in three major activities while foraging; flying, sitting on the water's surface and limited diving [51] and these activities have gained considerable attention in the academic literature. Many studies have focused on the energy used to forage [24,52–54], the composition of prey [7,55–57], wind driven effects on dynamic soaring [8,58], flight types [8,59,60] and the interactions of wandering albatrosses with fishing activity [35,61–64]. There are also several studies on the partitioning of albatross foraging activity during the day and night [65][66], including Phalan *et al* [10] and Pajot et al (2021) [67], who used satellite transmitters, GPS loggers and wet/dry activity loggers on 4 sympatric albatross species including the wandering albatross, to compare at sea differences in foraging activity by day and night. They found that brooding wandering albatross spent more time flying and more time landing and taking off from the surface of the sea in the day time and that they spent less time flying and more time sitting on the surface of the sea at night time. This data is especially valuable as some commercial fishing vessels mainly operate during the night by using lights to attract deep-sea squid [58,68–70] which could have a negative impact on the surface-seizing wandering albatrosses by increasing the risk of bycatch. There is a large body of literature on the main foraging behaviours observed in wandering albatrosses [10,13,65,66,71–74] and the general consensus is that when foraging, wandering albatrosses engage in two main behaviours; aerial searching and sitting on the water's surface and waiting [75]. However, given the depth distribution and high mobility of their principal prey, squid, it is unclear how either of these techniques might secure food. Given the vulnerable status of wandering albatrosses, any information that might clarify foraging techniques could be very valuable, especially given that conditions in the oceans are changing so fast as a result of man [76,77].

Aim.

The aim of this project is to determine how wandering albatrosses catch their prey. In particular, there is anecdotal evidence that wandering albatrosses might engage in a novel foraging behaviour described as ‘circling’ while sitting on the water’s surface. This project examines this circling using high resolution data acquired by Daily Diaries to examine the occurrence of circling behaviour and the external conditions associated with it. Specifically, the project will investigate whether; (i) there is any difference in the wandering albatrosses’ movements and general foraging behaviours between the day and night, (ii) they display circling behaviour on the surface of the water during a foraging trip, (iii) whether circling, if it occurs, is associated with daytime or night time foraging, and (iv) there is any indication of feeding behaviour associated with such circling. This investigation will hopefully help us to understand whether circling behaviour, if it occurs, is associated with foraging. This study focused on chick-brooding individuals, which have high energy requirements due to the need to provision for their young as well as maintaining their own requirements [24,78,79].

Methods:

Overview:

In order to determine if wandering albatrosses circle (spin) on the sea surface at night and to evaluate their foraging behaviour in general, data was collected using animal-attached tags used on individuals breeding in the Southern Ocean. Due to the Covid 19 pandemic and subsequent lockdowns I was personally unable to physically take part in the attachment process.

Data collection:

Location of tag deployment:

Tags were deployed on birds breeding at Marion Island in the southern Indian Ocean. Marion Island (46°54′S, 37°45′E) is one of two uninhabited islands in the sub-Antarctic Indian Ocean, collectively called the Prince Edwards Islands, and is part of South Africa (Figure 1) [80,81]. The island is 25 km long and 17 km wide and consists of 72 km of coastline and up to 490 m high [82]. The island has a tundra climate with strong regional north-westerly winds all year round [8,83]. The island was declared a Special Nature Reserve in 2003 and in 2013 the South African government declared 180,000 km^2 of the oceanic water surrounding the island a Marine Protected Area [18,37,83]. The Prince Edward Islands have also been designated an Important Bird Area (IBA) due to the many species of birds utilising the high cliffs and flat areas to breed, comprising an estimated 5 million breeding seabirds, including the wandering albatross [18]. The wandering albatross colonies where tagging occurred were located on the East coast of the island, at Skua Bay near the research base.

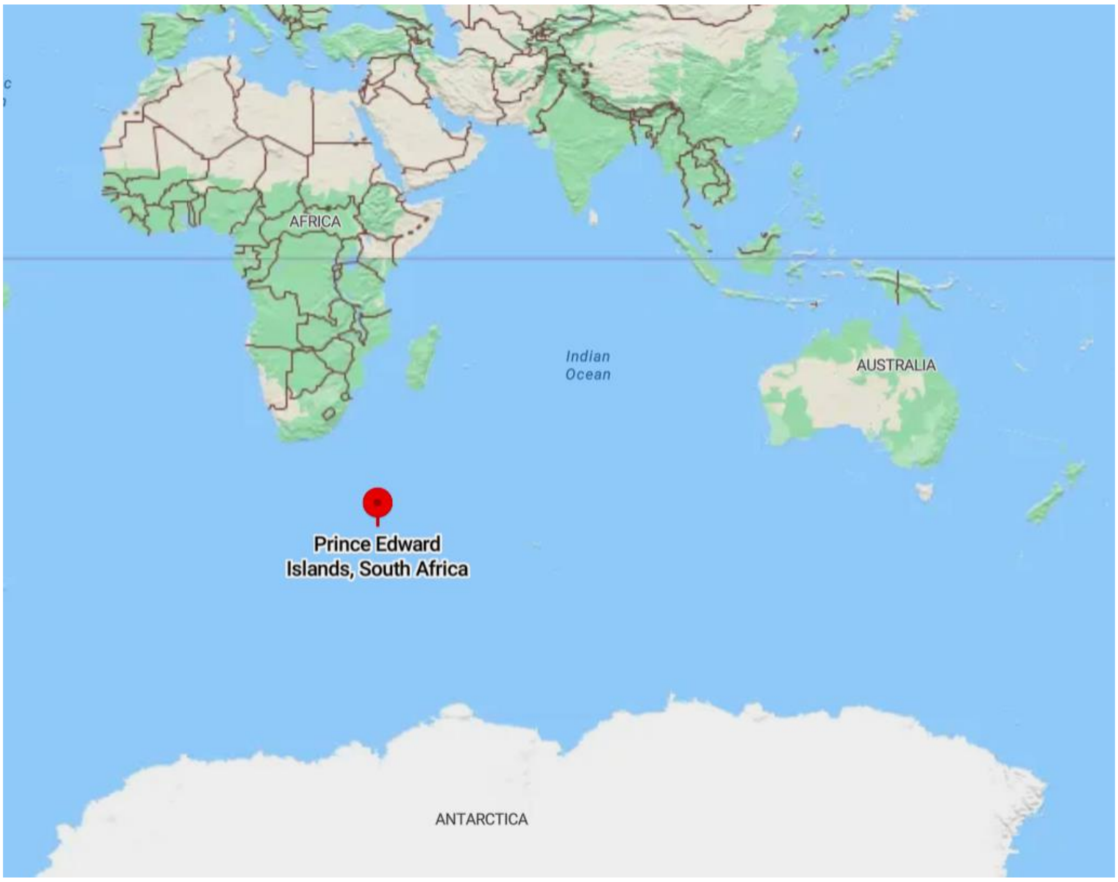
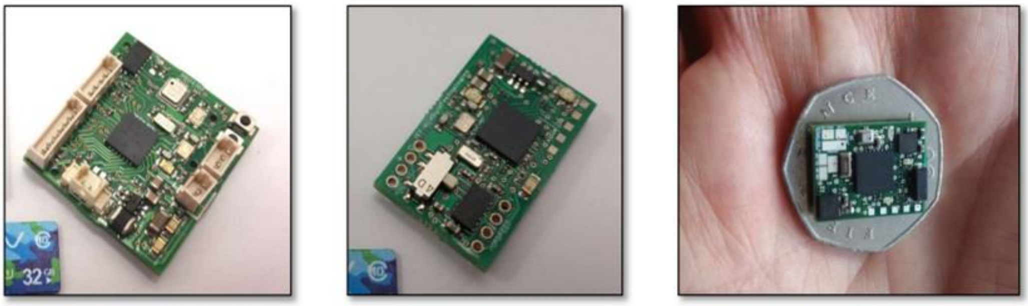


Figure 1. Location of the sub-Antarctic Prince Edward Islands, South Africa. The islands consist of two islands, Prince Edwards Island and the larger Marion Island. Data was collected from pairs brooding chicks from March 2007 to February 2018 from the colonies on Marion Island (46°54'S, 37°45'E). The islands are surrounded by the Southern Ocean. Map from Google Maps [84].

<u>Device for data collection:</u>

In order to qualify and quantify the albatrosses' movements and behaviours, bio-logging devices called 'Daily Diary' devices were used [85]. These devices had maximum dimensions of 42 x 26 x 10 mm with a 380 mAh battery, weighing 77-135 g (Figure 2) and were attached to the backs of the birds with waterproof Tesa tape [86]. The combined weight of the device (including housing, attachment tape and battery) was well below 3% of the body mass for adult wandering albatross (approx. 8.4-10.3 kg [87]). The devices contained an on-board Real-Time Clock (RTC) [accurate to better than 1.75 s drift per day, a light sensor, a tri-axial (orthogonal) accelerometer (measurement range -16 *g* to +16 *g*), a tri-axial magnetometer, a barometric pressure sensor, a temperature sensor and a MicroSD card for data storage. During deployment, data was collected from all channels at 40 Hz with 16-bit resolution.



Standard / original Daily Diary with connectors for battery/external sensors. Additional light sensor

Elongated Daily Diary with no connectors, power switch on/off. No light sensor. Battery / external sensors soldered to board.

Thumb Daily Diary with no connectors, no power switch on/off. No light sensor. Battery soldered to the board.

Figure 2. Daily Diary devices used to qualify and quantify the albatross's movements and behaviours. Devices were developed by Wildbyte technologies and the pictures were sourced from [85].

Data collection:

Daily Diary tags were attached to 28 wandering albatrosses (both sexes) which were brooding chicks from February 2007 to March 2018. Unfortunately, four of the tags were corrupt and unreadable so a total of 24 tags were used. All devices to be deployed were calibrated for time and in order to calibrate the responses of the magnetometers to the magnetic field intensity and so that correction for hard iron and soft iron distortions could be made before analysis [88].

Calibration for time took place by leaving the tags immobile for a period (typically > 1 minute) before, at precisely prescribed times, suddenly moving them sequentially back and forth along axes that represented the three orthogonal axes recorded by the accelerometers, and which were to become the heave, surge and sway of the birds after attachment (see below). On recovery of the tags, the sudden movement of these calibration manoeuvres could be found in the data so that the time could be set and so that the accelerometer axes could be properly ascribed to the heave, surge and sway axes with respect to the albatrosses.

To calibrate the magnetometers for the magnetic field, the tags were rotated in a figure of eight by the researchers who, at the same time, slowly rotated his/her heading, moving from facing

North, clockwise round the full 360º heading until he/she faced North again. Full details of this procedure are given in [88].

Before attachment, the colony was closely monitored in order to identify individuals returning from a foraging trip and so were known to be about to relieve their partner at the nest. Once a returning bird was spotted, the partner was removed from the nest and fitted with the Daily Diary tag. This process ensured that a full foraging trip was likely to be represented in the tag data. The devices were then attached to the underside of two central feathers in the tails of the albatrosses using waterproof tape following recommendations made by [89]. This tail attachment method was chosen because the tail feathers are strong, long and it is typically well tolerated by the bird meaning the device could be securely attached with no obvious detrimental effects [90]. Devices were so orientated that the three orthogonal acceleration axes represented the main body axes of the birds (Figure 3).

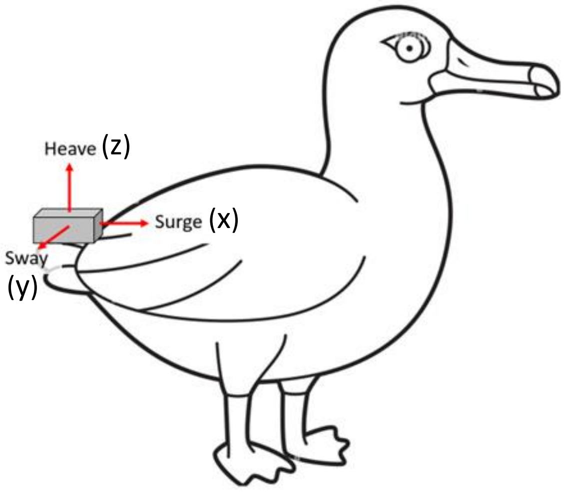


Figure 3. Schematic diagram of the attachment of a Daily Diary device to a wandering albatross on the tail showing how the main orthogonal acceleration axes recorded by the tag represented the main body axes of the bird: The surge was the longitudinal axis; the sway was the lateral axis and the heave was the dorso-ventral axis.

In order to minimise distress and interference, the attachment process was completed in under 15 minutes. The tagged birds were then left to forage normally, a process that typically lasted a number of days, once the individual returned back to the nest, the devices were immediately removed. The use of tape to secure the tags meant that, once the tape and device has been removed, there was no residue left on the feathers or any sign that the birds had been tagged. This research was approved by the University of Cape Town's Science Faculty Animal Ethics Committee and permission to tag the wandering albatross on Marion Island was granted by the Prince Edward Islands' Management Committee [86]. Logistical and deployment assistance was provided by the Department of Environmental Affairs and Tourism *via* the South African National Antarctic Programme.

Data Analysis:

All data collected from the Daily Diary tags was uploaded and analysed using custom-built software called DDMT, Daily Diary Multiple Trace [91], which allows 2D and 3D visualisation of motion, temperature, direction, GPS and barometric pressure data. In its most basic format, the program shows the data from all sensors as a series of lines against a (x-axis) time base, the length of which displayed can be varied by the user (Figure 4).

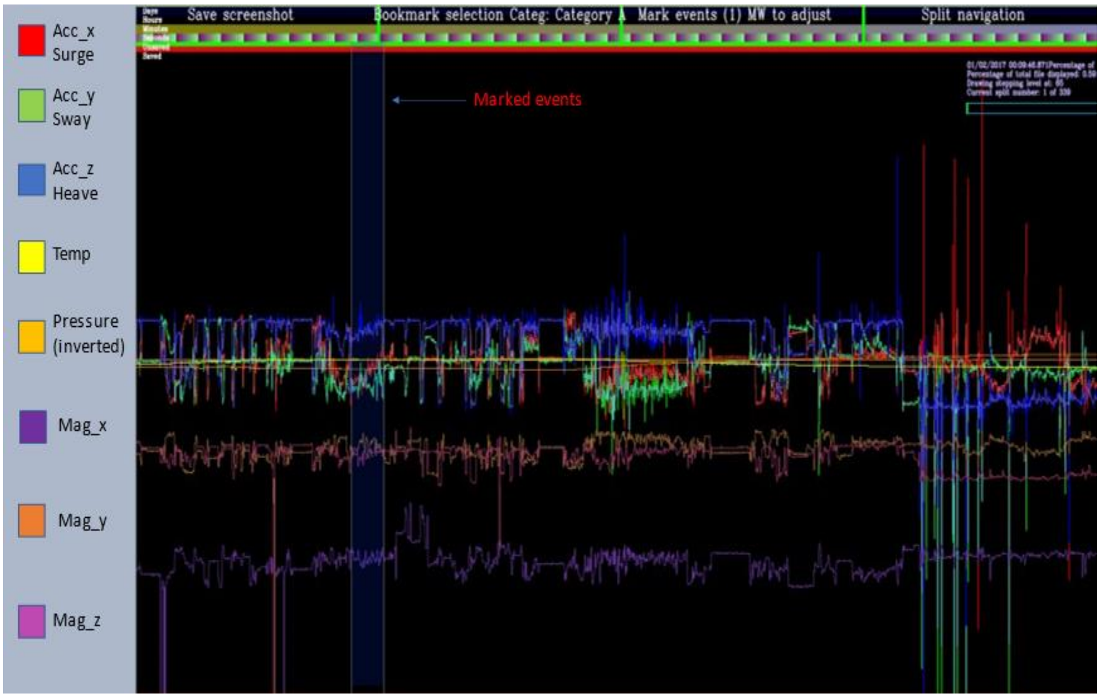


Figure 4. Screenshot of a section of data as a function of time (time is given by the unmarked x-axis) as shown by the DDMT software. This shows the x, y and z acceleration axes, the x, y and z magnetometry axes, the temperature axis and the (visually inverted for convenience) pressure axis recorded by a Daily Diary device taken off a wandering albatross. Note that scales are not given within DDMT because so many axes soon lead to confusion. Instead, the user can interrogate the time scale and particular data stream values by moving cursors across the display whereupon the specific values of the data crossing the cursors are displayed.

