Light-level geolocation reveals winter migration of the endangered Hutton's Shearwater (*Puffinus huttoni*)

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Author Contributions

The work in this thesis is primarily my own. The following people contributed in one or more ways:

Tim Guilford, Robin Freeman, Mike Bell and Elisabeth Bell were in charge of gathering the Hutton´s Shearwater data used in Chapters 2 and 3.

Tim Guilford, Holly Kirk, Annette Fayet, Akiko Shoji and Oliver Padget contributed to the data collection for the different seabirds in Chapter 2.

Tim Guilford has contributed with his ideas and feedback for all data chapters and all parts of the preparation of this thesis. I have also greatly benefitted from a number of comments and suggestions from Akiko Shoji, Holly Kirk, Oliver Padget, Rhiannon Meyer, Annette Fayet and from my advisors Chris Perrins and Alex Kacelnik.

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Contents

Chapter 1: General introduction 1

1.1 Hutton's shearwaters 2

1.2 Light-level geolocation. 4

1.3 Bibliography 6

Chapter 2: Latitudinal error around the equinox. Description of its structure and methods to deal with it. 9

2.1 Abstract 10

2.2 Introduction: 11

2.3 Materials and Methods 14

2.3.1 Data collection 14

2.3.2 Structure of the latitudinal error around the equinox 15

2.3.3 Comparison of filtering methods in Ground-Truthed data 15

2.3.4 Filters 17

2.3.5 Comparison of filtering methods in seabird tracks 19

2.4 Results 20

2.4.1 Structure of the latitudinal error around the equinox 20

2.4.2 Comparison of filtering methods in ground-truthed data 24

2.4.3 Comparison of filtering methods in live bird data 27

2.5 Discussion 35

2.5.1 Error structure around the equinox events: 35

2.5.2 Filters 1, 2 and 4: Omission-window filters 36

2.5.3 Filter 3 37

2.5.4 Filter 5 39

2.6 Bibliography 43

Chapter 3: Spatial description and phenology of the Hutton's shearwater (*Puffinus huttoni*) winter migration 47

3.1 Abstract: 48

3.2 Introduction: 49

3.3 Materials and Methods 52

3.3.1 Deployment of geolocators 52

3.3.2 Impact of geolocators 53

3.3.3 Light data analysis and filtering 54

3.3.4 Determination of itinerary and division of the year into different periods 54

3.3.5 Representation of the migration 56

3.3.6 Migratory phenology 56

3.3.7 Saltwater Immersion Data analysis 59
3.4 Results 63
3.4.1 Migration as a whole 63
3.4.2 Wintering Areas 74
3.4.3 Westwards Migration. 81
3.4.4 Eastwards migration: 86
3.4.5 Year to year differences in individuals tagged consecutive years 92
3.5 Discussion 94
3.5.1 Wintering areas of the Hutton's shearwater 94
3.5.2 Itineraries 96
3.5.3 Stopovers 98
3.5.4 Passage periods 100
3.6 Bibliography 101

Chapter 4: General conclusions 107
4.1 General conclusions 108
4.2 Final remarks 111
4.3 Bibliography 112

Appendices i
5.1 Appendix 1 ii
5.2 Appendix 2 xi
5.3 Appendix 3 xiii

Chapter 1:
General introduction

1.1 Hutton's shearwaters

Hutton's shearwaters (*Puffinus huttoni*) are a small (365g; Brooke, 2004) endangered seabird species endemic to the South Island of New Zealand. The breeding range of the species is limited to two colonies located on the Seaward Kaikoura Mountain Range between 1500m and 2000m above sea level (Sherley, 1992). The inaccessibility of the breeding location caused the breeding grounds to pass unnoticed until 1965 (Harrow, 1965) despite the species being described at the beginning of the XX century (Matthews, 1912).

Since the 1960s only, scientists have witnessed the loss of eight of the ten colonies originally discovered in the mountains around Kaikoura (Harrow, 1976; Sherley, 1992). Fossil evidence suggests the species could have had an even broader distribution ranging from North Canterbury to Mount Cookson before human settlers arrived (Worthy & Holdaway, 1995). This reduction in the breeding range is likely to have run parallel to a population decrease, but unfortunately there is no evidence for this assumption as the first population estimation was only made in 1986 (Sherley, 1992).

The causes behind the present day distribution is the introduction of a variety of fauna that has pressured the species back to the two most remote sites in their original range. The main impact is thought to have been caused by wild pigs (*Sus scrofa*) trampling on burrows and degrading burrowing habitat as their absence is the only difference between existing and extinct colonies (Cuthbert, 2001; Harrow, 2009). Chamois (*Rupicapra rupicapra*), red deer (*Cervus elaphus*) and goats (*Capra hircus*) have also played their role in eroding the burrowing grounds by grazing on the scarce vegetation (Harrow 1976, Sherley, 1992). Predators like stoats (*Mustela erminea*) and ferrets (*Mustela putorius*) have also been seen preying on both chicks and adults although they are not thought to be a major threat for the population (Cuthbert, 2001).

Nowadays threats at the breeding area have been taken care of through the culling of invasive fauna at the colonies (Clements & Griffin, 2011; Cuthbert & Sommer, 2009) and the banning of set nets around Kaikoura (Harrow, 2009). These measures are probably behind the stabilization in population numbers at around 300,000 – 350,000 individuals (Cuthbert & Sommer, 2009).

At sea Hutton´s shearwaters, like all other seabirds, face three main threats: Bycatch, pollution and overfishing (Croxall *et al.*, 2012). The only one of these three for which there are recorded data concerning the effect on the species is bycatch with up to eighty shearwaters having perished in a single set-net off Kaikoura (Harrow, 2009), at least demonstrating their inherent vulnerability.

The next step towards the long-term conservation of the species must be to assess whether and to what extent birds are threatened when they leave New Zealand coasts. This is especially relevant to seabirds, long-lived species with a low per-year reproductive output for which overwinter survival is key to the maintenance of population numbers (Croxall & Rothery, 1991). If on-land measures have stabilised the population, understanding of the threats at sea could be the key to increase the number of individuals out of endangerment.

To that end, the current thesis represents the first attempt to investigate the at-sea movements and behaviour of Hutton's shearwaters during the non-breeding season by using miniature on-board telemetry. In Chapter 3 of this thesis I make use of a data set derived from the deployment of light-level geolocation/salt-water immersion loggers (GLS) on 23 breeding individuals. Light data is used in order to determine the spatiotemporal distribution of the species outside of the breeding season and gain a detailed understanding of the winter

migration. Meanwhile, behaviour will be estimated from saltwater Immersion data. Its analysis will be used to study the phenology of the different stages of migration and to understand their functions within the year cycle. My aim for this third chapter is to gain an understanding of the species' migration that serves as a base for future accurate evaluation of threats and the eventual implementation of conservation measures.

1.2 Light-level geolocation.

Light-level geolocation is a tagging technique developed more than two decades ago that uses the time of sunset and sunrise to locate the device on the globe (DeLong *et al.*, 1992). In order to do this, Global Location Sensor tags –also known as geolocators or GLS- log light intensity allowing to draw the light curves for each day of the deployment. Once the device is recovered standard astronomical equations can be used to calculate two fixes per day: longitude is estimated from the times of sunrise and sunset and latitude from the proportion between day and night lengths (Hill, 1994).

Its simplicity has made it a relatively cheap, lightweight and long-lasting device that has made it a widespread tool for answering a number of fundamental ecological questions as well as for conservation. This has been especially beneficial for the study of seabirds, a group impossible to track with conventional methods over the vastness of the ocean. Below I summarize just a few examples of its use for seabird research.

The spatial description of the winter migration by itself already has great implications for conservation (Phillips *et al.*, 2007, Lewison *et al.*, 2012) by identifying important foraging grounds (Tranquilla *et al.*, 2013), stopovers in migration (Guilford *et al.*, 2008), the wintering grounds of an entire population (Frederiksen *et al.*, 2012) or even discovering unknown

migratory routes (Croxall *et al.*, 2005) and wintering areas (Fifield *et al.*, 2014). Geolocators have also been used to describe individual differences in migratory patterns (Dias *et al.*, 2011) and inter-specific segregation (Quillfeldt *et al.*, 2013; Linnebjerg *et al.*, 2013). They have also helped understand the species behaviour when at the breeding colony (Granadeiro *et al.*, 2009) and even to derive sex through the patterns of colony attendance (Guilford *et al.*, 2012).

When combined with environmental data the use of GLS has given us insight on the effect of moon phase on behaviour (Yamamoto et al, 2008, Guilford et al., 2012; Cruz *et al.*, 2013), the effect of wind on migration (Gonzalez-Solis *et al.*, 2009) or the relationship of bird distribution to particular environmental variables such as Chlorophyll a concentration (Ramírez *et al.*, 2013) or sea surface temperature (Quillfeldt *et al.*, 2013).

The great drawback of the method is its imprecision, chiefly the latitudinal unreliability around the equinoxes. Almost identical day lengths for the whole globe make it impossible to estimate latitude regardless of the accuracy in transition determination (Hill, 1994; Hill & Braun, 2001). This is very unfortunate as it is precisely with the change of the season that migratory animals migrate from wintering to breeding locations and vice versa. The study of this source of latitudinal error and of the possibilities to mitigate it will be the topic of Chapter 2 of this Thesis. To do that I will use empirical tracking data to study the error structure around the equinox and explore the possibilities of several new and existing filtering methods.

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Chapter 2:
Latitudinal error around the equinox.
Description of its structure and methods to deal with it.

2.1 Abstract

Latitude unreliability around the equinox events is probably the greatest drawback of using light-level geolocation to track migratory animals. Seasonal migrations by definition will have some degree of overlap with equinoctial error depriving researchers from important data for both science and conservation. Several theoretical studies have already described the expected magnitude and distribution of this error but here it is the first time that empirical tracking data is used for this purpose. In this chapter I will describe equinoctial error by using tracking data of six seabird species as well as stationary (ground-truthed) devices. This dataset will also be used to test the suitability of all previously described filtering methods plus two new suggested here for the first time. The conclusions of this study suggest a new source of error not foreseen in the theoretical studies and suggest a new filtering method based on the removal of fixes by latitude. This filtering method achieves on average less than 5 degrees of error during the equinox deleting only around 5% of the yearly fixes.

2.2 Introduction:

Technological development in the last few decades has transformed the study of wildlife. Our ability to build increasingly smaller and longer lasting devices has allowed us to gather information unimaginable only some decades ago, both in quantity and quality (Phillips *et al.*, 2008). The constant improvement in miniaturization and battery life have made it possible to track an increasingly greater number of bird species over a whole year cycle including small songbirds (Delmore *et al.*,2012; DeLuca *et al.*, 2015; Rodríguez-Ruiz *et al.*, 2014). Here I will focus on seabirds although the problems dealt with here are common for any other animals tracked using this technology.