Within DDMT, the calibration for time (see above) was used to set the time base to accord with East Africa Time (EAT) which is two hours behind Greenwich Mean Time (GMT) during British Summer Time (BST). Then, the magnetometer calibration (see above) was used to correct for hard- and soft iron distortions due to ferrous material within the tag. This process is complex but described in detail by and undertaken easily within DDMT. When this is complete, the magnetometer data can be used to determine the albatrosses' headings at all time [88].

The accelerometer data can be used to determine the roll and the pitch of the tag (and thereby the albatross). It does this by recording multiple times per second giving values that represent a combination of things which affect the signal. These include the angle of the accelerometer with respect to the earth's surface – the so-called 'static' acceleration [92]. When the accelerometer is pointing straight up, it gives a value of 1*g* and when it is pointing straight down it gives a value if -1 *g*. When, however, it is pointing parallel to the surface of the Earth, it gives a value of 0 *g*. Accelerometer values between these angles vary with the sine of the angle. There are three orthogonally mounted accelerometers in the daily diary devices. When positioned corrected on a bird's body (Figure. 3), each axis represents one of the three major axes of the body; the 'surge' which senses horizontal movement in the longitudinal axis; the 'sway' which senses the side-to-side movement on the lateral axis and the 'heave' which senses to the vertical movements in the dorso-ventral axis [46]. Smoothing the raw acceleration data, nominally over a two second running mean window [93] provides good estimates of the 'static acceleration' [94]. The 'static' acceleration is that imparted by the Earth's gravitational field [94]. Thus, inspection of the smoothed tri-axial acceleration axes (the axes can be smoothed within DDMT) allowed determination of the bird posture. Beyond this, the magnetometry data provided the bird heading which refers to the orientation of the bird in relation to the earth's magnetic field [43] while the barometric pressure showed changes in altitude (both of which can also be displayed within DDMT). For visual simplicity the barometric pressure axes was inverted so that gains in altitude were represented by an increasing value in the y-axis.

For the analysis, the data was evaluated by manually running through it in sequential time blocks (termed splits within DDMT). During this process, all behaviours such as flying, gliding, sitting on the water and circling at the water's surface were identified (for detail see the results section) using the differences in the tri-axial acceleration, barometric pressure and magnetometry axes. The timings and details of the identified behaviours were then marked and exported to excel for further analysis.

Identification of behaviours

Flight (Figure 5), consisted mostly of dynamic soaring where the bird used the energy from the wind to glide without flapping their wings. This was indicated by clear, repetitive waveforms in the magnetometry channels and unstable acceleration channels showing extensive variation.

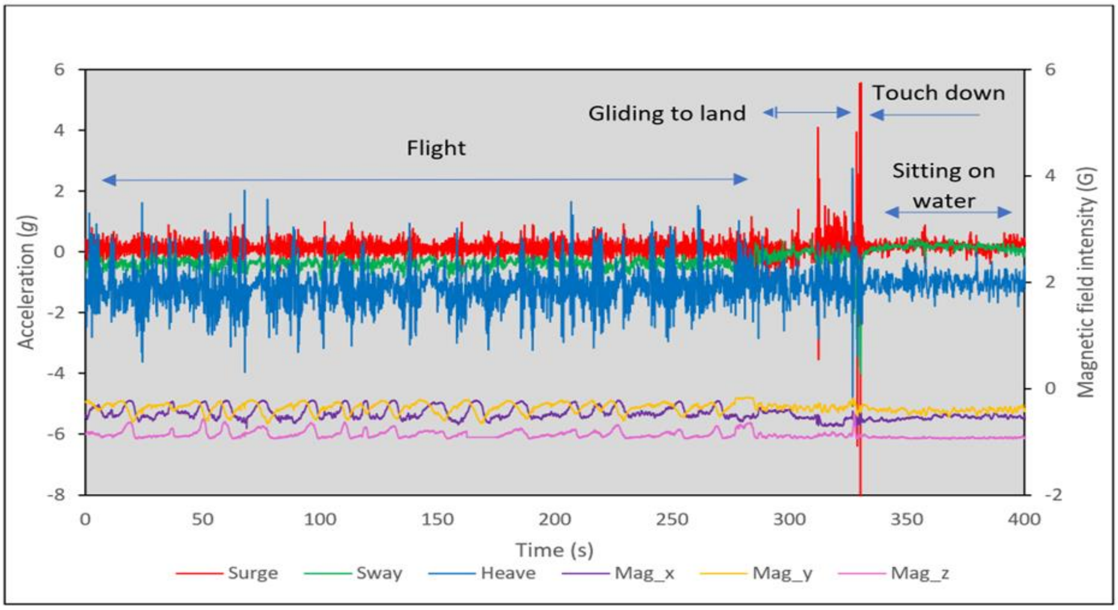


Figure 5. Daily Diary outputs showing data from the tri-axial accelerometers (surge, sway and heave) and magnetometers on a wandering albatross during a period when the bird flew for a while before it landed on the water. Note the clear waveform in the magnetometry data during flight due to the bird angling its body systematically during dynamic soaring. This pattern ceases once the bird sits on the water.

Figure 6- The Daily Diary output showing the tri-axial accelerometers (surge, sway and heave) and magnetometer channels during flight. Note the clear waveforms in the magnetometry channels and regular unstable acceleration channels.

Higher temporal resolution of the flight data also showed wing beats, which were manifest by fast, high amplitude waveforms in the surge and heave accelerations (Figure 7). These were particularly obvious during landing although, just before a bird actually touched down, it also typically maintained relatively stable magnetometry channel values as it maintained its directionality in the pre-touch-down glide (Figure 7).

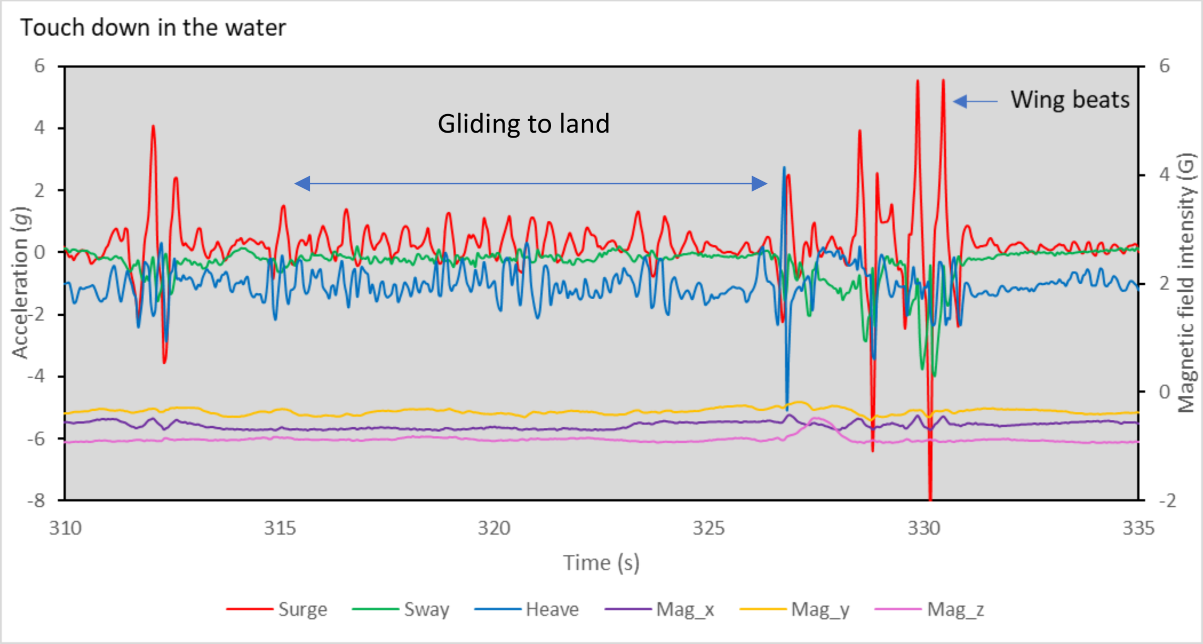


Figure 7 - The Daily Diary output showing the tri-axial accelerometers (surge, sway and heave) and magnetometers channels to highlight landing on the water. Here, regular stable magnetometry channels as flight terminates, indicate gliding to land which is then preceded by unstable acceleration values indicating high intensity wing beats which peak as the bird flaps on touching down on the water.

Rest on the water was indicated by stable accelerometery and magnetometry data (Figure 8).

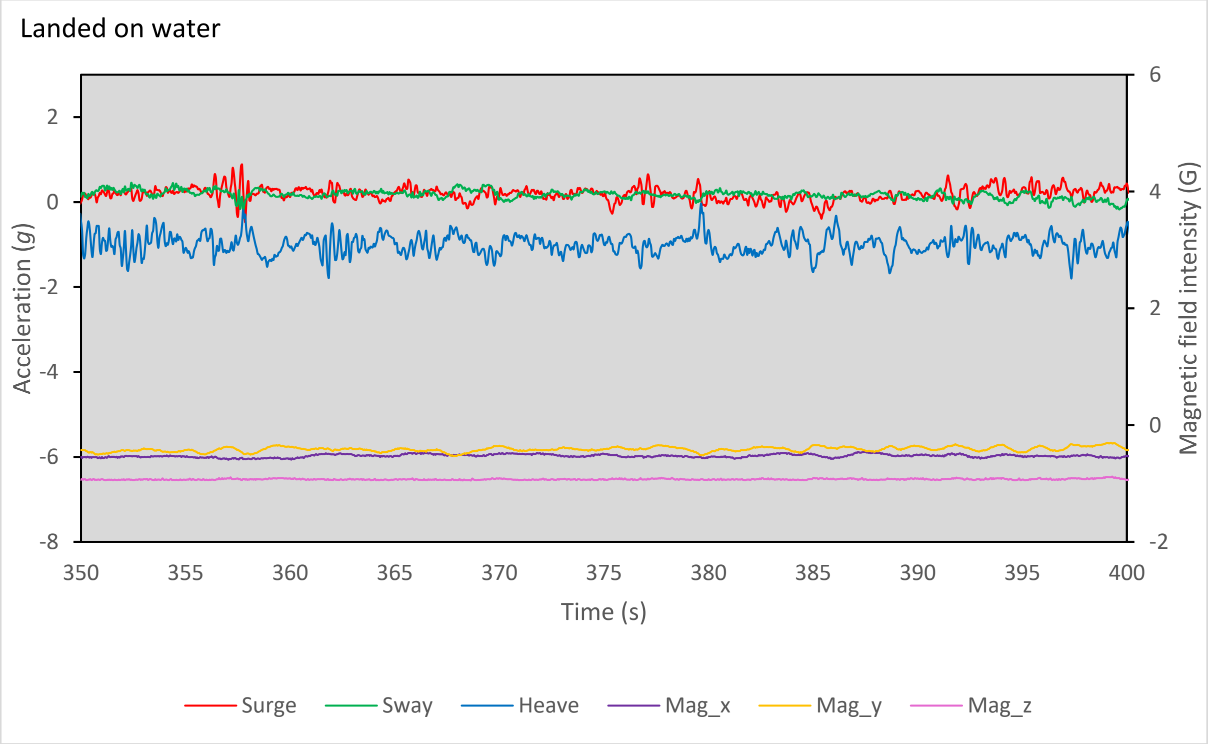


Figure 8 - The Daily Diary output showing the tri-axial accelerometers (surge, sway and heave) and magnetometers channels during a period when an albatross was resting at the sea surface. Note the regular, comparatively stable acceleration and magnetometry channels that characterize this condition.

Take off from the water was indicated by sudden unstable acceleration channels attributed to high amplitude wing beats (Figure 9).

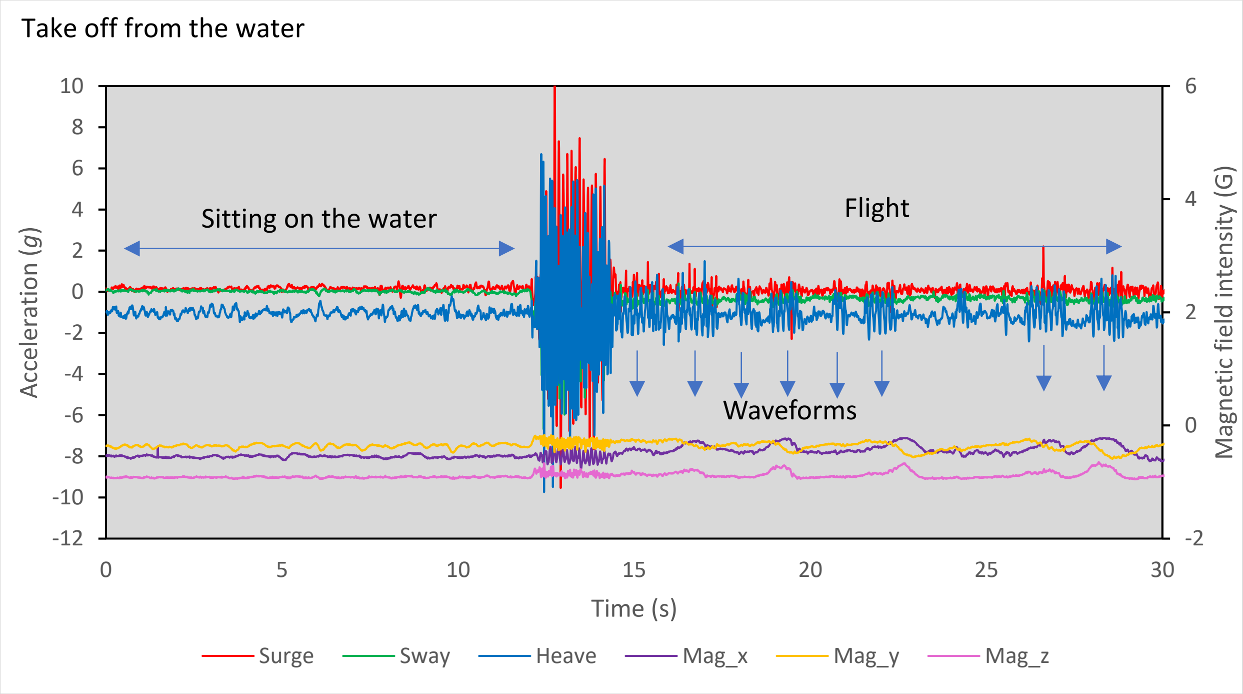


Figure 9 – Take off from the sea surface was typified by a sudden increase in variation on all acceleration channels (but most notably surge and heave), each showing a series of waveforms indicating wing beats. The take-off typically lasted about 3s. Following take-off, the characteristic flight pattern in sensor output resumed (cf. Figure 6). In the flight section above, the wing beat are particularly obvious as grouped, low amplitude waveforms in the heave acceleration values.

Circling (spinning) on the surface of the water was indicated by a highly regular waveform in the magnetometry channels while the acceleration channels were stable, one waveform period represents one full circle (Figure 10a). ‘Body lunges’ were identified by the surge acceleration dropping as the bird pitches forward (Figure 10b).

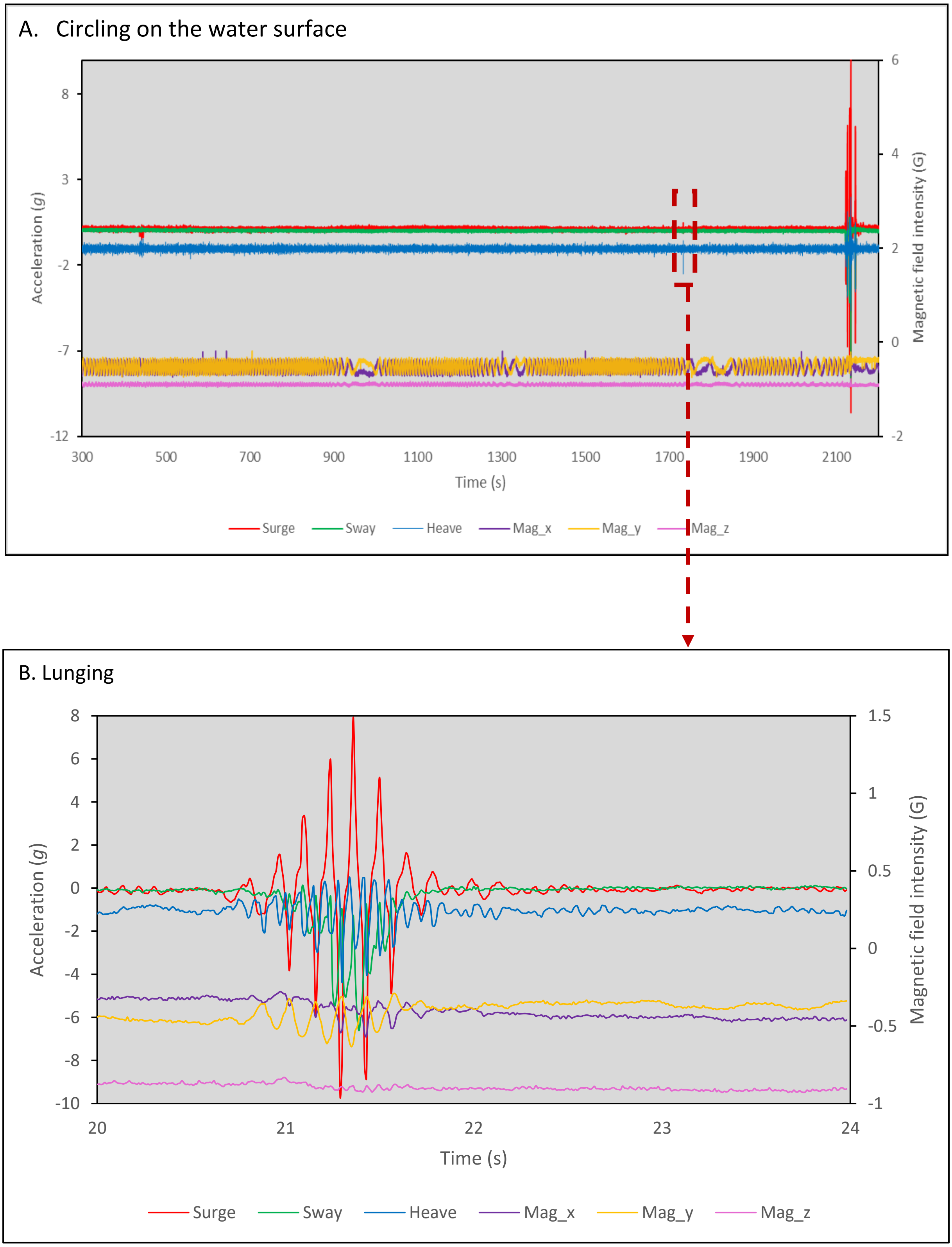


Figure 10 – (A) The Daily Diary output showing the tri-axial accelerometer and magnetometer outputs during circling at the water surface. Note the clear, regular waveform in the magnetometry channels with relatively stable acceleration values. The inset (B) highlights the sudden drop in the surge acceleration indicative of the bird pitching forward (interpreted as lunging). The short duration and irregularity of these events effectively rules out preening.

Treating the identified circling/spinning behaviour with the dead-reckoning process using DDMT, which uses vectors on the heading data and incorporates a constant travelling speed [88] showed the trajectory and rough form that the circles described by the spinning birds took. Assuming constant speed (taken from GPS data from a wandering albatross not included in this study), circling behaviour was very apparent although the process appeared to show some drift in movement rather than the albatrosses being entirely stationary (Figure 11).

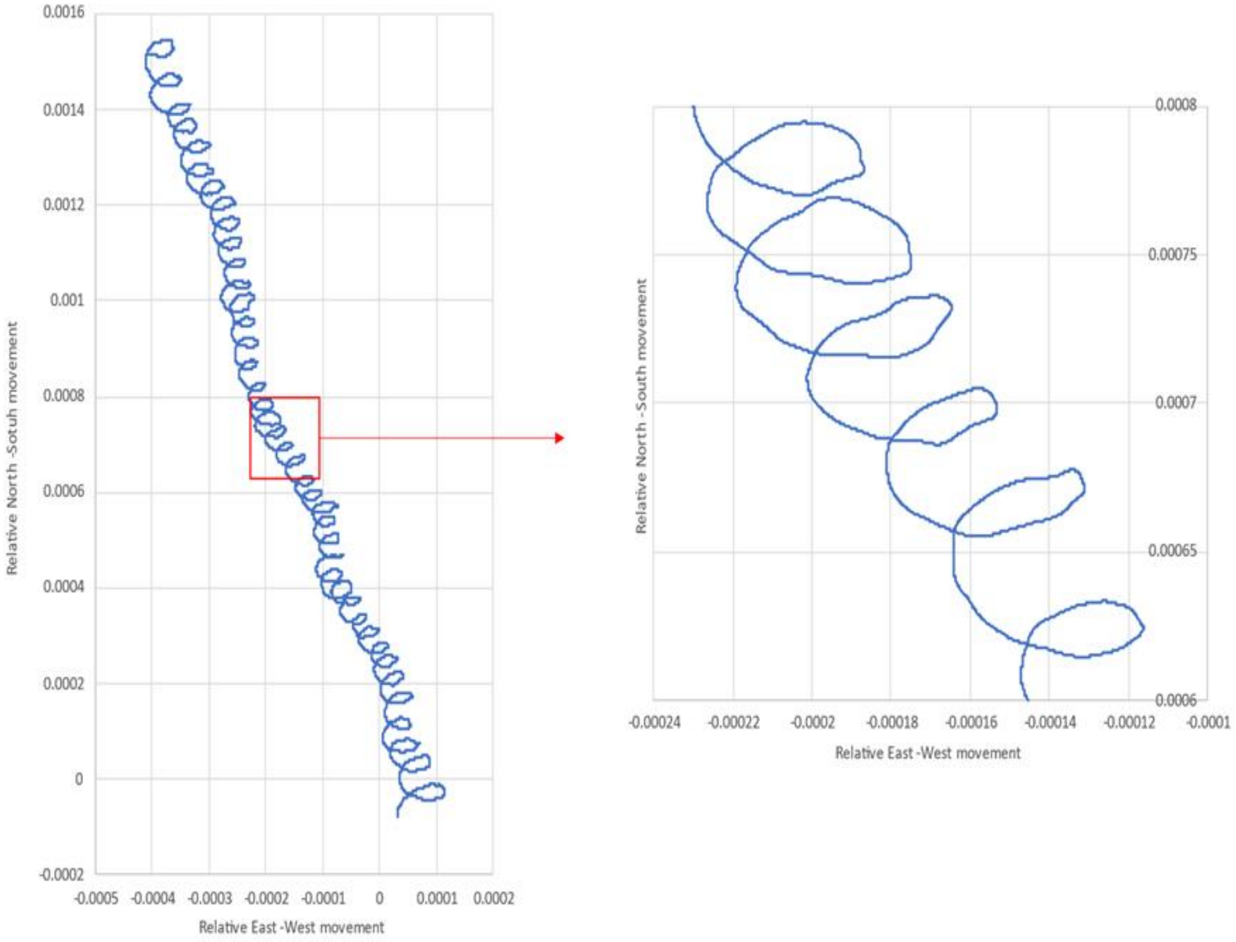


Figure 11 – Dead-reckoned section of a spinning wandering albatross track (WK00) created from DDMT showing a circling event lasting just over 7.5 mins. The inset shows just under a minute to highlight detail. The units are relative, and assume that the bird was paddling at constant speed.

Statistical analysis:

Statistics used were mainly descriptive and carried out within excel. In order to analyse if either day or night influenced the albatrosses' behaviour, a Shapiro-Wilk test was performed to confirm that the data was normally distributed (this test calculates a W statistic that can be compared to a critical value) before a Wilcoxon Signed Rank was carried out using IBM SPSS statistics.

Physical conditions:

The physical conditions (weather conditions, moon phase, sun rise/set and moon rise/set) operating at the times the albatrosses were wearing the tags were accessed using [95] which obtains their data from the meteorological station on Marion Island. Night time was defined as the hours of 00:00 - 07:12 and 17:42 - 00:00. This included astronomical twilight (when the sun elevation angle [the geometric centre] is between 12 and 18° below the horizon), nautical twilight (when the sun elevation angle is between 6 and 12° below the horizon) and civil twilight (when the sun elevation angle is between 0 and 6° below the horizon) However, within the period classified as night time, I also distinguished 'twilight', which was composed of astronomical, nautical and civil twilights, which occurred between 05:30 and 7:12 in the morning and 17:42 and 19:23 in the evening.

Results:

The foraging behaviour of 24 individuals was evaluated, comprised of nine females, four males and 11 individuals of unknown sex. The body movements of these individuals were identified by variations in data recorded by the tri-axial accelerometers and magnetometers and examples of the various behaviours and how they were defined by the sensor outputs are given above (Figure 5).

[88]

Summary data of behaviours

The total length of time that was evaluated from all tags was 74:10:26 (dd: hh:mm) and individual foraging trips lasted between 01:06:19 – 06:23:39 dd: hh:mm (x=03:03:26, SD= 01:13:37) (Table 1).

Table 1. The duration of flights and landings of all wandering albatrosses tagged based on Daily Diary deployments, during foraging trips where all individuals were provisioning for small chicks at Marion Island. Circling was recorded in 4 individuals.

Bird ID	Date	Sex	Total length of time monitored (dd: hh:mm)	Duration of flight (dd: hh:mm)	Duration of time sitting at sea (dd: hh:mm)	Circling present (Y/N)
WJ95	07/04/2014	F	4:21:40	4:4:43	0:16:57	N
WK00	07/04/2014	F	03:00:10	01:05:19	01:18:51	Y
Bum 3	01/02/2017	U	05:00:03	03:08:08	01:15:55	N
Bum 4	01/02/2017	U	02:17:03	01:14:49	01:02:14	N
Pitot 2	17/04/2016	U	01:08:57	01:05:13	00:03:44	N
Pitot 3	17/04/2016	U	03:21:11	02:06:00	01:15:11	N
Pitot 4	17/04/2016	F	01:10:30	01:09:22	01:00:08	N
Pitot 5	17/04/2016	U	01:06:19	00:15:38	00:14:41	N
DD1	14/04/2016	U	01:17:38	01:07:26	00:10:12	N
DD4	14/04/2016	F	01:22:12	01:02:04	00:20:08	N
DD7	14/04/2016	F	01:09:26	00:16:39	00:16:47	N
DD9	14/04/2016	M	01:21:00	00:21:51	00:23:09	N
DD10	14/04/2016	U	01:11:08	01:02:57	00:08:11	N
SA001	13/04/2018	F	06:23:39	03:22:48	03:00:51	N
SA02D	13/04/2018	M	02:22:47	02:04:59	00:17:48	N
SA06X	14/04/2018	F	03:12:36	01:16:31	01:20:05	N
SA009	13/04/2018	M	01:22:00	01:02:30	00:19:30	N
SA210	14/04/2018	F	06:01:30	03:22:15	02:03:15	Y
J11407	12/04/2007	U	04:07:49	03:03:14	01:04:35	Y
J10481	04/04/2007	F	03:03:35	02:05:49	00:21:46	N
J16180	28/03/2007	U	04:02:19	02:07:44	01:18:25	N
J16191	12/04/2007	M	04:05:28	0:15:50	02:13:38	Y
NC90	16/04/2015	U	03:10:31	02:02:02	01:08:29	N
NJ18	16/04/2015	U	02:19:05	01:14:01	01:05:04	N

The total time that all albatrosses' spent flying was 46:21:52 dd: hh:mm with total times spent flying per individual varying between 00:15:38-04:04:43 dd:hh:mm (x=01:22:55, SD=01:01:12). Across all birds, this constituted 22:05:47 dd: hh:mm (47%) of flight during the day time and 24:16:05 dd: hh:mm (53%) during the night time (Table 2).

Table 2. The total summed duration of behaviours from all individuals tagged at Marion Island, based on Daily Diary deployments. Periods of night were defined as the hours of 00:00 - [95]07:12 and 17:42 - 00:00, within which twilight was considered to be between the hours of 05:30 and 07:12 and 17:42 - 19:23 [95] however, because wandering albatrosses foraging for their chicks often involves them moving across time zones [96] and their locations were unknown, estimations of day and night periods must be considered to be very approximate.

	DD: HH:MM	Mean ± SD	Percentage of time spent
Foraging trip duration	74:10:26	03:03:26 ± 01:13:37	
Duration of flight per trip	46:21:52	01:22:54 ±01:01:12	62
Duration of time sitting at sea per trip	28:12:34	01:04:31 ± 00:17:56	38
Time circling per trip	00:03:45	00:00:56 ± 00:00:16	
Duration of flight during the day per trip	22:05:47	00:02:01 ± 00:01:57	47
Duration of flight at night per trip	24:16:05	00:02:17 ± 00:02:07	53
Duration of time landed at sea during the day per trip	15:09:12	00:01:35 ± 00:01:39	54
Duration of time landed at sea during the night per trip	13:03:22	00:01:29 ± 00:01:48	46
Duration of circling during the calculated day	00:01:24	00:00:28 ± 00:00:31	37
Duration of circling during the calculated night	00:02:21	00:00:35 ±00:00:20	63

The total time birds spent landed on the water was 28:12:34 dd: hh:mm, with individual landed times varying between 00:01:08-03:00:51 (x=01:04:31, SD=00:17:56). This comprised 15:09:12 (54%) during the day time and 13:03:22 (46%) during the night. On average, the individuals were observed to engage in specific flying bouts during the day time a collective total of 201 (x=8.4, SD=4.2) times per foraging trip, equating to 8.4 times per day, flying during the night time a total of 172 (x=7.2, SD=4.3) times, which equates to 7.2 flight bouts times per 24 h. They landed on the sea in the day time a collective total of 184 (x=7.7, SD=3.6) times per foraging trip (i.e., 7.7 times per 24 h during daylight) and they landed on the sea during the night time a total of 168 (x=7.0, SD= 4.1) times, (i.e., 7 times per 24 h during darkness). Although the daily diaries appeared to show that the birds tended to fly more times in the day time than in the night time (Figure 12), a Wilcoxon Signed Rank Test revealed that there was no statistically significant difference (Z = -1.637, P = 0.102). Similarly, although the tags also indicated that the birds landed on the water more times in the day than in the night, this was not statically significant (Z= -1.032, P = 0.302).