GLS technology (or light-level geolocation) has been a major contributor to this increase in information (Philips *et al.*, 2008). Its simplicity (Hill, 1994) has made it possible to have a relatively cheap, light and small sized positioning device with years-long battery life.

The drawbacks of this positioning technology are related to the accuracy of its estimates. First, the best average estimation error is in the range of the 100 to 200 kilometres (Phillips *et al.*, 2004; Fudickar *et al.*, 2011). The second cause of inaccuracy is seasonal, more precisely around the equinoxes. GLS technology estimates latitude from day-length and night-length and around the equinoxes when both become homogenous at all latitudes. This means that small changes in their estimation (due to weather, behavioural shading, changes in the orientation of the device, etc.) can lead to great latitudinal error (Hill, 1994). The closer a certain day is to the equinox the more similar the day-length is across all latitudes and the greater the error that can be caused by a small change in the estimation of sunrises or sunsets (Hill & Braun, 2001). Besides, this also means GLS cannot compensate for this two sources of unreliability by

taking a greater number of fixes, meaning that there are strict limitations to the questions that the technology can be used to answer.

Latitudinal unreliability due to the equinox is especially critical for migratory periods. Most seabird species have different wintering and breeding areas to exploit seasonal resources and the displacement between these areas often happens at the change of the seasons, around the equinoxes (Brooke, 2004; Newton, 2007). Having two fixes per day in migrations of up to 950 kilometres per (Croxall et al., 2005) further reduces the number of position estimates per actual location of the animal, making it impossible to get a second fix to validate or invalidate any given position estimate.

Movements during migration are therefore a poorly known aspect of seabirds' annual cycle but nonetheless an important part of it. Knowledge of migration can help us answer fundamental ecological questions (Newton, 2007), but is also basic to conservation, a major topic for seabirds now that nearly half of the seabird species are in decline (Croxall *et al.*, 2012). Detailed knowledge of the spatial and temporal movements of these birds is key to evaluating the threats they can be exposed to (Lewison *et al.*, 2012). Acquiring the greatest amount of information possible is therefore a priority.

The paucity of fixes together with the unpredictability of the error and the lack of a clear boundary for the equinox effect have made different researchers deal with this problem in different ways. Most papers reviewed have chosen a one-by-one eye inspection of the dataset to determine erroneous position estimates (Croxall *et al.*, 2005; Quillfeldt *et al.*, 2014; Gilg *et al.*, 2013; Raine *et al.*, 2013; Guilford *et al.*, 2009, 2011, 2012; Gonzalez-Solís *et al.*, 2009; Tranquilla *et al.*, 2013, 2014; Pollet *et al.*, 2014). Some authors have chosen a systematic, automated method that would provide some objectivity to their filtering. Most of these

involve the deletion of the fixes taken during a set period around the equinox event. These methods will be reviewed in the Materials and Methods section of this chapter (DeLong *et al.*, 1992; Phillips *et al.*, 2004, Delmore *et al.*, 2012; Fudickar *et al.*, 2012; Cresswell & Edwards, 2013; McKnight *et al.*, 2013, Frederiksen *et al.*, 2012; Fort *et al.*, 2013). Only one paper (Gaston *et al.*, 2011) has used the dataset itself to decide on the reliability of the fixes, this method will also be reviewed below.

In this chapter I will first describe the error structure around the equinox, something that to the best of my knowledge is being described with empirical tracking data for the first time here. To do this I will use GLS data from devices left stationary for a year (ground-truthed) and from animal tracks of seven different seabird species as test data. Ground-truth data will also be used to compare five -3 existent and 2 new- filtering methods to determine which renders the best estimate with the lowest number of fixes deleted.

All five filters will then be applied to bird tracks at the same deletion level that was found optimal for each filter in ground-truthed data. The species of choice to apply this filtering to is the Manx shearwater (*Puffinus puffinus*). The reasons behind this choice is the species' long-distance trans-equatorial migration (Guilford *et al.*, 2009) that provides a strongest possible challenge for methods developed using static ground-truthed data.

With this research I aim to provide future researchers with tools for understanding the behaviour of latitudinal error around the critical equinox periods and help them in choosing the best suited filtering method to their studies.

2.3 Materials and Methods

2.3.1 Data collection

Data for ground-truthed geolocators were collected from Copeland Island, Northern Ireland (54.675ºN, 5.529ºW) from June 2008 to June 2011 and from Skomer Island, Wales (51.736ºN, 5.296ºW) from June 2010 to September 2011. At Copeland devices were cable-tied to a railing on the top of an old lighthouse at the Copeland Bird Observatory, facing away from the mainland where the city of Belfast is located. At Skomer they were tied to a vertical metal pole located at the western end of the island above Tom's House, facing away too from the mainland, where the oil refineries from Milford Haven could cause light pollution at night. As a result: eight complete equinox periods over four years. In order to make data from these two locations comparable all fixes had the latitudes of their respective known locations subtracted.

Data for geolocators mounted on seabirds were obtained from seven different species. Five of them were tagged on Skomer Island: Manx shearwater (*Puffinus puffinus*), Atlantic puffin (*Fratercula arctica*), Razorbill (*Alca torda*), Common guillemot (*Uria aalge*) and Black-legged kittiwake (*Rissa tridactyla*). The two remaining species were the Balearic shearwater (*Puffinus mauretanicus*), tagged at Sa Cella cave in Majorca, Spain (Guilford *et al.*, 2012) and the Hutton's shearwater (*Puffinus huttoni*), tagged at Kowhai River Colony (Sherley, 1992) in New Zealand. Geolocators used for this study are makes MK-6, MK-9, MK-13 and MK-15 from British Antarctic Survey (Cambridge, UK). Devices were attached by two cable ties (Panduit, USA) to a custom-made Darvic ring mounted on one of the birds' legs. Total weight of the deployment never meant more than 2% of the individual's weight at the moment of tagging.

Filtering of GLS data was done by using a threshold of 10 light-intensity units to locate transitions (sunrises and sunsets) over the light-intensity curve. Erroneous transitions are often

encountered due to behavioural shading of the device, environmental features or artificial light sources during the night (Porter & Smith, 2013). These were deleted manually until only one sunrise and sunset were left per day using the 'TransEdit2' tool of the BASTrak program, edition v16 (BioTrack, UK). For this purpose the integrity and shape of the curve together with the times of sunset and sunrise on previous and successive days were taken into account. Only for some days in Kittiwake, Razorbill and Balearic Shearwater tracks was it impossible to retain any transition. The Hill-Ekstrom method was used for calibration of the sunset angle by using the 'GeoLight' package (Lisovski & Hahn, 2012) in R (R Core Team, 2012).

2.3.2 Structure of the latitudinal error around the equinox

The study of the equinox effect on latitudinal estimates is centred around the 20th of March and the 23rd of September. During these dates day-time and night-time are equal in length according to astronomical calculations, marking the limits between summer and winter. These days will be referred to as the 'equinox events' henceforth. In order to make sure that I included all possible effects of the equinox, the 'study period' will range fifty days both to the winter and the summer sides of the equinox events in question.

The basic plot used to visualize the effect of the equinox on location estimates consists of the latitudes of any given GLS plotted against the day of the year. These plots range for the whole 100-day study period both for ground-truthed and bird tracking data. This kind of plot is referred to as a 'latitudinal plot' from here on.

2.3.3 Comparison of filtering methods in Ground-Truthed data

Five different filtering methods were applied to the ground-truthed dataset. Three of them are given in the literature and two are newly described here. These filters were applied using

successively more restrictive thresholds or more 'costly' in terms of number of fixes deleted. The aim is to find the optimum level of deletion or 'optimal deletion threshold' for each filter: that which renders the best latitudinal estimate at a lower cost of deletion.

Before doing this it is necessary to take into account how estimates are, by default, slightly biased northwards and southwards (respectively northern winters and summers) even at times not close to the equinox (Lisovski *et al.*,2012). In order to avoid this bias from compensating for the errors of the opposite side of the equinox, the effect of the different filters was calculated separately for the two halves. However, the separation between the northern and southern bias –the 'bias-break'- does not coincide with the summer and winter halves marked by the equinox event. As predicted by Hill & Braun (2001), the greatest error in the equinox occurs on the winter side of the equinox. The precise moment of the year at which this happens will depend greatly on the latitude of the device and on the sunset angle used to make the astronomical calculations. From the observation of our data I can calculate this 'bias-break' to be on average seven days to the winter side of the equinox event. This is the day I used to divide the dataset so the underlying default bias did not interfere with deviation estimates. From here on, summer and winter sides of the equinox will be considered as those divided by the 'bias-break' instead of those delimited by the equinox event.

The five different filters were applied to the equinox as a whole but the resulting deviation in latitude was calculated separately for the summer and the winter sides. This was done separately for each equinox and then averaged together with the seven remaining equinox sides of the eight complete equinoxes I have information for. The values of optimal thresholds for each of the filters will allow us to draw comparisons among them.

The filters were compared with the estimated latitudinal deviation obtained outside of the equinox period. To calculate this I used the average latitudinal estimate of the months of June and December to compare for the summer and winter sides respectively.

2.3.4 Filters

All five filters were applied to the position estimate datasets without any other previous filtering:

A) Previously described filtering methods

*2.3.4.1 **Filter 1:** Removing a set number of days symmetrically around the equinox events.*

This is the most commonly described method in the literature. This method removes a set number of days (also called the 'omission window') symmetrically around the equinox event. Most authors in this category consider their omission window to be either 2 weeks (DeLong *et al.*, 1992; Phillips *et al.*, 2004; Gonzalez-Solís *et al.*, 2011; Delmore *et al.*, 2012) or 20 days/3 weeks (Fudickar *et al.*, 2012; Cresswell & Edwards, 2013; McKnight *et al.*, 2013) each side of the equinox. To apply this filter to ground-truthed data in successively more restrictive thresholds I have applied a symmetrical omission window increasingly wider around the equinox event.

*2.3.4.2 **Filter 2:** Removing days asymmetrically around the equinox events.*

Two other studies consider how the effect of the equinox on latitudinal estimation error is not symmetrical, but it is shifted towards the winter side of the equinox (Hill, 1994; Hill & Braun, 2001). Following this idea Frederiksen *et al.* (2012) effectively removed two weeks to the summer side of the equinox event and four to the winter side of it while Fort *et al.* (2013) remove one and three respectively. To implement this filter the omission window's origin was

located at the equinox event but the omission window was twice as wide to the winter side of the equinox as to the summer side.