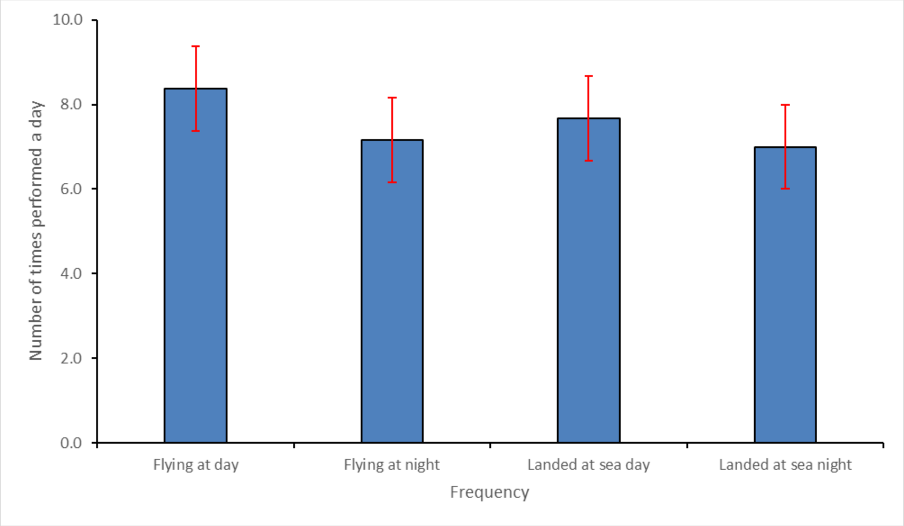


Figure 12. The mean number of times that wandering albatrosses performed the described behaviours (as bouts – i.e., flying refers to a single period during which the bird was flying without landing) per 24 h of their foraging trips. Bars show SDs.

The frequency distribution of flight lengths showed clearly that most flights were of short duration (within the 0–60-minute bracket), decreasing in occurrence with increasing length after that, this being true for both daytime flights and flights at night (Figure 13). There was no significant difference in the frequency of flight durations between day- and night-time flights for any of the birds (Wilcoxon Signed Rank Test Z = -1.861, P = 0.063).

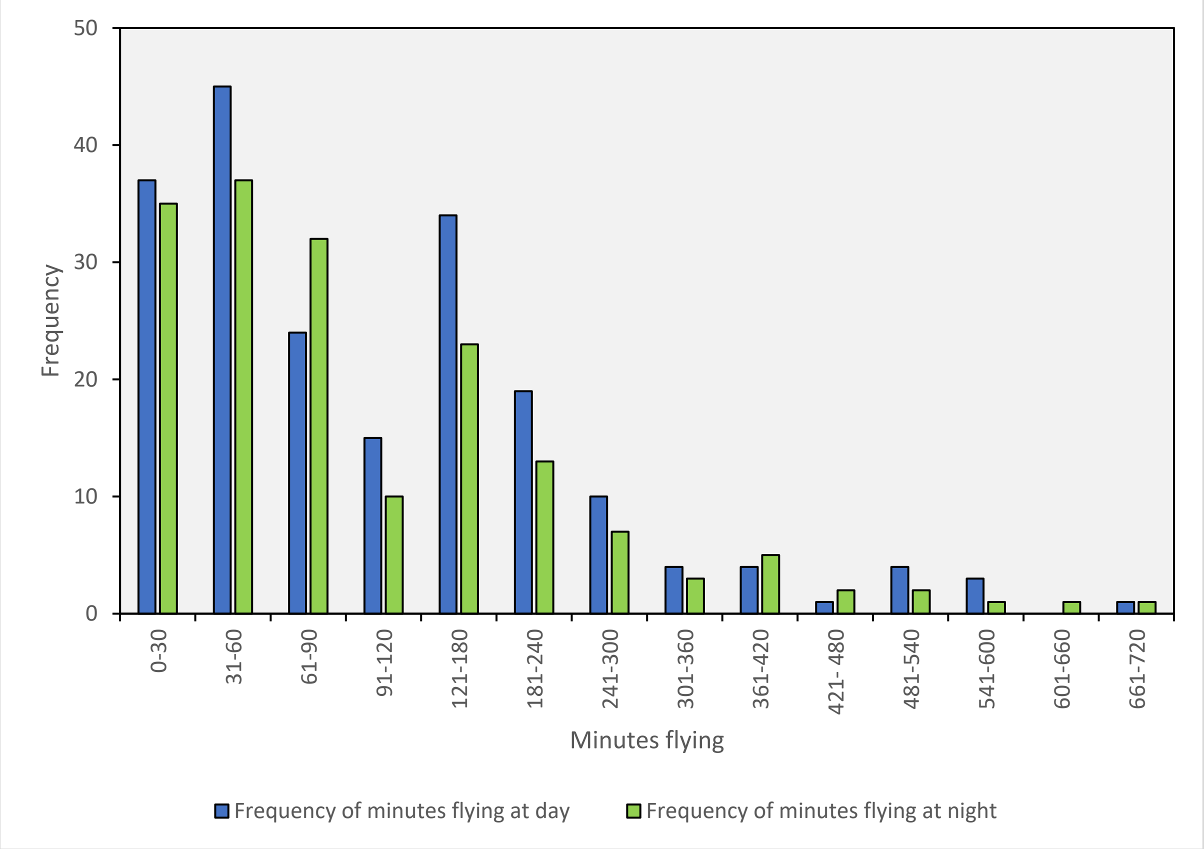


Figure 13. The frequency distributions of the times that wandering albatrosses spent flying. Note that an apparent bimodality is actually due to a doubling in bin width after 120 mins so that the actual trend is for the birds to have flight lengths that are most common for short periods (within the 0-30- and 30-60-min brackets), decreasing after that.

The frequency distribution of periods spent on the water followed a similar pattern, with short duration landings on the water of between 0-30 minutes long being the most common, with the incidence decreasing with increasing duration on the water after that (Figure 14). Although these short landing times apparently recorded a greater number of events occurring during the night than occurred during the day (with a total count of 73 (21%) compared to 60 (17%)) (Figure 14), this difference was not significant (Wilcoxon Signed Rank Test, P>0.05). Similarly, medium duration landings of between 31-120 minutes long happened 76 (22%) times during the day, whereas only 52 (15%) happened at night, and long periods on the water (121-420 minutes) also appeared to have occurred most during the day (with 48 (14%) landings compared to 37 (11%) during the night) although differences were not significant (Wilcoxon

Signed Rank Test, P>0.05). Very long periods on the water (421-720 minutes long) occurred 6 (2%) times during the night and did not occur during the day at all.

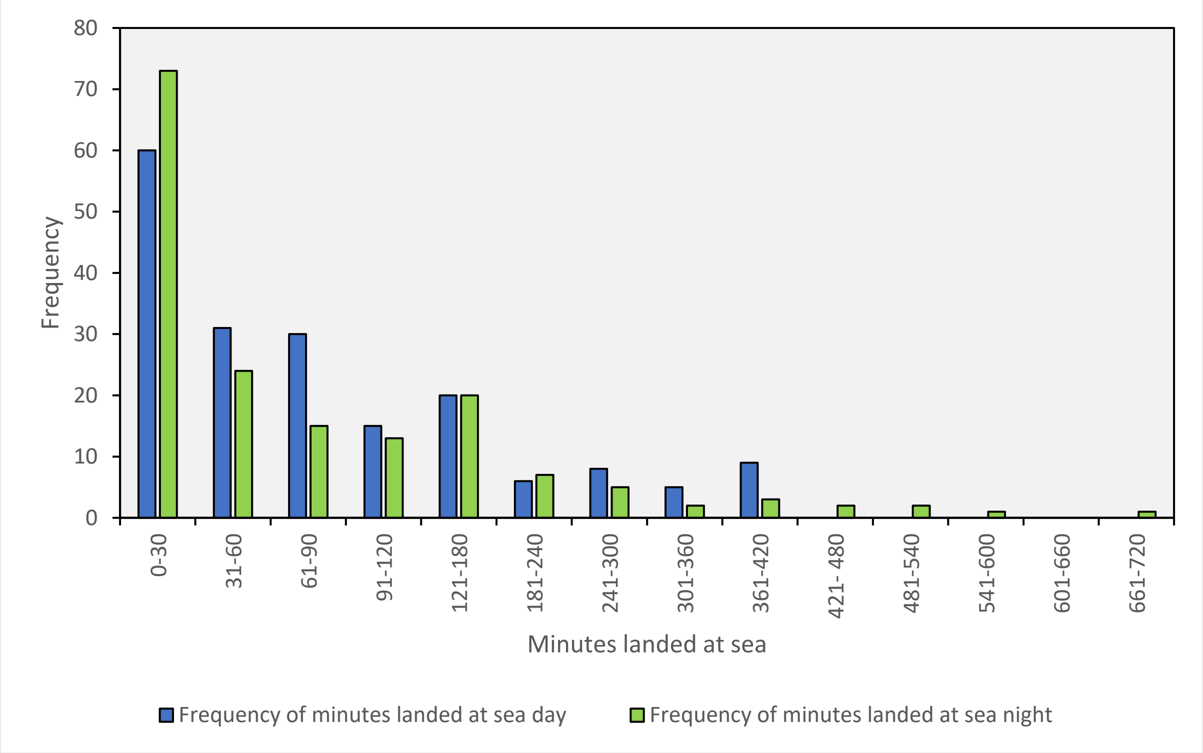


Figure 14. The frequency of time the birds spent at the sea surface without taking off. Note the change in bin width after 120 mins (cf. Figure.14).

<u>Circling behaviour</u>

Circling behaviour was observed seven times in four individuals of the 24 (17%) tagged and both sexes exhibited this behaviour. The circling events were observed in different years and all in the month of April (Table 1). The duration of these circling bouts ranged from 4-64 minutes (x=32, SD=24), with individuals spending between 0.61-0.91% (=0.76, SD=0.15) of their total foraging trip circling (Table 3). The mean time per circle was 10.7 s and the number of complete circles observed varied between 7 and 194 (x=74, SD=70) with circles being approximately equally clockwise and anti-clockwise (Table 4). The circling bouts began between 43-749 (x=373, SD=329) minutes after landing on the water and were shown to begin and stop suddenly, with five (71%) of the bouts concluding in lunges. Lunges also occurred within bouts, with the number of these lunges varying between 0 and 10 (x=4, SD=3) per circling bout (Table 4).

Table 3. The timings of the circling behaviour observed among wandering albatrosses at Marion Island based on Daily Diary deployments.

Bird ID	Sex	Date	Duration of circling (min)	Time started (EAT)	Time ended (EAT)	Time elapsed since sunset (min)	Time elapsed since landed (min)
WK00	F	09/04/14	64	06h57	08h01	536	681
WK00	F	09/04/14	15	08h06	08h21	605	749
SA210	F	16/04/18	5	17h34	17h39	1177	43
SA210	F	16/04/18	48	17h48	18h36	1191	58
SA210	F	16/04/18	4	19h40	19h44	1303	170
J11407	U	12/04/07	43	04h21	05h04	576	182
J16191	M	12/04/07	46	05h31	06h18	646	731

Table 4: Circling behaviour observed among wandering albatross at Marion Island based on Daily Dairy deployments.

Bird ID	Direction of circle	Number of circles	Circle dia. (assuming speed = 0.145 m/s) ±SD (m)	Lunges during or after circling
WK00	Anticlockwise	124	1.26 ± 2.48	0
WK00	Clockwise	18	1.77 ± 2.85	6
SA210	Anticlockwise	9	1.60 ± 1.73	0
SA210	Clockwise	99	1.82 ± 4.05	4
SA210	Anticlockwise	7	1.14 ± 1.37	5
J11407	Clockwise	67	1.75 ± 2.97	10
J16191	Anticlockwise	194	0.66 ± 1.12	2

Estimated lighting conditions during circling events.

Although proper night time is considered in some texts to occur when sun zenith angles are less than -18°, my consideration of ‘night time’ included ‘twilight’, when the sun angle is between 0 and -18°, equating to 05:30 to 07:30 in the morning and 17:42 to 19:23 in the evening

[95] for Marion Island. Assuming that the wandering albatrosses stayed within the same time zone as Marion Island (but see discussion), all but one individual bird commenced circling during a period of darkness/semi darkness (Figure 15). WK00 began circling at 06.57am (twilight) and continued to circle until 08.21am (daylight), and this occurred in two separate circling events. It was semi-dark when the bird began circling, the moon having set at 00.47am and there was no cloud cover. The bird's second circling event started 1 hour and 9 minutes after the sun had risen and there was no cloud cover until the circling ended. SA210 also began one of its three separate circling events during semi-darkness, 14 minutes before sunset. However, this occurred during a new moon (Figure 15) and in cloudy conditions. The third circling event occurred 2 hours and 6 minutes after sunset and it was fully dark with no moonlight and continued high cloud cover. Both J11407 and J16191 had circling events during the night hours with a waning crescent moon and high cloud coverage. Individuals showed a similar diel activity pattern, circling more when it was darker, with little moonlight and high cloud coverage (Table 5).

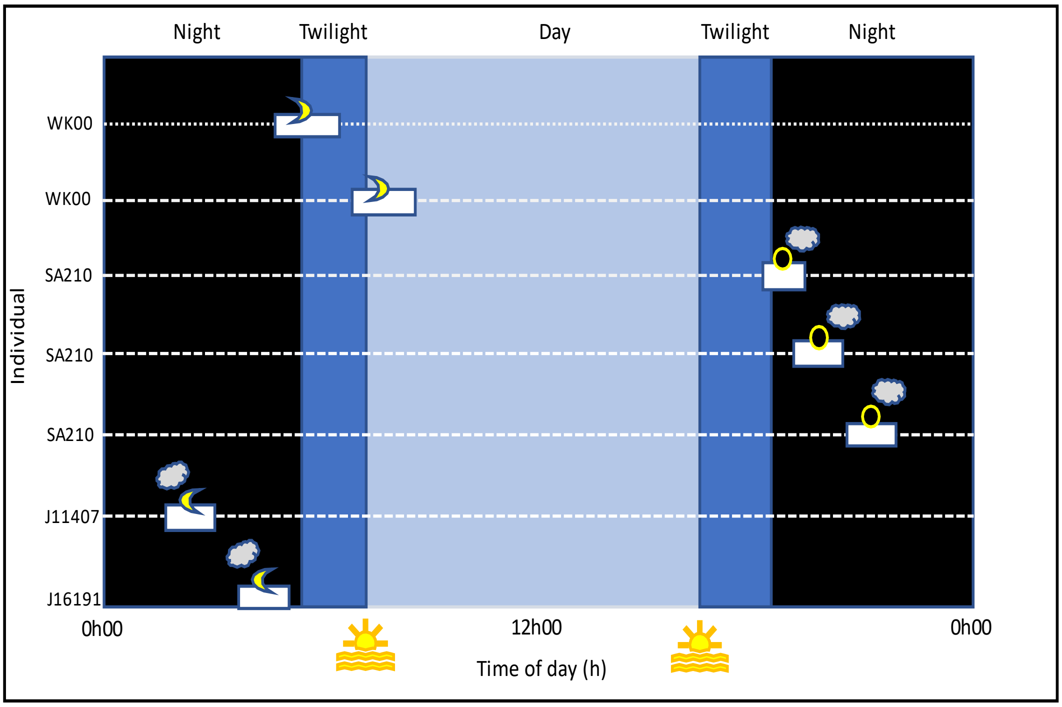


Figure 15. The lighting conditions and moon phases showing the projected level of light during each circling event. Assuming that the albatrosses were operating in the same time zone as Marion Island, one bird started circling during sunrise then had another circling event post morning twilight under clear conditions. One bird had a circling event during a new moon and two birds had circling events during night time with a waning crescent moon. It was cloudy during these latter events.

Table 5. Conditions at the time of the circling events at Marion Island based on information from the weather station based on the island and [95]. The time is in Eastern Africa Time (EAT) which is 2 hours ahead of Greenwich Mean Time (GMT) during British Summer Time (BST).

Bird ID	Date	Sunset (EAT)	Sunrise (EAT)	Moon phase	Moonrise (EAT)	Moonset (EAT)	Circling time (EAT)	Daylight length	Weather
WK00	09/04/14	18h01	06h57	2 days after first quarter	15h06	00h47	06h57 - 08h01	11h 3m	Clear
WK00	09/04/14	18h01	06h57	2 days after first quarter	15h06	00h47	08h06 - 08h21	11h 3m	Clear
SA210	16/04/18	17h48	07h07	New moon	07h06	18h26	17h34 - 17h39	10h 41m	Cloudy
SA210	16/04/18	17h48	07h07	New moon	07h06	18h26	17h48-17h39	10h 41m	Cloudy
SA210	16/04/18	17h48	07h07	New moon	07h06	18h26	19h40 - 19h44	10h 41m	Cloudy
J11407	12/04/07	17h56	07h01	2 days after third quarter	00h02	15h43	04h21 - 05h04	10h 53m	Cloudy
J16191	12/04/07	17h56	07h01	2 days after third quarter	00h02	15h43	05h31 - 06h18	10h 53m	Cloudy

Discussion:

There have been extensive studies into the foraging behaviour of wandering albatross however, to my knowledge, this is the first study into the possible novel forging behaviour described as 'circling while sitting on the water's surface. The aim of this research was to investigate (i) if there was any difference in the wandering albatrosses' movements and general foraging behaviours between the day and night, (ii) if they displayed circling behaviour on the surface of the water during a foraging trip, (iii) whether circling, if it occurs, was associated with daytime or night time foraging, and (iv) if there was any indication of feeding behaviour associated with such circling. In summary, the outcome of this investigation found no significant difference in the movement and foraging behaviour of chick-brooding wandering albatrosses between day and night. However, it provided evidence that they did occasionally engage in circling behaviour during periods of darkness/semi darkness and that this behaviour often concluded in potential feeding activity. It is, however, unlikely to be their dominant foraging technique.

The diet of wandering albatrosses.

It is widely thought that wandering albatrosses feed mostly on squid [103] found in pelagic waters although they also consume fish, crustaceans, cnidarians and carrion [10]. Investigations into the stomach contents of wandering albatross chicks at Marion Island discovered solid material comprising (by weight) 58.6% cephalopods, 36.5% fish and 4.9% crustacean and cetacean [56]. This study discovered that the squid species *Kondakovia longimana* was the most frequent species found with *Histioteuthis eltaninae*, *Onykia robsoni* and *Galiteuthis glacialis* also commonly found (Table 6) [56]. Two of these species are known to be bioluminescent (*H. eltaninae* and. *O. robsoni*) and all but *K. longimana* engage in diel vertical migration. Studies have determined that diet is, however, geographically variable as regurgitation studies taken at the Crozet Archipelago in the southern Indian Ocean reported that cephalopods accounted for 46% of their diet (Appendix 1) while fish, including the commercial Patagonian toothfish, dominated their diet, constituting 48% by weight [7] (Appendix 2). Xavier et al [104] discovered that adults may provide their chicks with as many as 60 different cephalopod species during his studies in the South Pacific. However, it is worth noting that some prey may be caught and digested before the birds return to their colony, providing a potential bias against species caught further away from the colony [31,105]. Another note of caution is that virtually all studies of wandering albatross diet are centred around what breeding birds feed on. This is because they represent the only opportunity for birds to be caught for (non-lethal) stomach sampling [55,57,106]. Thus, our knowledge of wandering albatross diet is inherently biased and this should be borne in mind in the following discussion.

Table 6. Sample of the squid and fish species found in the stomach of wandering albatross at Kerguelen and Crozet Islands, in the Southern Ocean. Squid was not their dominant prey in this study which amounted to 46%, while fish, including the commercial Patagonian toothfish, predominated, constituting 48%. This table is adapted from the results from Cherel et al. [7]. For complete list see (see appendix

Species	Common name	Bioluminescence	Size of living species (cm)	Distribution
Kondakovia longimana	Oceanic squid	No	74	Deep-sea
Onykia robsoni	Rugose hooked squid	Yes	75	Diel Vertically migrating
Histioteuthis eltaninae	Unknown	Yes	11	Diel Vertically Migrating
Psychroteuthis glacialis	Glacial squid	Yes	44	Mesopelagic
Dissostichus eleginoides	Patagonian toothfish	No	200	Mesopelagic

The foraging trips of wandering albatrosses are of considerable length (varying between two and 12 days [74], during which time birds may cover up to 6,091 km and range 256-1941 km from their breeding site [53,74]. They forage exclusively over open ocean and are believed to exploit highly patchy prey [11]. They have a particularly long breeding cycle that lasts over one year [54] and the success of their reproductive efforts is dependent on their own body condition [107] as well as meeting the energy requirements for their growing chick, so the timing of their breeding season is believed to match the peak prey resource availability [108].

Shaffer [54] stated that a breeding pair of wandering albatrosses on the Crozet Islands used a total of 2,733 MJ, which means that each adult has to consume an average of 1.7 kg of food a day to meet their own energy requirements and provision a chick for each day of the entire brooding period. During this brooding period, the parents take turns in sitting on the nest and in foraging [74]. At this time, foraging trips tend to be short (between 2 and 6 days [74]) because the small chicks are unable to fast for long [13]. My data were taken from birds during the brooding period, which also explains the lengths of time that the tag-equipped birds were at sea. Post-brooding wandering albatrosses do not stay with the chick for extended periods. Instead, both parents forage simultaneously, spending two to five days per trip at sea, sometimes longer, returning to feed the chick and typically spending just an hour or two at the nest before departing on the next foraging trip [87].

Basic activity patterns of foraging wandering albatrosses

Early authors stated that wandering albatrosses feed by surface seizing, although there had been no known direct observations in the period up to 1980. It was once thought that they time their chick brooding period during the austral autumn (March- May) in order to be the only other avian squid predator [109] however, more data has since become available to disprove this as other species such as the southern giant petrel have a similar breeding period [110]. These early studies stated that it was most likely that wandering albatross scavenged their prey during the day by regularly consuming whale regurgitate from the surface as well as frequenting whaling stations and feeding on discards, either directly from the carcasses or from floating discards [109]. The studies also stated that wandering albatrosses seize live vertically migrating squid from the surface during the night [109]. The behaviour of many marine organisms is structured around a 24-hour day and night cycle [111] and many of them undergo diel vertical migration (DVM) that might facilitate squid capture by albatrosses. Diel vertical migration is a behavioural pattern where the vertical distribution of many animals within the water column changes over a 24-hour period [111,112]. Many species, including several squid species, spend the daylight hours deep within the water column, ascending towards the surface at dusk where they reside during the night time hours before descending at dawn [111,113]. This is triggered by the diel changes in light intensity and possibly changes in water temperature and hydrostatic pressure [111] and it is likely motivated by increased prey availability and visibility as well as predator avoidance [114]. Research and technology have come a long way over the 43 years since these findings and although the fine scale details of the foraging strategies (location, timing and energetic costs) and prey species have become clearer, the main findings have not much changed.

Recent research has been able to ascertain that wandering albatrosses take prey that is widely spaced, unpredictable and patchy [12,26,115] so their precise foraging techniques have to deal effectively with that. Satellite tracking and activity monitoring studies [26,51] have shown that wandering albatrosses manage this due to their low energy cost flight based on dynamic soaring [8] which enables them to fly fast, covering long distances, a prerequisite for finding rare prey [116]. Indeed, [8] determined that wandering albatrosses can spend over 17 hours a day flying [26,51]. The general interpretation of this is that landings that break flight periods are primarily due to birds sighting prey near the sea surface and landing to exploit it.

This is consistent with my findings as data from the tri-axial accelerometers and magnetometers also showed flying for long periods with sudden short duration landings, lunging behaviour and then the bird takes off again (Figure 10). This is supported by the frequent number of shorter flight durations (0-180 minutes) (Figure 13) and regular short duration (<30 minutes) landings on the water, observed in the day (Figure 14). Short bouts on the water (<30 minutes) were the most common bouts and they occurred during both the day and at night (Figure 14) which is consistent with work by Weimerskirch, Wilson and Lys [26] and Weimerskirch and Guionnet [66]. However, my data shows that longer duration bouts on the water (>421 minutes) only occurred during the night.

The partitioning of foraging time was found to vary between individuals, Weimerskirch, Wilson and Lys [117] and Phalan et al [10] found that wandering albatrosses on average spend 60% of their foraging time in flight and 40% on the water. This study found no statistical difference in the number of times that the birds landed on the water at day and at night. It is worth noting, this may be the result of a small sample size (n=24) or possibly because of the extreme distances the wandering albatrosses can travel they may have travelled into an area with a longer duration of daylight.

Despite the fact that wandering albatrosses are reputed to take widely spaced and unpredictably located prey, conditions which will put the birds under selection pressure to travel far and fast to find them, there are clear cases where birds have caught prey after a long period of sitting at the water surface [8,105].This is enigmatic because it not clear how these widely spaced prey might be found by birds that are essentially not moving.

Irrespective of how this sit-and-wait foraging technique might work (see later), the two different foraging techniques – of flight to find prey or sit-and-wait to find prey - may be trade-offs between the rate of prey capture and the energetic cost of flying [26]. Despite their reliance on wind conditions to reduce their energy expenditure [27], searching flight involves multiple take-offs and landings (Figure 8) which is energetically expensive, particularly if not all landings lead to prey ingestion [72]. So, although searching during flight likely increases the probability of finding prey, wandering albatrosses may use the sit and wait method to forage since it is not as energetically onerous as flight [118]. One suggestion is that the birds switch foraging techniques, specifically sitting on the water when prey concentrations are especially high [12], although clearly, they are presumed to spend time to rest [26] or to digest their food [66].

The situation also seems to change according to the diel cycle, with wandering albatrosses apparently using the sit-and-wait method at night [31]. Certainly, they are considered to consume more prey during the daylight, presumably found during the extensive flying periods, than during the darkness [10,119,120]. There may be several reasons for this, one being that wandering albatross hunt by sight [121] so their foraging efficiency is reduced due to low light levels [67,122]. But at night, the albatrosses may also take advantage of the diurnal vertical migration of their prey. Another, untested motivation maybe predator avoidance, as species such as Orca (*Orcinus Orca*) have been observed off South Africa killing seabirds and 'playing' with them during the day [123] although this occurrence is rare. It is also germane to ask whether this behaviour might not also occur at night since Orca primarily use sonar to detect prey [124]. If so, we do not expect observers to 'see' this.

The dynamics of prey capture.

Wandering albatross are considered to be surface seizers [34] and pelagic squid are known to be fast and highly mobile, so how they feed on these deep-sea animals has long been a mystery [30,105]. In addition, these birds are generally considered to be poor divers, only diving infrequently and then to less than 1 m [125] which would preclude any substantive underwater prey pursuit.

Research has shown that there are five known methods used by wandering albatrosses to acquire food during the day time, one being feeding on moribund material [55]. This can work because many deep-sea dwelling squid are semelparous and die after spawning [126,127], some of them floating on the surface [65], presenting an opportunity for surface foraging seabirds.

The second feeding technique depends on the albatrosses' exploiting discards from fishing vessels [105]. Indeed, wandering albatross are renowned for following fishing vessels [35] and could possibly use other aggregating seabirds as visual and acoustic cues [27] to locate these craft.

The third proposed feeding strategy is to exploit the regurgitations of odontocete cetaceans [57]. Approximately 60 odontocete species consume squid [105], including the sperm whale (*Physeter macrocephalus*) which has a well-known association with albatrosses [128]. The sperm whale dives to depths of 200 - >1000 m to feed on deep-sea squid and fishes [129] and they periodically need to empty their stomachs of indigestible items such as squid beaks which do not pass further down the gut [57]. This regurgitate then floats on the surface of the water. However, birds would presumably need to be near constant escorts to capitalize on this, which may not be energetically profitable [130].

The fourth method is feeding on the scraps and/or live species pushed to the surface by other predators such as penguins or cetaceans [25]. Despite the possible predation risk, wandering albatrosses have been observed following pods of orca [123] because, when the orca feed, they often leave fragments of their prey on the sea surface [25]. In addition, prey availability may be enhanced by some orca hunting techniques such as 'bait-balling' [131] which pushes prey concentrations into the foraging range of the albatrosses.

The fifth method involves taking live prey at night [130], although prey is considered to be more difficult to catch due to the low light levels [10,78]. Thus, during night-time prey capture, it has been proposed that the wandering albatrosses remain sitting in a relatively fixed spot on the surface of the water, waiting for their prey to vertically migrate within their reach [119], doing so by starting at dusk and continuing until dawn [103]. Studies into the vertically migrating species fed upon by the wandering albatrosses have determined that many of them have bioluminescent organs which could make them more visible in the darkness [126] particularly when light from the moon is reduced or absent. Indeed, moon phase has a significant influence on vertically migrating squid, which reduce the extent and intensity of diel vertical migration due to the higher level of light [132]. This is consistent with my results as it was found that feeding activity during the night mostly occurred when the moon had set or at a phase when it was relatively dark and cloud cover was extensive. Wandering albatrosses have been also found to spend more time flying during a bright moon, [10,26,31,120].

Work by [105] provided evidence for some of these methods, although the authors worked on Laysan albatrosses (*Phoebastria immutabilis*) by using camera images to monitor 20 birds in Hawaii. For this sample, the authors observed the birds foraging on six intact floating squid, ten floating fragmented squid and observed them following fishing vessels nine times. The images did not show any cetaceans but associations cannot be ruled out as their distribution is sparse and it is possible that they often forage at depth. The camera could not take images during the night so there was no visual evidence what methods albatross may use to encounter their prey at night.

Circling Behaviour.

The foraging methods described above may only be some of multiple strategies for acquiring food. Given that the degree to which a predator can enhance its fitness may depend on their behavioural plasticity, and this is particularly true where prey distribution is not stable in space or time [12,133], there is perhaps room for other foraging options. Certainly, within Procellariforms, the ability to employ flexible foraging methods and the innovation of novel foraging techniques gives them a competitive advantage, thereby enhancing their survival and reproductive success [13]. My analysis of the wandering albatross data provides tantalising new insights into a novel behaviour which I suggest is a new foraging technique. This relates to the extended periods of circling (spinning) on the surface of the water which was often concluded in ‘lunges’, where the bird’s body suddenly pitched forward (Figure 10b). These lunges occurred straight after the circling ceased and then resumed afterwards, indicating feeding activity. All but one individual bird commenced circling behaviour during a period of darkness/semi-darkness (Figure 15). This individual had two separate circling events, the first of which occurred during a period of darkness, while the second event commenced just after sunrise. During the time of this circling event the moon had set and no cloud cover was recorded indicating that this individual apparently displayed circling behaviour during the day. Could this individual have been taking advantage of the diel vertical migration of the squid then or was it employing another method? However, all this assumes that the bird stayed within the same time zone as Marion Island. As previously mentioned, wandering albatrosses can fly thousands of kilometres while searching for prey [13] and this individual may easily have flown into a different time zone. For it to have foraged by circling in darkness, it would have had to have flown to the west of Marion Island, which may also have had different weather conditions than those indicated for the East of the island where the weather station records the data on the local weather [134]. It is also worth noting that the angle of the sun may influence the light intensity [135]. At high latitudes such as Marion Island the angle of the sun is low in the sky in the morning during autumn [136] which means the light intensity may have been low during this circling event, especially so near to sunrise.

Circling behaviour while foraging is not a new concept, having been documented in phalarope (Phalaropus sp) [137,138], humpback whales (*Megaptera novaeangliae)* [133] and narwhals (*Monodon monoceros)* [139]. In the case of the phalaropes, the circling is said to create a vortex in the water that serves to concentrate their zooplankton prey [138]. Humpback whales encircle their aggregating prey (fish or krill), causing them to concentrate by using a bubble curtain to contain them before ingesting them in one large gulp [133] while narwhals spin to increase the area swept by their echolocation beam by rotating its whole body [139]. None of these options seems viable as a reason for the circling behaviour observed in wandering albatrosses though.