2.3.4.3 Filter 3: *Filter based on latitudinal variance.*

Gaston *et al.* (2011) devised this method in which the dataset itself is used to decide on the validity of each fix. More precisely, they use a 7-day moving variance of the latitudinal estimates to decide on the reliability of the fixes. In their study they use a variance threshold three times greater than the variance of the last weeks of February and August for the respective equinoxes. In our study I have used the value of this 7-day moving variance as our reference to apply successively more restrictive thresholds.

B) Newly proposed filtering methods

2.3.4.4 *Filter 4: Symmetrical filtering around the mean distribution of erroneous locations.*

This method is a symmetrical omission-window filtering method like Filter 1. The difference lies in this method compensating for the equinox error being biased towards the winter side. To do this instead deleting more locations towards the winter side from the equinox event (as in Filter 2) the day around which the window is centred was located on the day in which the error is greatest. This day was chosen to be on the day at the bias-break (Lisovski *et al.*, 2012) which for my data was seven days to the winter side of the equinox event.

2.3.4.5 *Filter 5: Filtering by latitudes.*

The aim of this filter is to use the latitudinal plot and the knowledge of the error structure around the equinox to recognise and delete erroneous locations at a lower deletion cost. For ground-truth data the farthest latitudes are by definition those with the greatest error as there

is no movement to account for. To find the optimal deletion percentage increasingly restrictive thresholds will be applied at latitudes increasingly closer to the known location.

2.3.5 Comparison of filtering methods in seabird tracks

The optimal threshold for each of the filters calculated from ground-truthed data was then applied to tracking bird data except for Filter 5, for which no *a priori* considerations over the percentage of deletions were taken. The species chosen for this was the Manx shearwater, a trans-equatorial migrant involved in latitudinal changes of more than a hundred degrees of latitude in just a few weeks (Guilford *et al.*, 2009). These birds, as many others, attempt their outbound and return trips to Argentina near the equinoxes, making this species ideal for the study. The tracks of four Manx shearwaters will be shown for both the outbound and the return migration before and after being applied with each of the five filtering methods reviewed in this chapter. These maps will be shown together with the latitudinal plot indicating the data points filtered out with each of the methods. .

For illustration purposes tracks mapped show the latitudinal estimates corrected for fast displacement. As latitude is estimated from time differences between sunrises and sunsets fast directional movement can artificially alter day and night lengths by shortening (e.g. flying east) or lengthening them (e.g. flying west). The resulting track zigzags along the bird's trajectory rather than following a straight line. This can be easily detected by an algorithm and corrected, in my case this was done using the 'Locator' tool of the BasTrak software package v18.

2.4 Results

2.4.1 Structure of the latitudinal error around the equinox

The observation of the latitudinal plots corresponding to the ground-truthed data (Figure 2.1) show the error is not distributed randomly around the equinox but that it has a structure. This structure is consistent over both yearly equinoxes, over several years of ground-truthed data and over seven different seabird species (Figures 2.1 & 2.3).

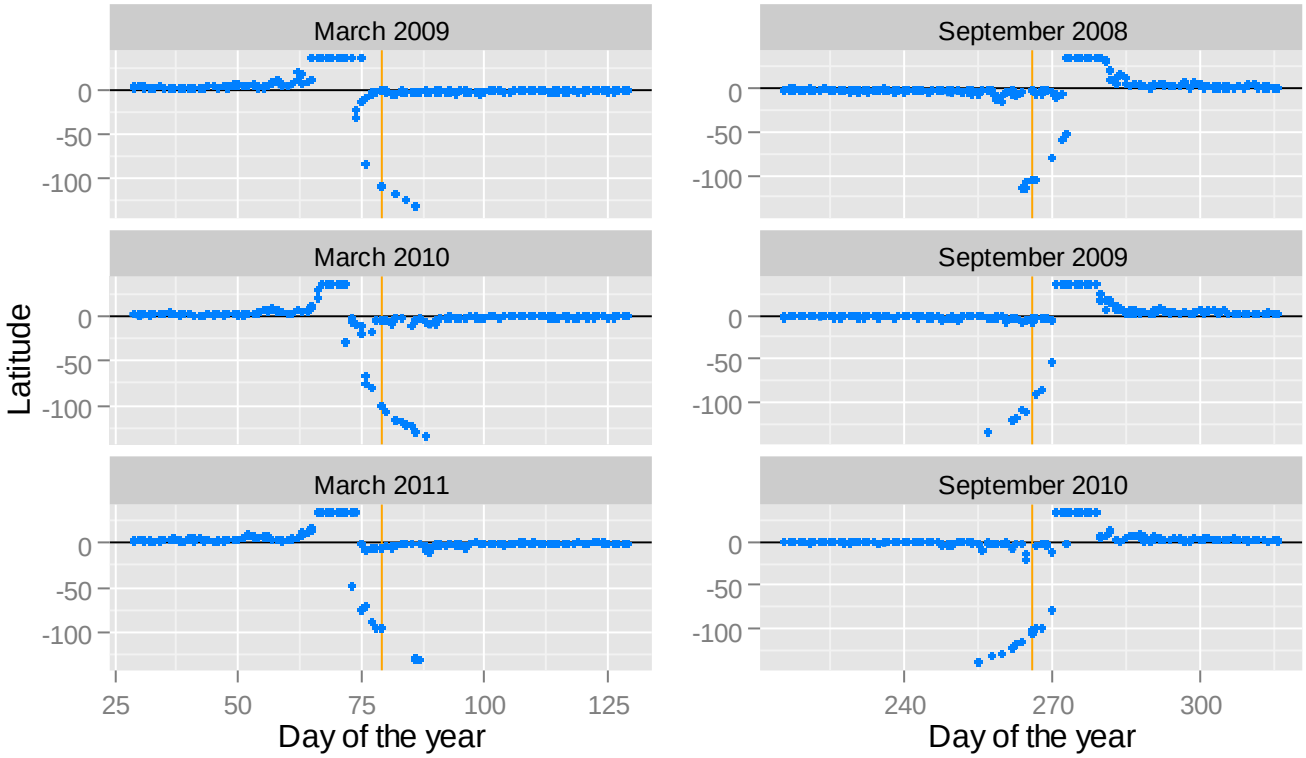


Figure 2.1: Latitudinal plots showing latitudinal estimates for six complete equinox periods for four different years of ground-truthed data at the northern hemisphere. Equinox events are represented by a vertical orange line and the known location by a black horizontal line.

This error structure in the equinox can be broken down into phases that help us describe it better. The phases will be described here as they happen chronologically at a March equinox in the northern hemisphere (Figure 2.2).

Phase 1: The only equinox effect on this phase is a slow increase of the northwards bias towards the equinox event reaching up to thirty five degrees of latitude in our sample (Figure 2.1 & figure 2.2).

Phase 2: Probably as a result of a total inability to calculate position in the days of greatest error this rising trend is interrupted and latitudes are estimated directly over the North Pole at 90ºN. This block of polar data points ranges from seven to fourteen days long and it shows both at the northern (Figures 2.1 & 2.3) and southern hemispheres (Figure 2.3*, P. huttoni*). This is true when using BASTrak software, the usage of other software like the R package 'GeoLight' or other applications based on it like IntiProc (Migrate technologies, Cambridge, UK) will result in the omission of these latitudinal estimates. The bias-break necessarily happens inside this phase as the error before is consistently biased northwards and southwards after it (Figures 2.1 & 2.3).

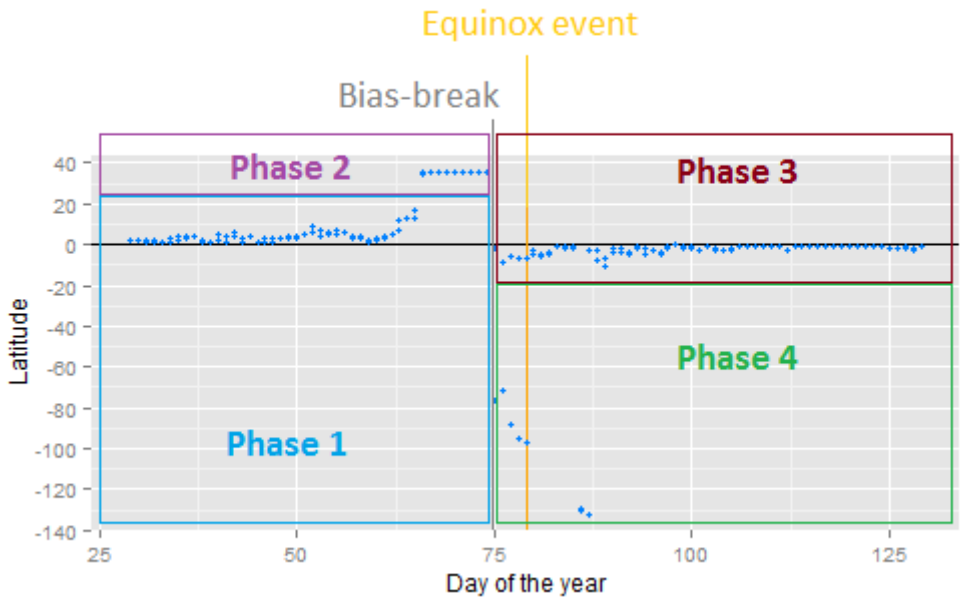


Figure 2.2: latitudinal plot showing an example ground-truthed March equinox in the northern hemisphere and the different phases it can be divided into. It also shows the positions of the bias-break (vertical grey line), the equinox event (vertical orange line) and the known location (horizontal black line).

The summer side of the equinox shows a completely different pattern, with latitudinal estimates distributed over two modes occurring simultaneously:

Phase 3: The main mode shows correct latitudinal estimates all through its extent except for those fixes closest to the bias-break. These are affected by southwards error that is greater the closer they are to the bias-break and reaching a deviation up to thirty degrees of latitude.

Phase 4: The other mode renders locations very far away from the known location and generally in the opposite hemisphere to where the GLS is at the moment (Figures 2.1, 2.3 & 2.5). These latitudinal estimates make a comma-like shape with the greatest error happening at the far end from the bias-break. In September these four phases happen in the opposite order, making for the mirror image of the March equinox (Figures 2.1 & 2.3).

In this study there is not many data for the southern hemisphere, only Hutton's shearwater data and Manx Shearwater data for when they cross the equator (Figure 2.3 & 2.5). In that hemisphere the biases are inverted for Phases 1, 3 and 4 and Phase 2 is still estimated at the North Pole.

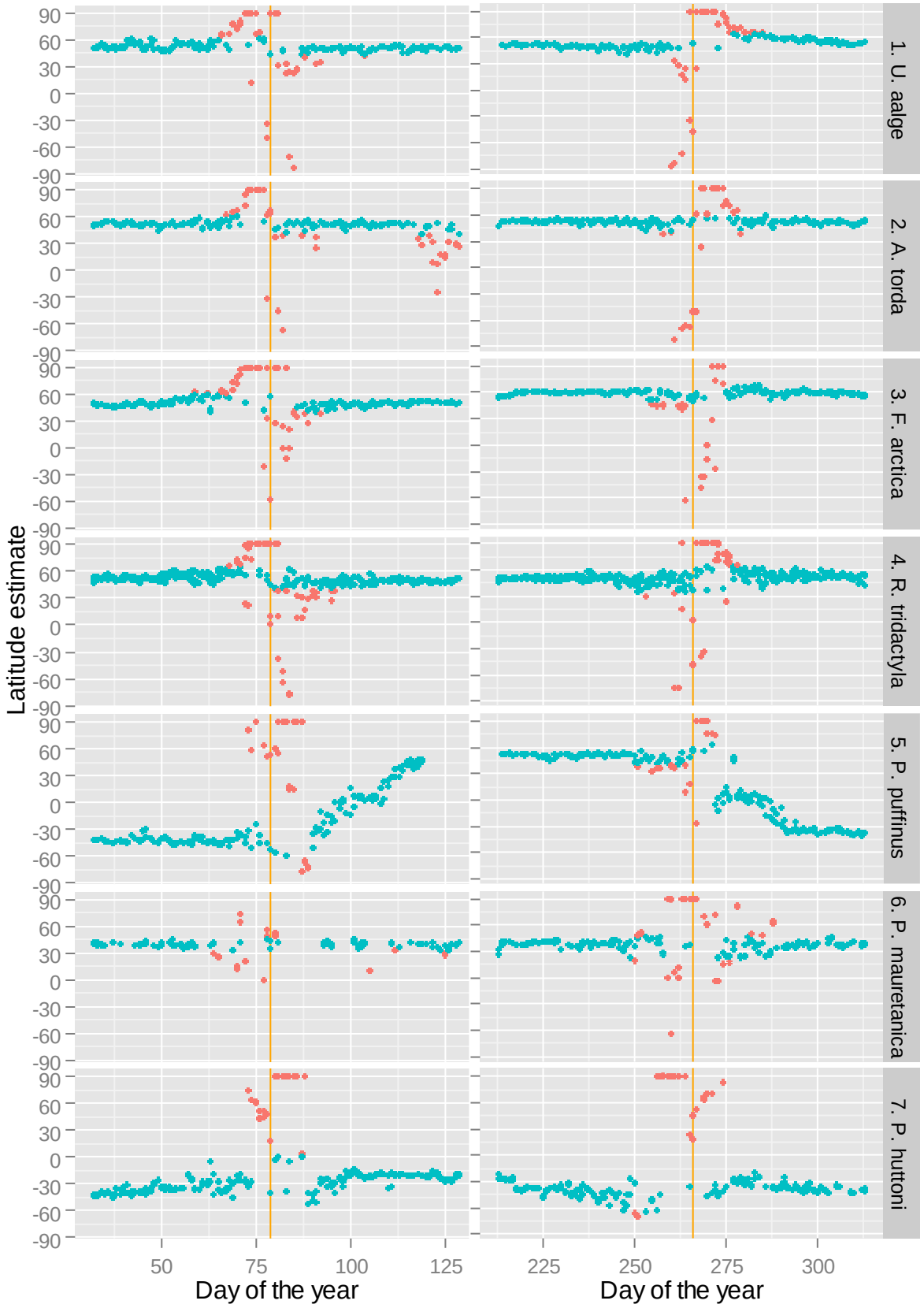


Figure 2.3: Latitudinal plots for a March and a September equinox for seven different seabird species: Common guillemot (*Uria aalge*), Razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica),* Black-legged kittiwake (*Rissa tridactyla*), Manx shearwaters (*Puffinus puffinus*), Balearic shearwater (*Puffinus mauretanicus*) and Hutton's shearwater (*Puffinus huttoni*). Equinox events are indicated by a vertical orange line. Latitudinal estimates considered erroneous by using Filter 5 are coloured red, those considered valid are coloured blue.

2.4.2 Comparison of filtering methods in ground-truthed data

Successively more restrictive thresholds achieve successively more accurate average estimates of the position, as expected. The rate of reduction in latitudinal deviation per unit of deleted fixes slows down until it asymptotes towards its respective value of the average latitudinal deviation during the equinox: 2ºN for the winter side and 1ºS for the summer side. This is true for all filters except for Filter 3 (Figure 2.4).

The optimal deletion threshold is considered to be the kink in the graph that precedes the asymptotic section as this is the point that achieves the best latitudinal estimate at the lowest deletion cost. The percentage of fixes deleted at that point will be considered from here on as the optimal deletion threshold.

Filters are applied to the whole equinox period but their efficiency has to be evaluated separately for the winter and the summer sides, meaning that filters can present a different threshold for each of both sides. Taking a conservative approach, the optimal deletion threshold of each filter will be considered the highest of both (Table 2.1).

By this criterion the best filter in performance is the latitudinal filter or Filter 5. It achieves an average of 3 and 2 degrees of deviation from the known location (for the winter and summer sides respectively) at only five percent of deleted fixes both at the winter and the summer sides (Figure 2.4, Table 2.1). Application of this filter at that threshold results in deleting all datapoints further than 7.5 degrees from the known location. As a result only some of the individual fixes closer to the bias break deviate over 5 degrees. If we consider all the data together we can see the daily average only very rarely crosses that 5 degree limit (Figure 2.5).

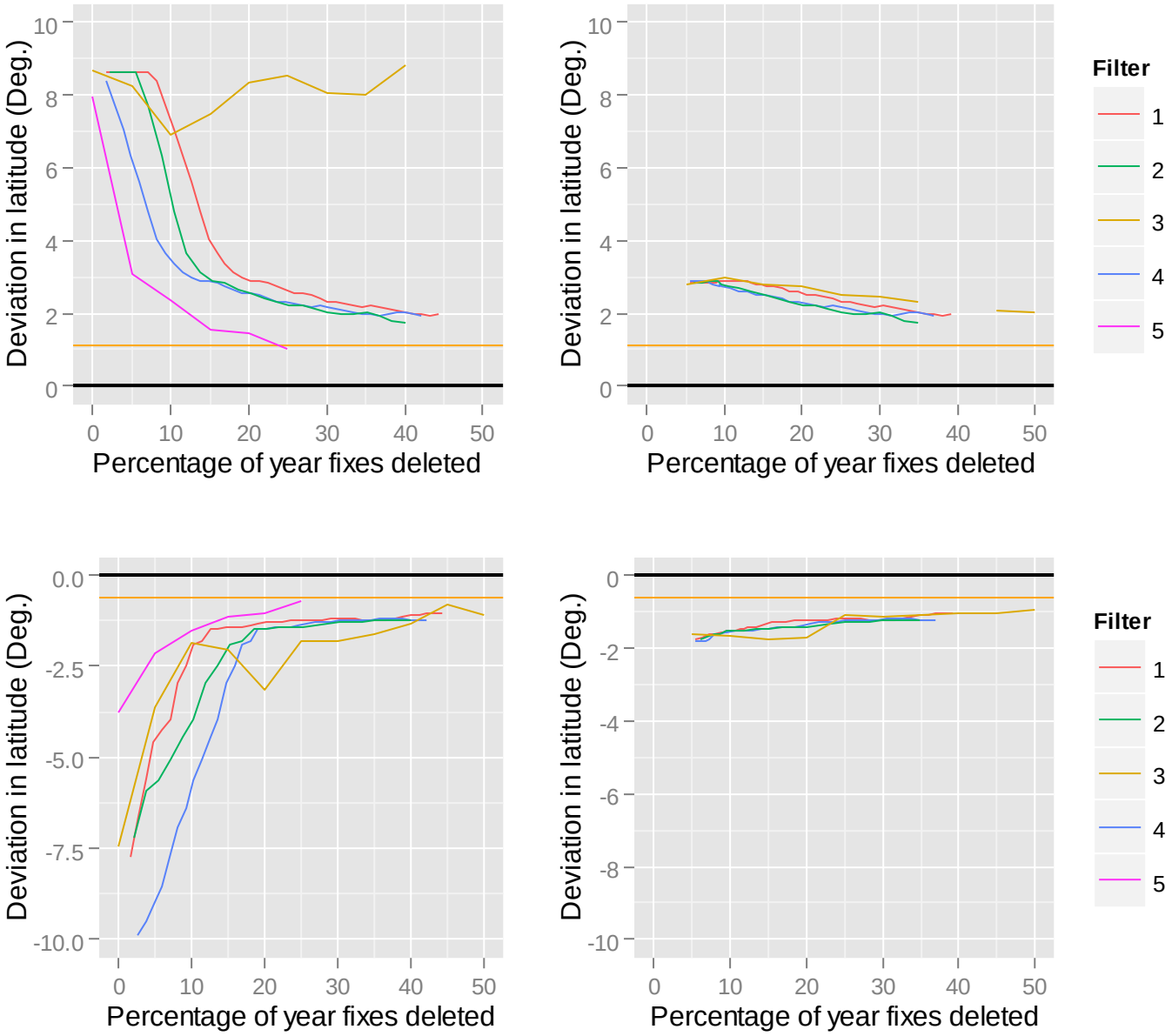


Figure 2.4: Graphs showing the application of successively more restrictive thresholds for all five filters tried on ground-truthed data. Filter trials are analysed differently for the winter (**top** half) and summer side (**bottom** half) of the equinox. **Left)** Filtering applied to unfiltered data. **Right)** Filtering after filter 5 has been applied to the dataset.

Table 2.1: Table showing the optimal deletion thresholds for the five filtering methods studied as extracted from figure 2.4. Thresholds chosen to apply for tracking data are highlighted in red.