I suggest that the action of paddling and circling may induce the production of bioluminescence by dinoflagellates such as *Noctiluca scintillans* and *Pyrocytis fusiformis* among many others [140] *via* the phenomenon known as 'marine phosphorescence'. The word bioluminescence comes from the word "bios" meaning life in Greek and "lumen" meaning light in Latin and it is a powerful mechanism that has evolved separately 40 times [141]. It is thought that 40% of marine organisms are bioluminescent and these animals can be found from the surface of the water to down to 4000 metres [141]. This light, which is created when the chemicals luciferin–luciferase interact with oxygen, is in the blue-green spectrum [141–144]. Specifically, though, these dinoflagellates emit light when disturbed, something that has been documented for the waters around ships [140], swimming marine organisms [145,146] and breaking waves [140]. Thus, I propose that the action of albatrosses circling at night, paddling as they do, will, under the right oceanographic conditions (see below), produce a ball of light, the circling serving to concentrate the agitation in a certain volume of water thereby increasing the intensity of the light ball. Many wandering albatross prey species show positive phototaxis and are attracted to the light, associating the light with their own prey, mates or conspecific competition [69] so I suggest that the circling behaviour acts to attract prey to the albatross. Importantly, potential prey may be attracted from the depths – as they are by humans jigging for squid using light [58,68,70] so that the circling behaviour would act to allow wandering albatrosses to access prey that they otherwise could not reach.

Wandering albatross are opportunistic [35] and given their enhanced olfactory senses [11], it is possible that they are familiar with the smell of the microbes when primary production levels are high and there are bioluminescent organisms in the water column, with the odour being transported by the wind and currents [27,144]. Meteorological elements such as precipitation and cloud cover, as well as the moon phases, may factor into the motivation behind circling, as visibility will be reduced [27]. My findings support this as all the circling events bar two occurred when there was extensive cloud cover and no moonlight. This creates darker conditions [147] which works in favour of diel vertically migrating species and the visibility of bioluminescence.

The oceanographic processes and bioluminescence.

The marine environment is highly spatially variable in terms of oceanographic and biological processes [108] and marine predators showing clumped distributions as they exploit aggregated prey resources [52]. Indeed, these marine predators themselves play an important role in these processes *via* trophic flows and nutrient cycling [44]. However, predators such as wandering albatrosses are rare and highly mobile, travelling thousands of kilometres [106], which makes determining which processes influence their foraging behaviour a challenge as they move across the variable conditions. Studies have shown that the larger Procellariforms, particularly wandering albatrosses, can only exploit the upper few metres of the water column so that oceanic frontals systems, such as eddies, and bathymetric features, such as continental shelves and ridges, are likely to be the main factors that influence their prey availability [82,148]. Abiotic factors such as Sea Surface Temperature (SST), salinity and chlorophyll (Chl-a) levels are also significant factors influencing local prey availability [69], and it is the complex interactions between these and other factors which makes the waters around Marion Island so productive.

The prince Edward Islands are approximately 0.45 million years old and exist on complex bathymetry including the Southwest Indian Ridge (SWIR) and the Andrew Bain Fracture Zone

(ABFZ) [83]. Marion Island lies in the subantarctic zone of the Southern Ocean, situated in the eastward flowing Antarctic Circumpolar Current (ACC) and to the north of the Antarctic Polar Front (APF) and the Sub Antarctic Front (SAF) [81,149]. The ACC is one of the strongest ocean currents in the world and it transports cold, nutrient rich waters around Marion Island and the interaction between this current and the SWIR creates anticyclonic and cyclonic eddies which influence the Sea Surface Height (SSH) [83]. These mesoscale eddies can cause elevated plankton and fish biomass within the vicinity of the island [81]. The Agulhas Current, also within the Marion Island wandering albatross foraging area, is important to productivity as it is a fast-flowing current originating in the Indian Ocean that carries warmer waters which influences the salinity and temperature of the surrounding waters and promotes upwelling which carries nitrates, phosphates and silicates [150]. The warmer water is less dense than the cooler water and it rises to the surface where the strong westerly winds mix it up and then when the organic material dies it sinks to the bottom which creates a nutrient rich subsurface layer [126]. The SAF separates the colder oxygen rich waters from the ACC and the warmer waters from the Agulhas Current creating favourable conditions for phytoplankton blooms and associated phosphorescence [150]. Marion Island itself contributes to the high productivity in the surrounding waters as it is an active volcano and is a major breeding ground for millions of different species, both of which act as additional sources of organic matter and minerals [151]. Mesoscale eddies then aid in transporting the nutrient rich water from its origin and transport it around the surrounding areas, resulting in a diverse spectrum of biota such as phytoplankton, zooplankton and diatoms [21,82,83].

The species composition of these organisms is highly variable and often includes many bioluminescent species [142,152] and these organisms provide an important food source for many species at varying life stages, including squid and fishes [153]. It is thought that approximately 76% of marine species, including squid, can emit light [141] and use it as a way to communicate with mates, escape from predators or to attract prey in the limited visibility of the ocean [154–156]. When it gets dark the prey becomes harder to detect so another way in which the wandering albatrosses may use bioluminescence when foraging is by sitting on the surface of the water and waiting for vertically migrating squid and fishes to come to the surface [10]. Many of these species such as *Pyroteuthids* and *Myctophids* have photophores (light-producing organs) which can produce bright flashes making them visible in the darkness [157]. Even prey species such as the Deep-sea squid (*Grimalditeuthis bonplandi)*, which does not have photophores, may still become more visible during the night as when they move, they may instigate bioluminescence in other surrounding species [127]. Some studies have doubted this theory and state that many species' photophores are under complete control of the emitting organism or that their photophores are directed downwards for counter illumination [55,158]. However, work by Imber and Russ (1975) found that 80% of the cephalopods found in the stomach of a wandering albatross in Auckland were bioluminescent. Research has shown that Procellariforms have remarkable neuro anatomy and their eyes have high levels of rhodopsin, which is a photosensitive chemical involved in nocturnal vision [115,121]. This, coupled with their significant olfactory senses, indicates that wandering albatross are well adapted for night time forging.

The future.

This study has provided new insights into the foraging behaviour of wandering albatrosses. However, there are several limitations which, if addressed in future, could provide a clearer picture of novel foraging techniques utilised by not just wandering albatross but all far ranging species operating in their changing environment. The use of biologging such as the Daily Diaries used here has revolutionised our understanding of the behaviour and biology of many free-living species [159] however, with such sophisticated and complex technology, comes its own set of challenges. One such challenge is that the interpretation of such data is complex and the classification of behaviours requires prior knowledge of the subject's behaviour in the first place [160] and is subject to human error. Also, behaviours that occur over a short period of time may not be detected [31]. Another consideration is that the behaviour of many species is highly dependent on the surrounding abiotic and biotic factors such as wind conditions, the presence of conspecifics and the presence of other predators or fishing vessels, all of which may influence their behaviour. The tags do not record these factors which may give clues as to the elicitors of the behaviours [27,43]. One way of beginning to deal with this is to use low-light cameras in combination with the tags as demonstrated by Sakamoto, Takahashi, et al [25]. This approach provides visual evidence of certain behaviours as well as the motivation behind them [40]. However, recording duration is extremely limited [25], especially for far ranging species like wandering albatrosses. Two other restrictions when using cameras, especially while used on seabirds is the non-standardisation, and limitation, of the visual field. For example, in addition to the restricted lens angle, the camera's visual field may be obscured by the water, the bird's feathers or in due to the position of the camera itself. Indeed, the bird with its camera may be positioned in such a way that the camera may not record an event such as the presence of another predator or a fishing vessel even though it is present [40]. The other restriction is the size of camera tags. These animal-borne cameras tend to be larger and heavier than the 'movement tags', which may interfere and impair the elements being measured e.g., flight distances, diving or specialist foraging techniques such as circling [41]. These can have negative effects including increased foraging effort and reduced provisioning for their chicks [41].

With the Earth's population reaching over eight billion [161], the dependence on the world's oceans has grown exponentially [162] and the resulting environmental changes is significantly affecting its biodiversity and productivity [163]. The Prince Edward Islands marine biodiversity is globally important and despite the measures taken to protect it i.e., MPAs, the area including Marion Island, is subject to overfishing, pollution, habitat loss, invasive species and climate change [164] . This is thought to have a negative impact on wandering albatrosses as they mature slowly and have a low reproductive output so that high adult mortality can have a major implication for population well-being [165]. One of the major threats to wandering albatrosses is commercial and illegal fishing because, as well as depleting prey resources, such operations often catch birds in their fishing equipment [20,165,166] including when the albatrosses scavenge from long-lined baited hooks [35]. Previous studies have shown a high spatial overlap between the wandering albatross breeding grounds at Marion Island and local Patagonian toothfish long-line and pelagic tuna fisheries during the chick brooding period with, notably, several fishery related items such as plastic and hooks being found in diet samples [35]. Wandering albatrosses are well known to follow fishing vessels [13] with high mortality rates due to bycatch. Thus, although fisheries might provide an abundant and predictable food resource for opportunistic and scavenging seabirds such as wandering albatross by giving them their discards [64,166], the consequences of increased mortality need to be factored in. Another harvesting method which may negatively impact wandering albatross is jigging, which uses light to attract squid [167], in a manner similar to that proposed here by wandering albatrosses catch their prey using the circling behaviour. Jigging, like circling, works by taking advantage of the squid's natural diel vertical migration and their attraction to light. Spindle shaped structures with baited hooks and incandescent lights are lowered into the water to attract squid and then hauled up slowly to concentrate the catch near to the surface [68]. As wandering albatrosses are surface seizers, they can become stuck on the hooks and drown [28].

As top predators, wandering albatross are useful bioindicators of the changing marine ecological conditions [167] and biologging studies such as this are an efficient way to monitor such changes, particularly as the growing human population requires more and more resources and the effects of climate change have a worsening impact on our ecosystems. Future research is needed into the current anthropogenic threats putting wandering albatrosses at risk in order to establish future threats and allow early mitigation if possible.

Conclusion:

The purpose of this study was to look into the foraging behaviour of free-living wandering albatrosses using high resolution tri-axial accelerometery and magnetometry data, with the goal of understanding how wandering albatrosses capture their prey, specifically if they engage in circling behaviour while on the surface of the water. The results of this study support the hypothesis that wandering albatrosses use circling behaviour to forage. However, the prey distribution is not static in space and time and it is highly influenced by several abiotic and biotic factors such as oceanographic processes and planktonic blooms. Although circling behaviour was identified, it is likely to be energetically expensive so is unlikely to be their main foraging technique, only being used when the environmental conditions are right, i.e., when primary production levels are high and the bioluminescent microorganisms are present in the water column. Given the increased anthropogenic levels of eutrophication in the oceans today, this foraging technique may become more prevalent in the future and these results highlight the need for future research into the novel foraging behaviours utilised by predators such as wandering albatrosses. The ability to identify and quantify free living predators' movements, foraging behaviour and prey resources has great value in ecological studies and it can provide a greater understanding of the motivation behind behaviours and ultimately the factors which influence the distribution of resources. This is particularly important within the Southern Ocean region which is often considered a window into the state of the world's marine environments. A greater understanding of our oceans is vital for our rapidly changing ecosystems and is essential to establish efficient conservation and management strategies to protect the number of wandering albatrosses from depleting further.

References:

1. Marohnić J. Diomedove Ptice: The Birds of Diomedes. VAPD. 2010; 103:41–61.

2. Gotch AF. Latin Names Explained: A Guide to The Scientific Classification of Reptiles, Birds & Mammals. Blandford Press; 1996.

3. Froy H, Lewis S, Catry P, Bishop CM, Forster IP, Fukuda A, et al. Age-related variation in foraging behaviour in the wandering albatross at South Georgia: No evidence for senescence. PLoS One. 2015; 1:19-10.

4. Weimerskirch H, Delord K, Guitteaud A, Phillips RA, Pinet P. Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. Sci Rep. 2015; 1:7-5.

5. Travis J. Do Wandering Albatrosses Care About Math? Science mag. 2007; 318:742–3.

6. Peterson I. Trails of The Wandering Albatross. Sci News. 1996; 150:104–7.

7. Cherel Y, Xavier JC, De Grissac S, Trouvé C, Weimerskirch H. Feeding ecology, isotopic niche, and ingestion of fishery-related items of the wandering albatross (*Diomedea exulans)* at Kerguelen and Crozet Islands. Mar Ecol Prog Ser. 2017; 565:197–215.

8. Schoombie S, Wilson R, Ryan P. Wind driven effects on the fine-scale flight behaviour of dynamic soaring wandering albatrosses. Mar Ecol Prog Ser. 2023;

9. Richardson PL. Upwind Dynamic Soaring of Albatrosses and UAVs. Prog Oceanogr. 2015; 130:146–56.

10. Phalan Ben, Phillips A Richard, Silk RD Janet, Afanasyev Vsevolod, Fukuda Akira, Fox J, et al. Foraging behaviour of four albatross species by night and day. Mar Ecol Prog Ser. 2007; 340:271–86.

11. Nevitt GA, Losekoot M, Weimerskirch H. Evidence for olfactory search in wandering albatross, (*Diomedea exulans)*. Pnas. 2008; 105:4576–81.

12. Weimerskirch H, Pinaud D, Pawlowski F, Bost CA. Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. American Naturalist. 2007; 170:734–43.

13. Weimerskirch H, Cherel Y, Delord K, Jaeger A, Patrick SC, Riotte-Lambert L. Lifetime foraging patterns of the wandering albatross: Life on the move! J Exp Mar Biol Ecol. 2014; 450:68–78.

14. Westrip J, Cooper J, Crawford R, Croxall J, Gales R, Phillips R, et al. The IUCN Red List of Threatened Species. 2018; 1:15.

15. Phillips RA, Croxall JP, Silk JRD, Briggs DR. Foraging ecology of albatrosses and petrels from South Georgia: Two decades of insights from tracking technologies. Aquat Conserv. 2007; 17:6–21.

16. Rackete C, Poncet S, Good SD, Phillips RA, Passfield K, Trathan P. Variation among colonies in breeding success and population trajectories of wandering albatrosses (*Diomedea exulans*) at South Georgia. Polar Biol. 2021; 44:221–7.

17. Croxall JP, Rothery P, Pickering SPC, Prince PA. Reproductive Performance, Recruitment and Survival of Wandering Albatrosses (*Diomedea exulans*) at Bird Island, South Georgia. Journal of Animal Ecology. 1990; 59:775–96.

18. Barnes SKN, Johnson DJ, Anderson MD, Taylor PB. Important Bird Areas in Africa and associated islands-South Africa. In: Fishpool LDC, editor. Important Bird Areas in Africa and associated islands Priority sites for conservation. BirdLife International; 2001; 793:876.

19. Nel DC, Ryan PG, Crawford RJM, Cooper J, Huyser OAW. Population trends of albatrosses and petrels at sub-Antarctic Marion Island. Polar Biol. 2002; 25:81–9.

20. Cooper J. Antarctica and Islands. Cape Town; 2006.

21. Chown Steven, Froneman P William. The Prince Edward Islands: land-sea interactions in a changing ecosystem. 1st ed. SunPress; 2008.

22. Sumner PD. Rock weathering rates on subantarctic Marion Island. Arctic Antarctic Alpine Rescue. 2004; 36:123–7.

23. Riotte-Lambert L, Weimerskirch H. Do naive juvenile seabirds forage differently from adults? Proceedings of the Royal Society B: Biological Sciences. 2013; 1:9-280.