	Filter 1	Filter 2	Filter 3	Filter 4	Filter 5
Winter	18.82%	13.70%	-	11.51%	5%
Summer	12.60%	18.63%	10%	19.18%	5%
Mean	15.71%	16.15%	10%	14.85%	5%

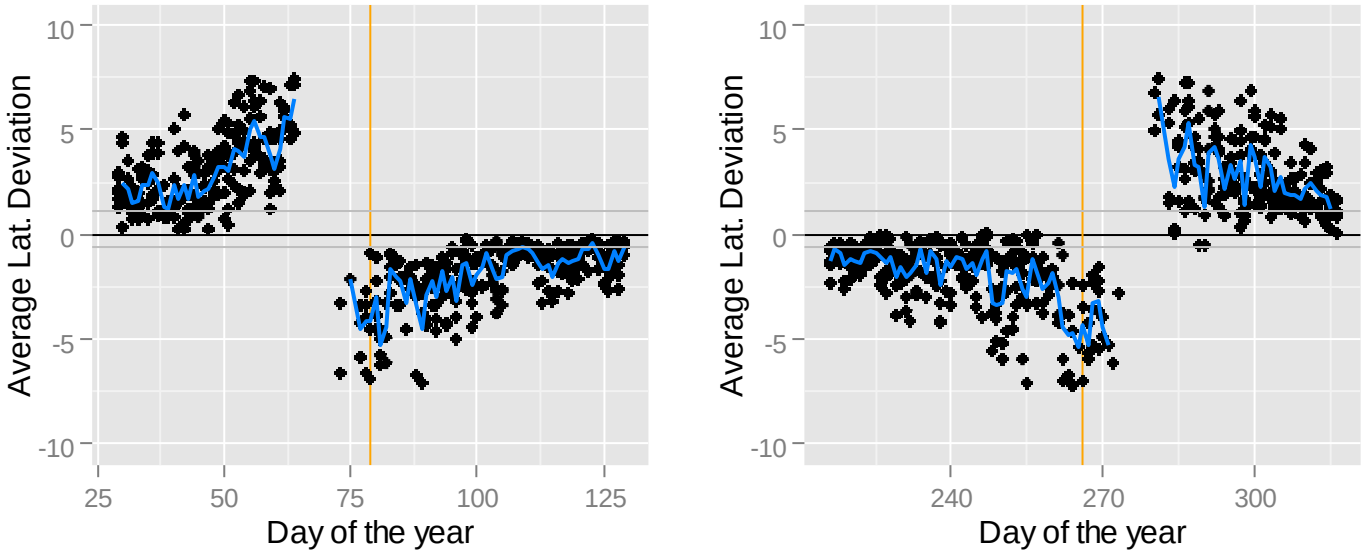


Figure 2.5: latitudinal plots for the eight equinox periods of ground-truthed data available. Black dots show the remaining fixes after deleting 5% of the yearly datapoints using Filter 5 or deleting all fixes further away than 7.5º from the known location. Blue line represents the daily average latitudinal deviation. Horizontal black line represents the known location. Horizontal grey lines represent the average deviation in two months not affected by the equinox: June and December. Vertical orange line represents the equinox events. **Left:** March equinox. **Right:** September equinox.

The second best filter is Filter 3, achieving its optimum at 10% of the data points deleted on the summer side. There are however, two problems with Filter 3. First, on the winter side it fails to achieve an estimate better than a very poor average deviation (Figure 2.4). And second, the results achieved by this filter vary greatly between devices (not shown), causing the erratic behaviour on both sides of the equinox (Figure 2.4).

All three omission-window filters show good performance for one of their sides, but very poor for the other (Table 2.1). In the discussion section a 29-day-wide omission will be suggested as the optimal length for a filter of this kind. In Figure 2.6 I aim to find the optimal day around which such window should be centred. According to the graph best result is rendered when the summer and the winter sides of the equinox are both closest to the known location (zero latitudinal deviation) and this shows to be the sixth day to the winter side of the equinox.

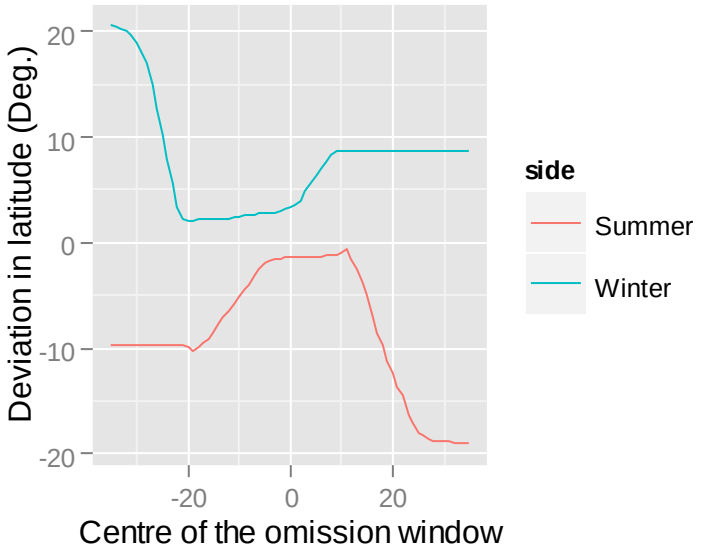


Figure 2.6: Average latitudinal deviation for the winter (Blue) and summer (Red) sides after applying all the different possibilities of a 29-day-long omission window for the 100-day study period in ground-truthed data. On the x axis zero indicates the equinox event (both March and September), positive numbers indicate the number of days to the summer side and negative numbers to the winter side.

2.4.3 Comparison of filtering methods in live bird data

The optimal threshold value of each filter as extracted from Figure 2.3 is applied to live bird data (Table 2.1). This means an omission window of 16 days for filter 4, 17 days for filter 2 and 18 days for filter 1. As it is impossible to find an optimum threshold for the winter side of Filter 3 I decided to use the 10% optimum of the summer side. This means the threshold is set at a value of 130 for the 7-day moving variance. For Filter 5 no goal of deletion was set beforehand. Instead the latitudinal plots were used to decide on where to draw the limits (Figure 2.12).

Figure 2.7 shows the outbound and return migration tracks for four Manx shearwaters before any filtering is undertaken. The route they follow in both migratory directions is broadly appreciable even without any filtering but there are many erroneous data points throughout both migratory periods.

On the outbound trip Filters 2 (Figure 2.9) and 4 (Figure 2.11) miss the whole migration and 1 (Figure 2.8) and 3 (Figure 2.10) only show the second half of it. Only filter 5 retains the first half of the migration for one of the birds (Figure 2.12).

On the return migration, the equinox event happens during the first half of the migration, making it almost impossible to retrieve much information from any of the birds. Nevertheless it is also clear how filter 1 (Figure 2.8) and filter 3 (Figure 2.10) fail to retrieve almost any information from the first half of the trip. Filter 2 (Figure 2.9) and Filter 4 (Figure 2.11) show one complete track of the four and filter 5 (Figure 2.12) achieves two of them.

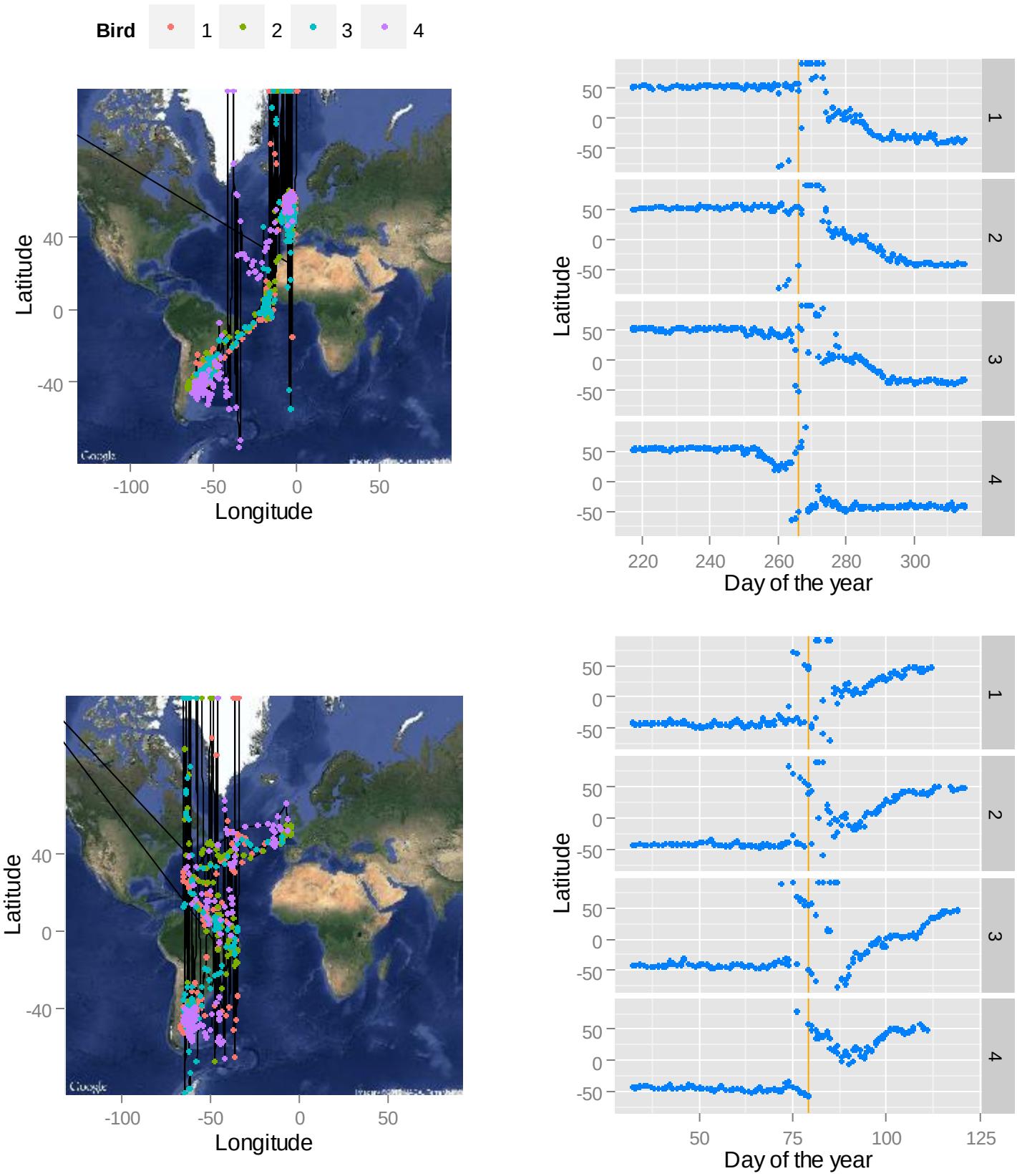


Figure 2.7: Four unfiltered Manx shearwater tracks for their outbound (top) and return migration (bottom). Left: maps displaying all fixes. Right: Latitudinal plots spanning a hundred days around the respective equinox event (vertical orange line). In this map the block of polar datapoints corresponding to phase 2 are plotted at the top of the map (latitude 80ºN) despite their real latitudinal estimate is 90ºN.

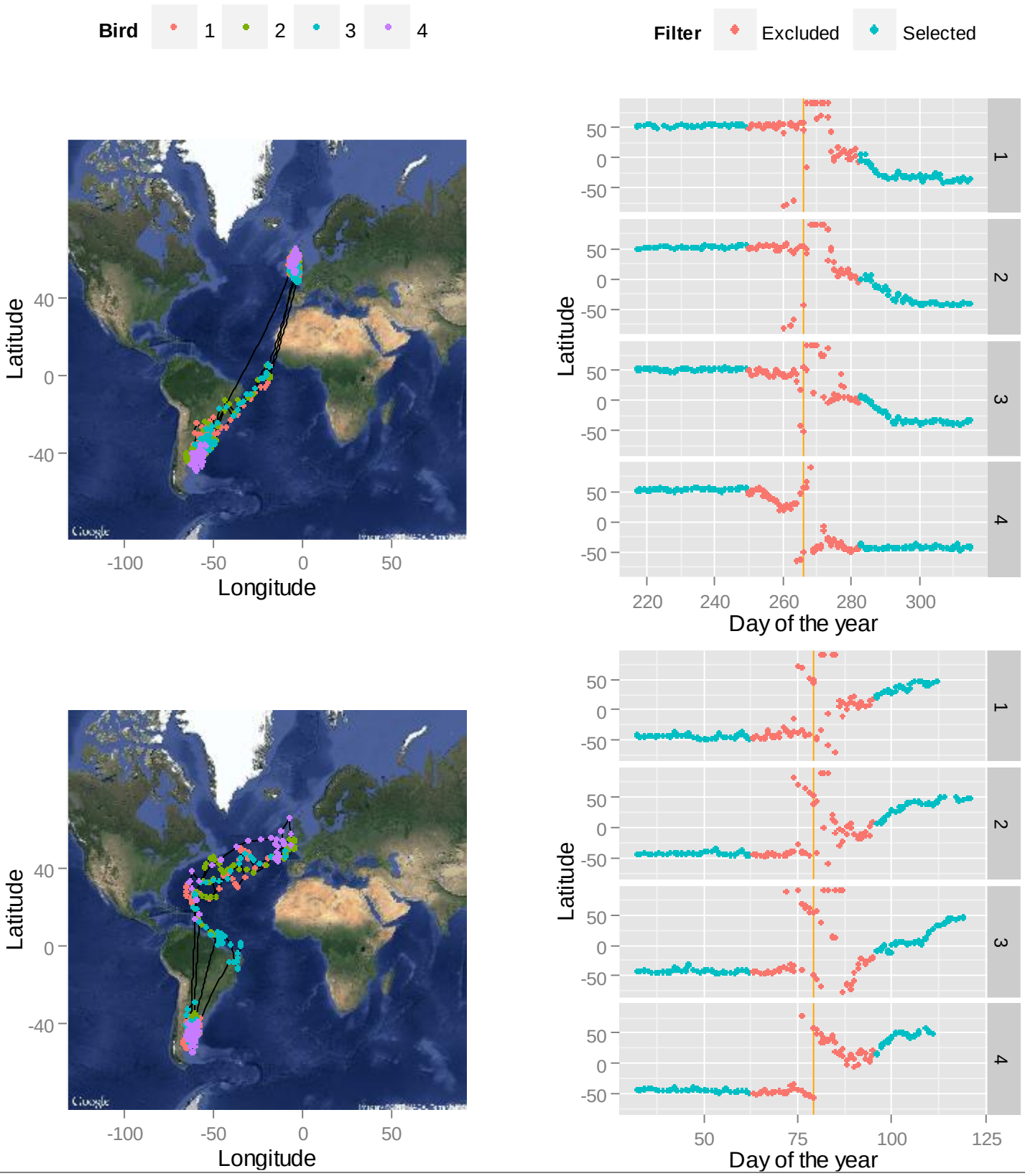


Figure 2.8: Filter1 applied to four Manx shearwater tracks for their outbound (top) and return migration (bottom). Left: maps displaying filtered fixes. Right: Latitudinal plots spanning a hundred days around the respective equinox event (vertical orange line). Selected datapoints are coloured blue and red for those excluded.

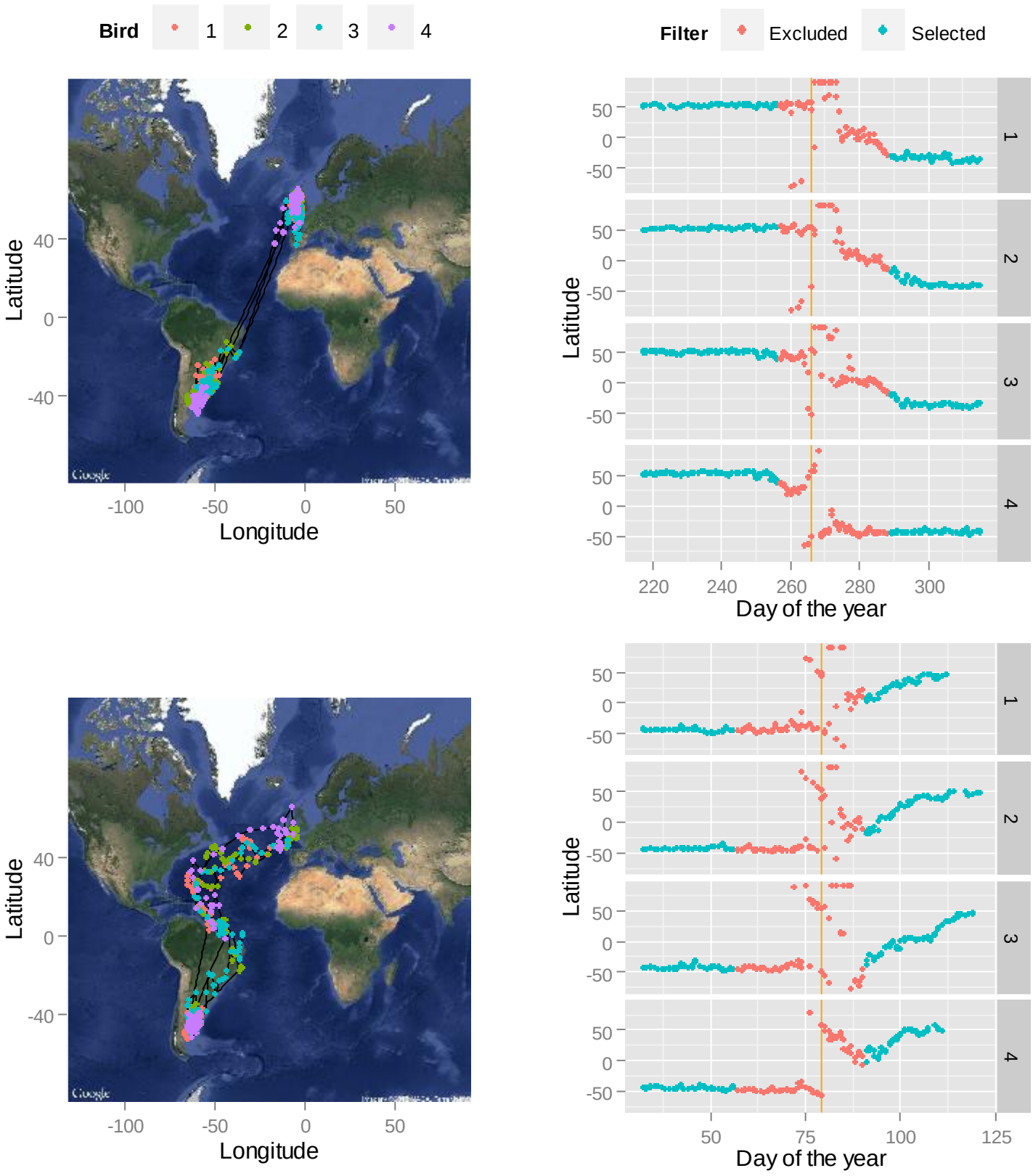


Figure 2.9: Filter 2 applied to four Manx shearwater tracks for their outbound (top) and return migration (bottom). Left: maps displaying filtered fixes. Right: Latitudinal plots spanning a hundred days around the respective equinox event (vertical orange line). Selected datapoints are coloured blue and red for those excluded.

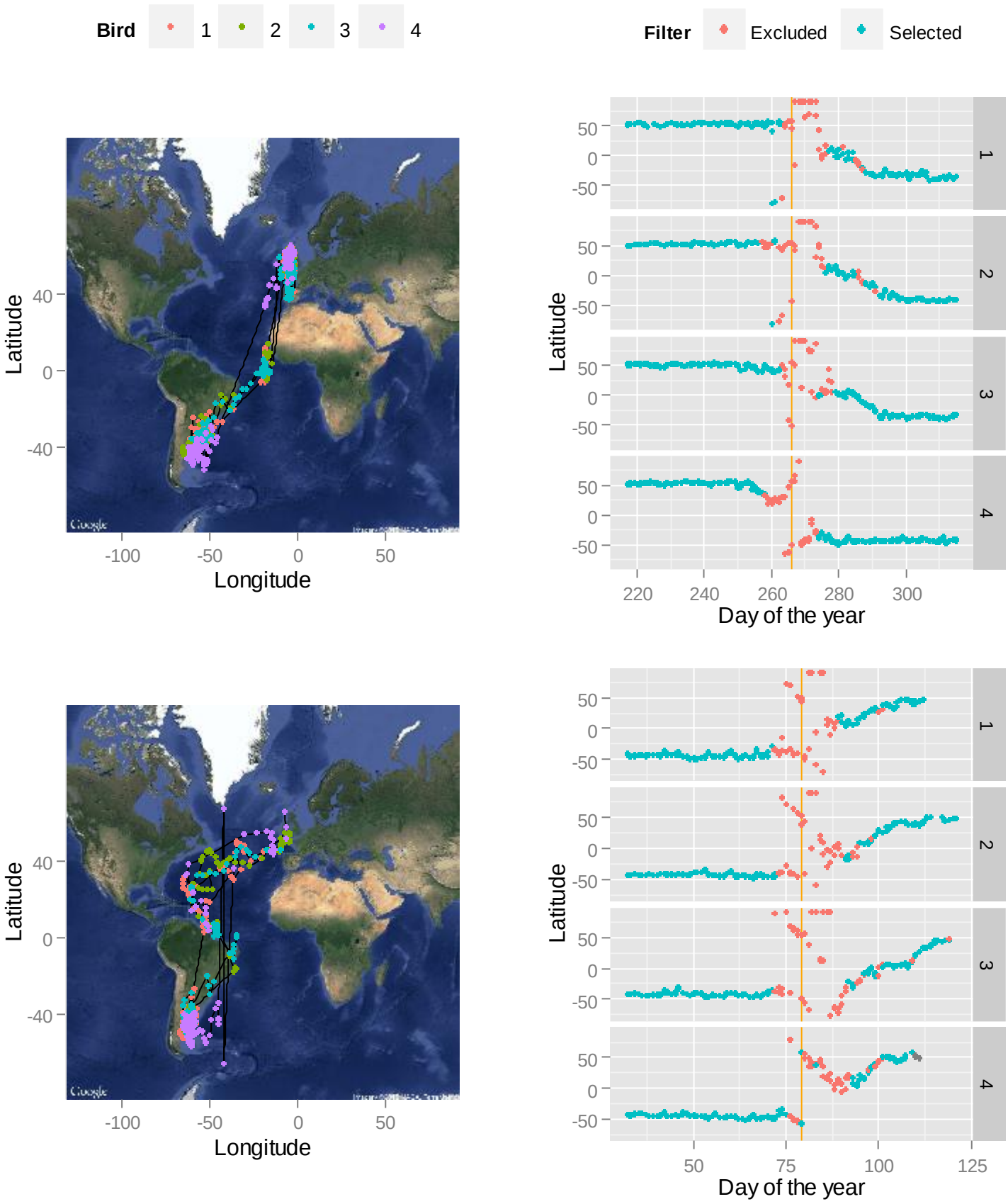


Figure 2.10: Filter 3 applied to four Manx shearwater tracks for their outbound (top) and return migration (bottom). Left: maps displaying filtered fixes. Right: Latitudinal plots spanning a hundred days around the respective equinox event (vertical orange line). Selected datapoints are coloured blue and red for those excluded.