24. Salamolard M, Weimerskirch H. Relationship Between Foraging Effort and Energy Requirement Throughout the Breeding Season in the Wandering Albatross. Ecology. 1993.

25. Sakamoto KQ, Takahashi A, Iwata T, Trathan PN. From the eye of the albatrosses: A bird-borne camera shows an association between albatrosses and a killer whale in the Southern Ocean. PLoS One. 2009; 1:4-10.

26. Weimerskirch Henri, Wilson P Wilson, Lys P. Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. Mar Ecol Prog Ser. 1997; 151:245–51.

27. Gutowsky ES. A Conceptual framework for the drivers of albatross movement. Mar Ornithol. 2017; 45:23–38.

28. Young L, VanderWerf E. Conservation of Marine Birds. Young L, VanderWerf E, editors. Hawaii: Academic Press; 2023.

29. Meese EN, Lowe CG. Active acoustic telemetry tracking and tri-axial accelerometers reveal fine-scale movement strategies of a non-obligate ram ventilator. Mov Ecol. 2020; 1:17-8.

30. Fernandez P, Anderson~ DJ. Nocturnal and diurnal foraging activity of Hawaiian albatross detected with a new immersion monitor. The Cooper Omithological Society. 2000; 102:577–84.

31. Weimerskirch H, Cherel Y, Cuenot-Chaillet F, Ridoux V. Alternative foraging strategies and resource allocation by male and female wandering Albatrosses. Ecology. 1997; 78:2051–63.

32. Jamieson AJ, Vecchione M. Hadal cephalopods: first squid observation (*Oegopsida, Magnapinnidae*, Magnapinna sp.) and new records of finned octopods (*Cirrat*a) at depths > 6000 m in the Philippine Trench. Mar Biol. 2022; 169:10–5.

33. Weimerskirch H, Huin N. Diving Depths of Albatrosses. Antarct Sci. 1994; 6:353–4.

34. weimerskirch H, Jouventin P., Claude Stahl J. Comparative ecology of the six albatross species breeding on the Crozet Islands. IBIS. 1985; 128:195–213.

35. Nel DC, Ryan PG, Nel JL, Klages NTW, Wilson RP, Robertson G, et al. Foraging interactions between Wandering Albatrosses (*Diomedea exulans*) breeding on Marion Island and long-line fisheries in the southern Indian Ocean. Ibis. 2002; 144:141–54.

36. Guiry EJ, James M, Cheung C, Royle TCA. Four millennia of long-term individual foraging site fidelity in a highly migratory marine predator. Commun Biol. 2022; 5:1–9.

37. Kirkman SP, Mann BQ, Sink KJ, Adams R, Livingstone TC, Mann-Lang JB, et al. Evaluating the evidence for ecological effectiveness of South Africa's marine protected areas. Afr J Mar Sci. 2021; 43:389–412.

38. Wilmers C, Nickel B, Bryce C, Smith J, Wheat R, Yovovich V. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology. 2015; 96:1741–53.

39. Wilson ADM, Wikelski M, Wilson RP, Cooke SJ. Utility of biological sensor tags in animal conservation. Conservation Biology. 2015; 29:1065–75.

40. Wilson RP, Vandenabeele SP. Technological innovation in archival tags used in seabird research. Source: Marine Ecology Progress Series. 2012; 451:245–62.

41. Burger EAlan, Shaffer AS. Application of tracking and data-logging technology in research and conservation of seabirds. The American Ornithological Society. 2008; 125:253–64.

42. Ripperger SP, Carter GG, Page Supervision RA, Duda N, Koelpin A, Weigel R, et al. Thinking small: Next-generation sensor networks close the size gap in vertebrate biologging. PLoS Biol. 2020; 1:25-18.

43. Williams HJ, Holton MD, Shepard ELC, Largey N, Norman B, Ryan PG, et al. Identification of animal movement patterns using tri-axial magnetometry. Mov Ecol. 2017; 47:60-5.

44. Andrzejaczek S, Gleiss AC, Lear KO, Pattiaratchi CB, Chapple T, Meekan M. Biologging tags reveal links between fine-scale horizontal and vertical movement behaviours in tiger sharks (*Galeocerdo cuvier*). Front Mar Sci. 2019; 1:13-6.

45. Yoda K, Naito Y, Sato K, Takahashi A, Nishikawa J, Coudert-Robert Y, et al. A New Technique for Monitoring the Behaviour Of Free-Ranging Adelie Penguins. J Exp Biol. 2001; 685–90.

46. Whitney NM, Pratt HL, Pratt TC, Carrier JC. Identifying shark mating behaviour using three-dimensional acceleration loggers. Endanger Species Res. 2010; 10:71–82.

47. Watanabe S, Izawa M, Kato A, Ropert-Coudert Y, Naito Y. A new technique for monitoring the detailed behaviour of terrestrial animals: A case study with the domestic cat. Appl Anim Behav Sci. 2005; 94:117–31.

48. Wilson RP, Liebsch N, Davies IM, Quintana F, Weimerskirch H, Storch S, et al. All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. Deep Sea Res 2 Top Stud Oceanogr. 2007; 54:193–210.

49. Brownscombe JW, Lee FG, Gutowsky AJ, Danylchuk S. Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. Mar Ecol Prog Ser. 2014; 505:241–51.

50. Jiménez S, Domingo A, Brazeiro A, Defeo O, Wood AG, Xavier JC, et al. Sex-related variation in the vulnerability of wandering albatrosses to pelagic longline fleets. Anim Conserv. 2016; 19:281–95.

51. Wilson RP, Weimerskirch H, Lys P. A Device for Measuring Seabird Activity at Sea. Source: Journal of Avian Biology. 1995; 26:172–5.

52. Antolos M, Shaffer SA, Weimerskirch H, Tremblay Y, Costa DP. Foraging behaviour and energetics of albatrosses in contrasting breeding environments. Front Mar Sci. 2017; 4:1–12.

53. Arnould JPY, Briggs DR, Croxall JP, Prince PA, Wood AG. The foraging behaviour and energetics of wandering albatrosses brooding chicks. Antarct Sci. 1996; 8:229–36.

54. Shaffer SA. Annual energy budget and food requirements of breeding wandering albatrosses (*Diomedea exulans*). Polar Biol. 2004; 27:1–14.

55. Rodhouse PG, Clarke MR, Murray AWA. Cephalopod prey of the wandering albatross (*Diomedea exulans*). Mar Biol. 1987; 96:1–10.

56. Cooper J, Henley SR, Klages NTW. The diet of the Wandering Albatross (*Diomedea exulans*) at Subantarctic Marion Island. 1992; 12:477–84.

57. Clarke MR, Croxall JP, Prince PA. Cephalopod Remains in Regurgitations of The Wandering Albatross (*Diomedea exulans*) At South Georgia. Marine Biological Association of the United Kingdom. 1981; 54:9–21.

58. Masuda D, Kai S, Yamamoto N, Matsushita Y, Suuronen P. The effect of lunar cycle, tidal condition and wind direction on the catches and profitability of Japanese common squid (*Todarodes pacificus*) jigging and trap-net fishing. Fisheries Science. 2014; 80:1145–57.

59. Humphries NE, Weimerskirch H, Queiroz N, Southall EJ, Sims DW. Foraging success of biological Lévy flights recorded in situ. 2012; 109:7169–74.

60. Williams HJ, Shepard ELC, Duriez O, Lambertucci SA. Can accelerometery be used to distinguish between flight types in soaring birds? Animal Biotelemetry. 2015; 1:11-3.

61. Rich Catherine, Longcore Travis. Ecological consequences of artificial night lighting. Island Press; 2006.

62. Ogunola OS, Onada OA. Fishing with light: Ecological consequences for coastal habitats. Int J Fish Aquat Stud. 2016; 4:474–83.

63. Amaral EH, Carr HA. Experimental Fishing for Squid with Lights in Nantucket Sound. Marine fisheries review. 1980; 51–6.

64. Torres LG, Thompson DR, Bearhop S, Votier S, Taylor GA, Sagar PM, et al. White-capped albatrosses alter fine-scale foraging behaviour patterns when associated with fishing vessels. Mar Ecol Prog Ser. 2011; 428:289–301.

65. Cooper' J, Wilson~ RP, Adams' NJ. Timing of foraging by the Wandering albatross (*Diomedea Exulans*). Polar Biol. 1993; 6:55–61.

66. Weimerskirch H, Guionnet T. Comparative activity pattern during foraging of four albatross species. Ibis. 2002.

67. Pajot A, Corbeau A, Jambon A, Weimerskirch H. Diel at-sea activity of two species of great albatrosses: the ontogeny of foraging and movement behaviour. J Avian Biol. 2021; 1:13-52.

68. Asokan K, Krishnan AR. Techniques to squid jigging in India: A review. J Entomol Zool Stud. 2021; 9:415–22.

69. Renjith RK, Paras NJha, Chinnadurai Shunmugavel, Remesan MP. Automated Squid Jigging and Prospects in Indian waters. ResearchGat. 2019;1–34.

70. Yamashita Y, Matsushita Y, Azuno T. Catch performance of coastal squid jigging boats using LED panels in combination with metal halide lamps. Fish Res. 2012; 113:182–9.

71. Nicholls DG, R Robertson CJ, Prince PA, Murray MD, Walker KJ, Elliott GP. Foraging niches of three Diomedea albatrosses. Source: Marine Ecology Progress Series. 2002; 231:269–77.

72. Weimerskirch H, Bonadonna F, Bailleul F, Mabille G, Dell'Omo G, Lipp HP. GPS tracking of foraging albatrosses. Science (1979). 2002; 1259:1262-295.

73. Weimerskirch H, Gault A, Cherel Y. Prey Distribution and Patchiness: Factors in Foraging Success and Efficiency of Wandering Albatrosses. 2005; 86:2611–22.

74. Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P. Foraging strategy of Wandering albatross through the breeding season: A study using satellite telemetry. Auk. 1993; 110:325–42.

75. Wilson RP, Weimerskirch H, Lys P. A Device for Measuring Seabird Activity at Sea. J Avian Biol. 1995; 26:172–5.

76. Lyu K, Zhang X, Church JA, Wu Q, Fiedler R, Dias FB. Roles of Surface Forcing in the Southern Ocean Temperature and Salinity Changes under Increasing CO2: Perspectives from Model Perturbation Experiments and a Theoretical Framework. J Phys Oceanogr. 2023; 53:19–36.

77. Cheung WWL. The future of fishes and fisheries in the changing oceans. J Fish Biol. 2018; 92:790–803.

78. Cianchetti-Benedetti M, Catoni C, Kato A, Massa B, Quillfeldt P. A new algorithm for the identification of dives reveals the foraging ecology of a shallow-diving seabird using accelerometer data. Mar Biol. 2017; 164:177-4.

79. Shaffer SA, Costa DP, Weimerskirch H. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. Funct Ecol. 2003; 17:66–74.

80. Nel DC, Ryan PG, Crawford RJM, Cooper J, Huyser OAW. Population trends of albatrosses and petrels at sub-Antarctic Marion Island. Polar Biol. 2002; 25:81–9.

81. Nel D, Omardien A. Towards the Development of a Marine Protected Area at the Prince Edward Islands WWF South Africa Report Series-2008/Marine/001. 2008; 1:201.

82. Pistorius P, Hindell M, Crawford R, Makhado A, Dyer B, Reisinger R. At-sea distribution and habitat use in king penguins at sub-Antarctic Marion Island. Ecol Evol. 2017; 7:3894–903.

83. Toolsee T, Lamont T, Rouault M, Ansorge I. Characterising the seasonal cycle of wind forcing, surface circulation and temperature around the sub-Antarctic Prince Edward Islands. Afr J Mar Sci. 2021; 43:61–76.

84. https://maps.google.com/. Google maps. 2023.

85. Wildbytestechnologies.com. Wildbytes technologies.2023

86. The efficiency of detecting seabird behaviour from movement patterns. MovEcol_2023.

87. Berrow SD, Croxall JP. Provisioning Rate and Attendance Patterns of Wandering Albatrosses at Bird Island, South Georgia. Condor. 2001; 103:230–9.

88. Gunner RM, Holton MD, Scantlebury MD, van Schalkwyk OL, English HM, Williams HJ, et al. Dead-reckoning animal movements in R: a reappraisal using Gundog. Tracks. Animal Biotelemetry. 2021; 1:37-9.

89. Wilson RP, Piitz K, Peters G, Culik B, Scolaro JA, Charrassin J-B, et al. Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildl Soc Bull. 1997; 1:101–6.

90. Yeap L, Shephard JM, Bouten W, Jackson B, Vaughan-Higgins R, Warren K. Development of a tag-attachment method to enable capture of fine- and landscape-scale movement in black-cockatoos. Australian Field Ornithology. 2017; 34:49–55.

91. https://github.com/DDMT-Software/DDMT. DDMT. 2023.

92. Shepard ELC, Wilson RP, Halsey LG, Quintana F, Laich AG, Gleiss AC, et al. Derivation of body motion via appropriate smoothing of acceleration data. Aquat Biol. 2008; 4:235–41.

93. Shepard ELC, Wilson RP, Halsey LG, Quintana F, Laich AG, Gleiss AC, et al. Derivation of body motion via appropriate smoothing of acceleration data. Aquat Biol. 2008; 4:235–41.

94. Shepard ELC, Wilson RP, Quintana F, Laich AG, Liebsch N, Albareda DA, et al. Identification of animal movement patterns using tri-axial accelerometery. Endanger Species Res. 2010; 10:47–60.

95. https.timeanddate.com. Timeanddate. 2023.

96. Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P. Foraging Strategy of Wandering Albatrosses Through the Breeding Season: A Study Using Satellite Telemetry. Auk. 1993; 110:325–42.

97. Fehlmann G, O'Riain MJ, Hopkins PW, O'Sullivan J, Holton MD, Shepard ELC, et al. Identification of behaviours from accelerometer data in a wild social primate. Animal Biotelemetry. 2017;5.

98. Pagano AM, Rode1 KD, Cutting A, Owen MA, Jensen S, Ware J V., et al. Using tri-axial accelerometers to identify wild polar bear behaviours. Endanger Species Res. 2017; 32:19–33.

99. Conners MG, Michelot T, Heywood EI, Orben RA, Phillips RA, Vyssotski AL, et al. Hidden Markov models identify major movement modes in accelerometer and magnetometer data from four albatross species. Mov Ecol. 2021; 1:7-9.

100. Ropert-Coudert Y, Wilson RP. Trends and perspectives in animal-attached remote sensing. Front Ecol Environ. Ecological Society of America; 2005; 437:44.

101. Ryan PG, Cooper J. Observer precision and bird conspicuousness during counts of birds at sea. South African Journal of Marine Science. 1989; 8:271–6.

102. Harper P. Feeding behaviour and other notes on 20 species of Procellariiformes at sea. Notornis. 1987; 34:169–92.

103. Imber M j, Russ R. Some Foods of The Wandering Albatross (*Diomedea exulans*). Journal of the Ornithological Society of New Zealand. 1975; 1:101-22.

104. Xavier JC, Walker K, Elliott G, Cherel Y, Thompson D. Cephalopod fauna of South Pacific waters: Mar Ecol Prog Ser. 2014; 513:131–42.

105. Nishizawa Bungo, Sugawara Takanori, Young LC, Vanderwerf EA, Yoda K Watanuki. Albatross-borne loggers show feeding on deep sea squids: implications for the study of squid distributions. 2018;257–65.

106. Richoux NB, Jaquemet S, Bonnevie BT, Cherel Y, McQuaid CD. Trophic ecology of Grey-headed albatrosses from Marion Island, Southern Ocean: Insights from stomach contents and diet tracers. Mar Biol. 2010; 157:1755–66.