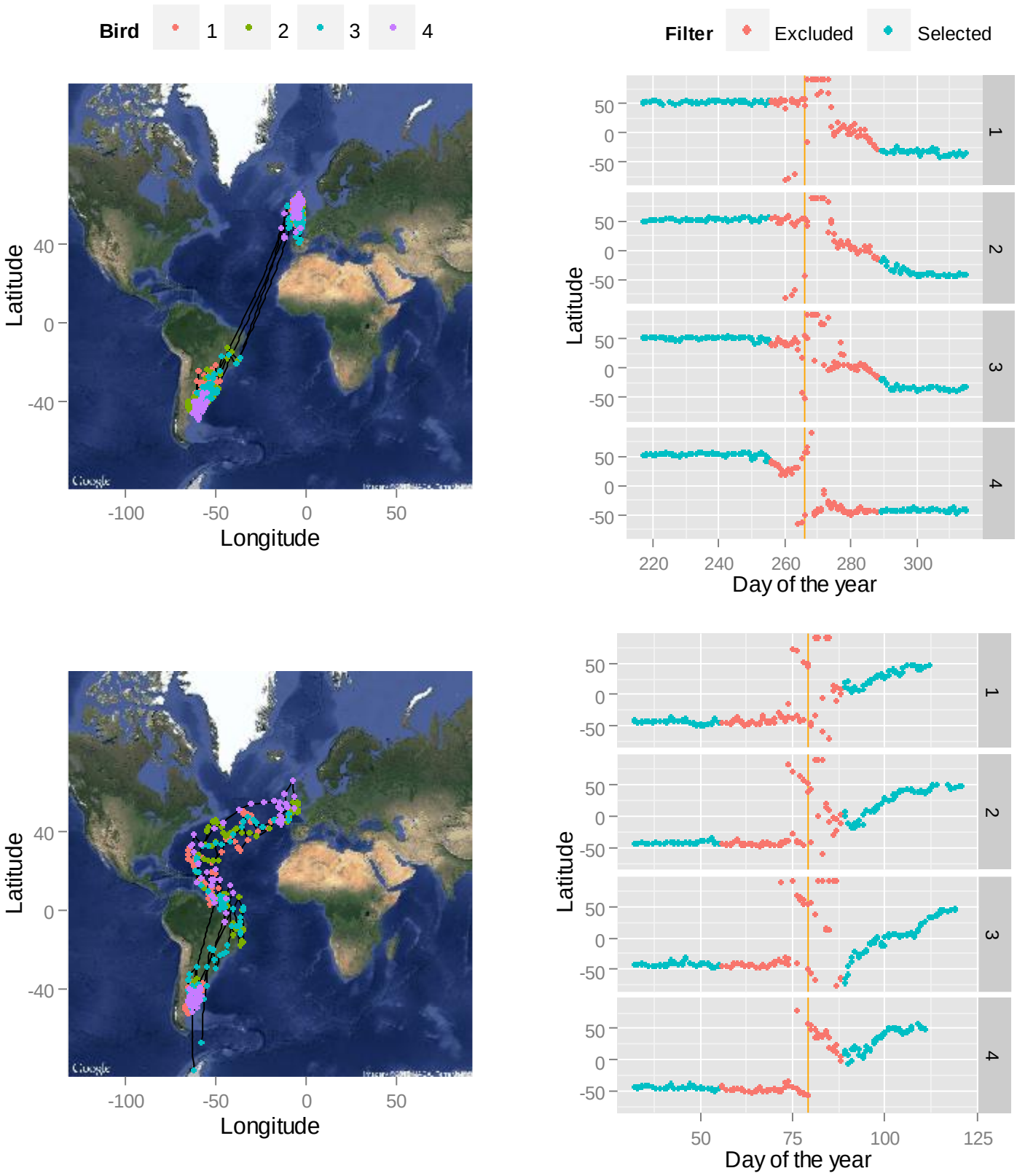


Figure 2.11: Filter 4 applied to four Manx shearwater tracks for their outbound (top) and return migration (bottom). Left: maps displaying filtered fixes. Right: Latitudinal plots spanning a hundred days around the respective equinox event (vertical orange line). Selected datapoints are coloured blue and red for those excluded.

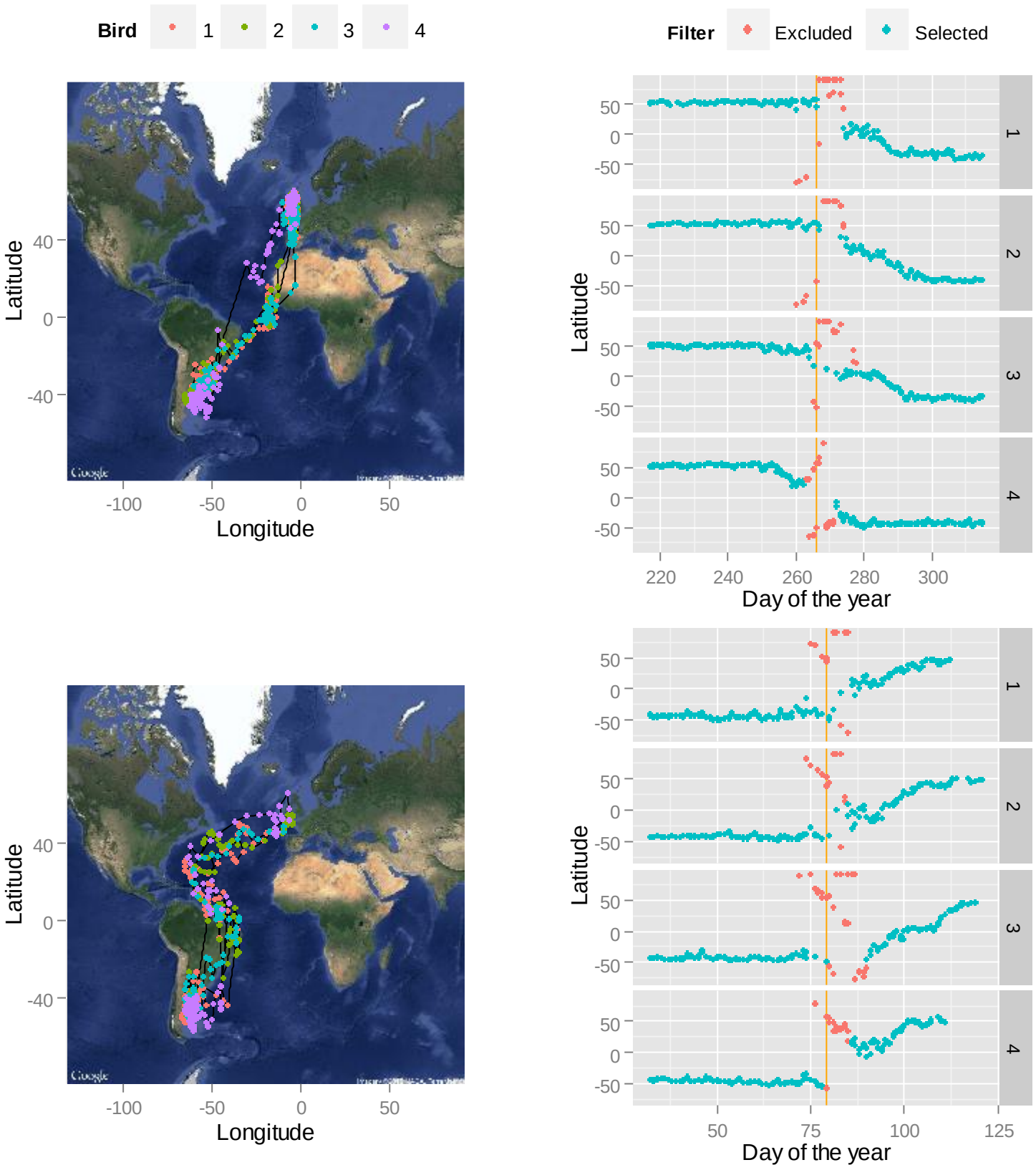


Figure 2.12: Filter 5 applied to four Manx shearwater tracks for their outbound (top) and return migration (bottom). Left: maps displaying filtered fixes. Right: Latitudinal plots spanning a hundred days around the respective equinox event (vertical orange line). Selected data points are coloured blue and red for those excluded.

2.5 Discussion

2.5.1 Error structure around the equinox events:

Our findings concerning the error structure around the equinox are consistent in many aspects with those found in the published literature. A bias-break happens as shown in Lisovski *et al.* (2012) with fixes being biased northwards in the winter side and southwards in the summer side. This is true for the northern hemisphere and the opposite for the southern hemisphere. Also the magnitude of the error in the latitudinal estimation is greater the closer fixes are to the effective equinox (Figure 2.5) as expected from Hill (1994). These theoretical studies describe the facts observed in Phases 1 and 3 (Figures 2.2 and 2.5), but not the other two.

Phase 2 corresponds to the period of greatest error when it is impossible to determine any latitude. At this period the BASTrak program defaults the latitude to 90ºN just as other algorithms (Lisovski et al., 2012 and programs based on it like IntiProc) return 'NA' for this same period. As expected by Hill (1994) and Hill & Braun (2001) this happens to the winter side of the equinox, further from the equinox event the further the device is from the equator. Also the bias-break seems to happen somewhere inside this phase of greatest error (Figure 2.2) as predicted in Lisovski *et al.* (2012).

Phase 4 is simultaneous to phase 3 on the summer side of the equinox. It could be caused by behavioural or weather shading, making the sunrises appear to be later -or sunsets earlier- than they really are. This is probably why the algorithm of the program allocates fixes in the opposite hemisphere, where it is now winter time and the days get shorter. The comma-like shape of the tail and how its error gets bigger the further the fixes are from the equinox had not been described yet and it is still unexplained.