107. Weimerskirch H. How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. Journal of Animal Ecology. 1998; 67:99–109.

108. Poupart TA, Waugh SM, Miskelly CM, Kato Akiko, Angel LP, Rogers KM, et al. Fine-scale Foraging Behaviour of Southern Buller's Albatross, The Only Thalassarche That Provisions Chicks Through Winter. Mar Ecol Prog Ser. 2019; 625:163–79.

109. Croxall JP, Prince PA. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biological Journal of The Linnean Society. 1980; 14:103–31.

110. Hunter S. Breeding biology and population dynamics of giant petrels Macvonectes at South Georgia. The Zoological Society of London. 1984; 203:441–60.

111. Häfker NS, Connan-McGinty S, Hobbs L, McKee D, Cohen JH, Last KS. Animal behaviour is central in shaping the realized diel light niche. Commun Biol. 2022; 1:8-5.

112. Cohen JH, Forward RB. Zooplankton Diel Vertical Migration — A Review of Proximate Control. Oceanography and Marine Biology. 1st ed. CRC Press; 2016; 89:122.

113. Bower JR, Takagi S. Summer vertical distribution of paralarval gonatid squids in the northeast Pacific. J Plankton Res. 2004; 851:857-26.

114. Mehner T. Diel vertical migration of freshwater fishes - proximate triggers, ultimate causes and research perspectives. Freshw Biol. 2012; 1342–1359.

115. Bastos R, Martins B, Cabral JA, Ceia FR, Ramos JA, Paiva VH, et al. Oceans of stimuli: an individual-based model to assess the role of olfactory cues and local enhancement in seabirds' foraging behaviour. Anim Cogn. 2020; 23:629–42.

116. Wilson RP, Neate A, Holton MD, Shepard ELC, Scantlebury DM, Lambertucci SA, et al. Luck in Food Finding Affects Individual Performance and Population Trajectories. Current Biology. 2018; 3871:3877-28.

117. Weimerskirch H, Wilson RP, Lys P. Activity pattern of foraging in the wandering albatross: A marine predator with two modes of prey searching. Mar Ecol Prog Ser. 1997; 151:245–54.

118. Weimerskirch Henri, Wilson P Rory. Oceanic respite for Wandering albatross. Nature. 2000; 406:955–6.

119. Weimerskirch H, Wilson RP. When do wandering albatrosses (*Diomedea exulans*) forage? Mar Ecol Prog Ser. 1992; 86:297–300.

120. Catry Paulo, Phillips A Richard, Phalan Ben, Silk RD Janet, Croxall P John. Foraging strategies of grey-headed albatrosses (*Thalassarche chrysostoma*): integration of movements, activity and feeding events. Mar Ecol Prog Ser. 2004; 280:261–73.

121. Lindsey Terence. Albatrosses. Csiro Publishing; 2008.

122. Prince PA, Huin N. Diving behaviour of the grey-headed albatross. Antarct Sci. 1997; 9:243–9.

123. Williams A, Dyer B, Randall R, Komen J. Killer Whales (*Orcinus Orca*) And Seabirds: Play, Predation and Association. Mar Ornithol. 1990; 37:41.

124. Ford JKB, Ellis GM. You Are What You Eat: Foraging Specializations and Their Influence on the Social Organization and Behaviour of Killer Whales. Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies. Japan; 2014; 75:98.

125. Prince P, Huin N, Weimerskirch H. Diving depths of albatrosses. Antarct Sc. 1994; 6:353–4.

126. Shealer DA. Biology of Marine Birds. Schreiber EA, Burger J, editors. CRC Press; 2002.

127. Hoving HJT, Zeidberg LD, Benfield MC, Bush SL, Robison BH, Vecchione M. First in situ observations of the deep-sea squid (*Grimalditeuthis Bonplandi*) reveal unique use of tentacles. Proceedings of the Royal Society B: Biological Sciences. 2013; 1:5-280.

128. Hodges CL, Woehler E. Associations Between Seabirds and Cetaceans In The Australian Sector Of The Southern Indian Ocean. Mar Ornithol. 1993; 22:205–12.

129. Fristrup KM, Harbison GR. How do sperm whales catch squids? Mar Mamm Sci. 2002; 18:42–54.

130. Júnior TV, Henrique D. Are deep-sea cephalopods really common prey for oceanic seabirds? Biota Neotrop. 2011; 11:177–81.

131. Jourdain E, Vongraven D. Humpback whale (*Megaptera novaeangliae*) and killer whale (*Orcinus orca*) feeding aggregations for foraging on herring (*Clupea harengus*) in Northern Norway. Mammalian Biology. 2017; 86:27–32.

132. Conners MG, Hazen EL, Costa DP, Shaffer SA. Shadowed by scale: Subtle behavioural niche partitioning in two sympatric, tropical breeding albatross species. Mov Ecol. 2015; 1:20-3.

133. McMillan CJ, Towers JR, Hildering J. The innovation and diffusion of "trap-feeding," a novel humpback whale foraging strategy. Mar Mamm Sci. 2019; 35:779–96.

134. Nyakatya MJ, McGeoch MA. Temperature variation across Marion Island associated with a keystone plant species (*Azorella selago* Hook. (Apiaceae)). Polar Biol. 2008; 31:139–51.

135. Cordero RR, Feron S, Sepúlveda E, Damiani A, Jorquera J, Rowe PM, et al. Ground-based measurements of the weather-driven sky radiance distribution in the Southern Hemisphere. Dunea D, editor. PLoS One. 2023; 18:1–14.

136. https://www.suncalc.org. SunCalc. 2023.

137. Obst BS, Hamner Peggy P Hamner WM, Wolanski E, Rubega M. Kinematics of phalarope spinning. Nature. 1996; 384:121–2.

138. Digiacomo A' PM, Hamnerb WM, Hamnerb PP, Caldeirab RMA. Phalaropes feeding at a coastal front in Santa Monica Bay, California. Journal of Marine Systems 2002; 37:199–212.

139. Tervo OM, Ditlevsen S, Ngô MC, Nielsen NH, Blackwell SB, Williams TM, et al. Hunting by the Stroke: How Foraging Drives Diving Behaviour and Locomotion of East-Greenland Narwhals (*Monodon monoceros*). Front Mar Sci. 2021; 1:18-7.

140. Valiadi M, Iglesias-Rodriguez D. Understanding bioluminescence in dinoflagellates—how far have we come? Microorganisms. MDPI AG; 2013; 3:25.

141. Martini S, Francis W, Francis WR. The Dark Ocean Is Full of Lights. Biodiversity. 2020;8.

142. Haddock SHD, Moline MA, Case JF. Bioluminescence in the sea. Ann Rev Mar Sci. 2010; 2:443–93.

143. Widder EA. Marine Bioluminescence. Bioscience; 2001; 3:9.

144. Ofer N, Bell F, Alistar M. Designing Direct Interactions with Bioluminescent Algae. DIS 2021 - Proceedings of the 2021 ACM Designing Interactive Systems Conference: Nowhere and Everywhere. Association for Computing Machinery, Inc; 2021; 1230:1242.

145. Haddock SHD, Moline MA, Case JF. Bioluminescence in the Sea. Ann Rev Mar Sci. 2010; 2:443–93.

146. Rohr J, Latz MI, Fallon S, Nauen JC, Hendricks E. Experimental approaches towards interpreting dolphin-stimulated bioluminescence. Journal of Experimental Biology. 1998; 201:1447–60.

147. Prince PA, Francis MD. Activity Budget of Foraging Gray-Headed Albatross. Condor. 1984; 86:297–300.

148. Waugh SM, Weimerskirch H, Waugh SM, Weimerskirch H. Environmental heterogeneity and the evolution of foraging behaviour in long ranging greater albatrosses. OIKOS. 2003; 103:374–84.

149. Perissinotto R, Lutjeharms JRE, Van Ballegooyen RC. Biological-physical interactions and pelagic productivity at the Prince Edward Islands, Southern Ocean. Journal of Marine Systems. 2000; 327:341-24.

150. Bryden. Harry, Beal L, Duncan L. Structure and Transport of the Agulhas Current and its Temporal Variability. J Oceanogr. 2005; 61:479–92.

151. Smith VR. Energy flow and nutrient cycling in the Marion Island terrestrial ecosystem: 30 years on. Polar Record. 2008; 44:211–26.

152. Herring PJ. Systematic Distribution of Bioluminescence in Living Organisms. J Biolumin Chemilumin. 1987; 1:147–63.

153. Lischka A, Piatkowski U, Hanel R. Cephalopods of the Sargasso Sea: distribution patterns in relation to oceanography. Marine Biodiversity. 2017; 47:685–97.

154. Young RE, Mencher FM. Bioluminescence in mesopelagic squid: Diel colour change during counterillumination. Science (1979). 1980; 208:1286–8.

155. Burford BP, Robison BH. Bioluminescent backlighting illuminates the complex visual signals of a social squid in the deep sea. Pnas. 2020; 117:8524–31.

156. Widder EA. Bioluminescence in the Ocean: Origins of Biological, Chemical, and Ecological Diversity. Science (1979). 2010; 328:704–10.

157. Vacquié-Garcia J, Royer F, Dragon AC, Viviant M, Bailleul F, Guinet C. Foraging in the Darkness of the Southern Ocean: Influence of Bioluminescence on a Deep Diving Predator. PLoS One. 2012; 1:11-7.

158. Cronin HA, Cohen JH, Berge J, Johnsen G, Moline MA. Bioluminescence as an ecological factor during high Arctic polar night. Sci Rep. 2016; 1:9-6.

159. Walker JS, Jones MW, Laramee RS, Holton MD, Shepard ELC, Williams HJ, et al. Prying into the intimate secrets of animal lives; software beyond hardware for comprehensive annotation in 'Daily Diary' tags. Mov Ecol. 2015; 1:16-3.

160. Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, et al. Can ethograms be automatically generated using body acceleration data from free-ranging birds? PLoS One. 2009; 1:12-4.

161. www.Worldometers.info. Worldometer.2023.

162. Gelcich S, Buckley P, Pinnegar JK, Chilvers J, Lorenzoni I, Terry G, et al. public awareness, concerns, and priorities about anthropogenic impacts on marine environments. PNAS. 2014; 111:15042–7.

163. Hautier Y, Tilman D, Isbell F, Seabloom E, Borer E, Reich P. Anthropogenic Environmental Changes Affect Ecosystem Stability Via Biodiversity. Plant Ecol. 2015; 348:336–9.

164. Prakash S, Verma AK. Anthropogenic Activities and Biodiversity Threats. International Journal of Biological Innovations. 2022; 04:94–103.

165. Bentley LK, Kato A, Ropert-Coudert Y, Manica A, Phillips RA. Diving behaviour of albatrosses: implications for foraging ecology and bycatch susceptibility. Mar Biol. 2021; 1:10-168.

166. Kuepfer A, Votier SC, Sherley RB, Ventura F, Matias R, Anderson O, et al. Prey-switching to fishery discards does not compensate for poor natural foraging conditions in breeding albatross. ICES Journal of Marine Science. 2022;

167. Perold V, Schoombie S, Ryan PG. Decadal changes in plastic litter regurgitated by albatrosses and giant petrels at sub-Antarctic Marion Island. Mar Pollut Bull. 2020; 1:8-159.

Appendix:

Appendix 1. Full list of squid species found in the stomach of wandering albatross at Kerguelen and Crozet Islands, in the Southern Ocean. This table is adapted from the results from Cherel et al. [7].

Species	Common name	Bioluminescence	Size of living species (cm)	Distribution
Architeuthis dux	Giant Squid	No	1300	Deep- sea
Illex argentinus	Argentine shortfin squid	No	30	Diel Vertically Migrating
Martialia hyadesi	Flying squid	Yes	40	Epipelagic
Todarodes pacificus	Japanese flying squid	No	30	Epipelagic
Filippovia knipovitchi	Smooth hooked squid	No	45	Mesopelagic
Kondakovia longimana	Oceanic squid	No	74	Deep-sea
Moroteuthopsis longimana	Giant warty squid	No	150	Epipelagic
Notonykia africanae	African club hook-squid	Yes	18	Deep-sea
Onychoteuthis banksii complex	Common club hook squid	Yes	35	Epipelagic
Onychoteuthis bergii	Hooked squid	Yes	35	Epipelagic
Onykia ingens	Greater hooked squid	Yes	94	Ontogenetic migrating
Onykia robsoni	Rugose hooked squid	Yes	75	Diel Vertically migrating

Species	**Common name**	**Bioluminescence**	**Size of living species (cm)**	**Distribution**
Psychroteuthis glacialis	Glacial squid	Yes	44	Mesopelagic
Slosarczykovia circumantarctica	Antarctic arm squid	Yes	17	Deep-sea
Gonatus antarcticus	Antarctic squid	No	23	Ontogenetic migrating
Lycoteuthis lorigera	Crowned firefly squid	Yes	8	Diel Vertically Migrating
Taningia danae	Dana octopus squid	Yes	230	Diel Vertically Migrating
Lepidoteuthis grimaldii	Grimaldi scaled squid	Yes	100	Deep-sea
Histioteuthis atlantica	Cock-eyed squid	Yes	35	Diel Vertically Migrating
Ancistrocheirus lesueurii	Sharpear enope squid	Yes	25	Mesopelagic
Histioteuthis eltaninae	Unknown	Yes	11	Diel Vertically Migrating
Histioteuthis macrohista	Deep-webbed jewel squid	Yes	7	Diel Vertically Migrating
Histioteuthis miranda	Unknown	Yes	26	Deep-sea
Stigmatoteuthis hoylei	Flowervase jewel squid	Yes	20	Diel Vertically Migrating
Alluroteuthis antarcticus	Antarctic neosquid	No	27	Epipelagic
Nototeuthis dimegacotyle	Unknown	No	8	Epipelagic
Cycloteuthis sirventi	Sirvent's disc-fin squid	Yes	1	Mesopelagic

Species	**Common name**	**Bioluminescence**	**Size of living species (cm)**	**Distribution**
Discoteuthis laciniosa	Crenellate disc-fin squid	Yes	7	Diel Vertically Migrating
Mastigoteuthis psychrophila	Whip-lash squid	Yes	14	Diel Vertically Migrating
Asperoteuthis lui	Whip-lash squid	Yes	20	Unknown
Chiroteuthis veranyi	Long-armed squid	Yes	130	Epipelagic
Batoteuthis skolops	The bush-club squid	Yes	4	Deep-sea
Galiteuthis glacialis	Glass squid	No	50	Diel Vertically Migrating
Mesonychoteuthis hamiltoni	Colossal squid	Yes	1000	Diel Vertically Migrating
Taonius belone	Glass squid	Yes	66	Diel Vertically Migrating
Teuthowenia pellucida	Googly-eyed glass squid	Yes	20	Diel Vertically Migrating

Appendix 2. Full list of fish species found in the stomach of wandering albatross at Kerguelen and Crozet Islands, in the Southern Ocean. This table is adapted from the results from Cherel et al. [7].

Species	**Common name**	**Bioluminescence**	**Size of living species (cm)**	**Distribution**
Bathyraja sp	Skate sp	No	Unknown	Deep-sea
Magnisudis prionosa	Southern barracudina	No	55	Mesopelagic
Lampadena notialis	Notal lanternfish	Yes	14	Mesopelagic
Muraenolepis marmoratus	Marbled moray cod	No	44	Deep-sea
Macrourus holotrachys	Bigeye grenadier	Yes	80	Deep-sea
Antimora rostrata	Blue antimora	Yes	75	Deep-sea
Halargyreus johnsonii	Slender codling	No	56	Deep-sea
Dissostichus eleginoides	Patagonian toothfish	No	200	Mesopelagic
Champsocephalus gunnar	Mackerel icefish	No	45	Deep-sea