Before discussing the filtering results it must be taken into account that even a month away from the equinox the average deviation from the known location is 2ºN in the winter side and 1ºS on the summer side (Figure 2.7). This average error is much greater that those calculated for June and December (1.01ºN and 0.63ºS) or those calculated previously by other authors (Phillips *et al.,* 2004, Fudickar et al., 2011). This is caused by the expected increase in the north or south bias (for winter and summer in the northern hemisphere respectively) towards the equinoxes (Lisovski *et al.,* 2012). This means that this is the optimal deletion that can be achieved even by applying a very conservative filtering. This can be explored visually in Figure 2.6 and it is the reason for all filtering methods in Figure 2.4 (but Filter 5) to asymptote towards 1ºS and 2ºN rather than towards the average estimates for June and December.

2.5.2 Filters 1, 2 and 4: Omission-window filters

Filters 1, 2 and 4 have a very similar performance pattern. The three of them show a very similar shape when applied in increasingly more restrictive thresholds to GT data (Figure 2.4) just happening at different values over the X axis. Also the three of them show two different thresholds for the winter and the summer sides of the equinox (Table 2.1). While Filter 1 reaches its optimal threshold at a lower cost in the winter side, filter 4 does so at the summer side and vice versa. Filter 2 having an intermediate position (Figure 2.4). This imbalance means that, as filters are applied to the whole equinox, it is necessary to use the most restrictive threshold to ensure a good estimate on both sides. This causes an unnecessary deletion of data points on the side with a less restrictive threshold that means losing seven and five percent of the yearly estimates for filters 1 and 2 respectively.

A desirable filter of this kind would have the same threshold on both sides, reducing the need to delete data points that do not contribute to achieve a better estimate. Averaging the

thresholds for both sides in Filters 1, 2 and 4 it is possible to see that this balancing should occur around 14.85-16.15% of deletion of the yearly estimates for the three filters (Table 2.1).

This similarity in the average for the three filters (Table 2.1) together with the similarities in curve shape (Figure 2.4) probably indicate that these three filtering methods are nothing but three facets of the same filter. This 'omission-window' kind of filter would involve the exclusion of a block 29 days wide around both equinoxes (15.5% of the yearly data points) and its optimal location would be centred seven days to the winter side of the equinox (Figure 2.6). Probably this window should be centred closer to the equinox event near the equator and further away from it when closer to the poles (Hill, 1994).

The omission window method is not the best approach to deal with the equinox problem. Even at the estimated best deletion rate of 15.5% is still much greater than that of filters 3 and 5. This is due to the need for the omission-window filters to have to delete days in a block, needing to stretch the window in order to get rid of phase 2 and 4 while deleting many valid Phase 1 and 3 points (Figure 2.2). This massive deletion deprives us of a great deal of information that could otherwise be useful (Figures 2.8, 2.9 & 2.11).

2.5.3 Filter 3

Filter 3 is probably the best option to carry out the filtering in a systematic and automated way. The deletion percentage needed is quite low, around 10% (Figure 2.3) and when applied to seabird tracks it seems to remove most of the phase 2 and 4 locations (Figure 2.10).

This percentage is far less than the 20% of the dataset that Gaston *et al.* (2011) claimed to delete in their original study. In that study they chose a conservative method to set the

threshold; they used three times the latitudinal variance of the last week of February and August for all tracks as threshold to filter for the respective March and September equinoxes. Applying this method to my dataset would mean a 7-day variance value of 29 that would cause the deletion of 37% of the yearly estimates. This difference in deletion percentage probably comes from our sample size being smaller than in the original paper (n = 4 here vs. n = 31 in Gaston *et al*., 2011). An analysis with fewer birds will achieve a smaller variance value and consequently achieve a greater deletion percentage. To avoid this dependence of the method on sample size I recommend the usage of the 10% deletion percentage obtained here as a guide when choosing a threshold for this method rather than a variance value, as the number of erroneous locations is likely to be similar among tracks.

This filter might encounter several problems, the greatest of them related to Phase 2 data. The presence of several estimates in the same position renders a 7-day moving variance of 0 for those far from the edges, making them invisible for our filter and affecting the averages for the winter side. This is the reason behind the failure in finding an optimal threshold for the winter side on the ground-truthed data (Figure 2.4 Left). Even if the Phase 2 and 4 are removed this filter shows no improvement over the omission-window filters (Figure 2.4 Right). In Manx shearwater tracking data this does not seem to be such a big problem (Figure 2.7) as tracks show noticeably fewer Phase 2 fixes than ground-truthed data (Figure 2.1). This is probably due to the trans-equatorial nature of the Manx´s migration. As showed in Hill (1994) and Hill & Braun (2001), the further the device is from the equator the further the time of greatest error will be biased towards the winter side. Therefore, if the bird moves towards the equator as winter approaches, the migration itself will reduce the number of datapoints affected by the worst part of the equinox error. The best example of this can be seen by observing the latitudinal plot for bird 4 on the outbound migration (Figure 2.7) that shows no Phase 2 error because it crosses the equator exactly during the equinox, effectively not being in winter at all

during its migration. This coincidence is unlikely to apply to the vast majority of studies as most seabird species are not trans-equatorial migrants (Brooke, 2004). The six other seabird species reviewed here show greater Phase 2 errors and it is likely they will need further filtering if applying filter 3 (Figure 2.3).

Another big problem for filter 3 in tracking data is the proximity in latitude that many phase 4 data points exhibit (Figures 2.3 & 2.10). This makes their 7-day variance value very low, not being removed by the filter creating the need for further processing (see bird 4 on its return migration; Figure 2.10).

This likely need for further processing after application of Filter 3 is not, in my opinion, a drawback of the method. What I suggest here is to take these decisions from the very beginning with the aim of preserving a greater amount of information. This is what I intend when suggesting the use of Filter 5.

2.5.4 Filter 5

This filter has proved to render the best estimates at the lowest cost both on ground-truthed (5%, Figure 2.3) and on empirical tracking data (5.4%, Figure 2.12). The effectiveness of the method is based on the knowledge of the error structure around the equinox. Most erroneous datapoints are those that have the greatest error (Figures 2.1, 2.2 & 2.3). This means removing those located farthest from the main trend (Phases 2 and 4) will remove most of the error in a minimal number of fixes. This is true and quite clear-cut for both ground-truthed data and seabird tracks, including most of those involving great latitudinal variation (Figures 2.1, 2.3 & 2.12).

The error in phases 1 and 3 is more difficult to filter as its contribution to the estimate only grows very gradually towards the bias-break. Knowing on which side of the equinox and which hemisphere the bird is at can give us a hint as to whether the observed movement in the estimates is due to the error or to the birds' movements (Figure 2.1) but it is not possible to be certain. This is going to make the decision on the quality of the estimate much less clear-cut (Birds 2 and 4 in Figure 2.12). This decision will be more complicated the faster the migration and the noisier the data are. In these cases the use of further knowledge including information on the biology of the species (e.g. previous sightings) or the usage of longitudinal and activity data from the logger (saltwater immersion, SST, TDR) is encouraged. If these data are unavailable the filter's low percentage of deletion allows for being conservative and still delete fewer datapoints than other filters.

Filter 5 needs to be applied to each equinox of each bird independently. This can be seen as a disadvantage due to the increase in labour, but I think that accounting for individual variability is a better way of dealing with equinox error. Individual differences in phenology will result in different passage and stopover periods for different individuals at different equinox phases. This will cause a different error structure for each bird that must therefore be dealt with individually. An example of this can be seen in how different Manx shearwater latitudinal plots look depending on the time at which the birds cross the equator (Figure 2.7). The same could be said if the different birds happened to take different routes in their migrations. This advantage of individual filtering over omission-window methods can be seen in Manx Shearwater tracks applied with filters 1, 2 and 4 (Figures 2.8, 2.9, 2.11). In these filters differences in the resulting filtered track mainly depend on the bird's displacement coinciding or not with the omission windows rather than on the effectivity of the filters as a method.

Filtering birds individually also has the advantage of not needing to take into account the variability in timing of the equinox error as it occurs at different times from the equinox event depending on the latitude and the sun elevation angle used (Hill, 1994, Hill & Braun, 2001). In the case of omission window filters this needs to be taken care of.

The application of Filter 5, however, can have two main sources of criticism: 'Cherrypicking' and inaccuracy.

Cherrypicking is the (usually unwittingly) biased choice of results based on the researcher's preconceived ideas. It can be argued that Filter 5 can offer a risk for this as sometimes the boundary between correct and incorrect fixes has to be set in a grey area due to the birds' movement together with the equinox error (Birds 2 and 4 in Figure 2.12). However, this is a risk that is always present when dealing with equinox error, be it setting up a variance threshold, the length and position of an omission window or deleting "obviously" erroneous datapoints. In order to avoid this it is necessary that filter 5 is applied in an informed and explicit manner.

In other words, reasons for deciding on a threshold must be made explicit as well as the thresholds themselves in order to make the use of this filter repeatable and assessable. Thresholds can be described very easily as a line in the Cartesian plane of the latitudinal plot. For birds that do not endeavour in a migration with a great latitudinal variation this filtering can be done just by stating the two latitudes that serve as upper and lower limits for the filtering (Figure 2.3).

For birds that have greater latitudinal changes in their migration the latitudinal threshold will need to vary with the date as the bird moves. This can be described using an equation of the

following kind: Latitude = slope · date + intercept as it is the case of the Manx shearwater (Figure 2.12). It would also be advised to make explicit the percentage of deleted fixes removed with this method to assess the level of conservatism applied by the researcher as this is an easy way to compare among studies.

The other criticism that can be made of the method concerns the accuracy of the resulting fixes. From ground truthed data we know that in the best case scenario the application of Filter 5 would result in the mean deviation ranging from 3.5 degrees at the closest days to the bias break to 1.25 degrees at 30 and 20 days from the equinox respectively for the winter and the summer sides (Figure 2.5). The greatest latitudinal deviation expected could be of up to 7.5 degrees (Figure 2.5). To put this in perspective this is a degree less than the whole island of Great Britain. This is a good result considering data from this period were discarded with other methods, however in real tracks such an efficient filtering is likely to be much more difficult due to error being confounded with the birds' displacement. For example, the gradual increase in error can cause a stationary period to look like a displacement period and displacement periods to have their trajectories altered.

To avoid this it is first advised to contrast the observed track from the estimates with the expected bias for the time of the year and to use several tracks with different phenologies before describing any migratory period spatiotemporally. As mentioned above the use of other data from the logger like longitude or activity data (e.g. Saltwater Immersion Data/SID, Sea Surface Temperature) is of great help when determining the trajectory of the bird. Saltwater immersion Data, for example, can very reliably determine when the animal has endeavoured in sustained flight helping assess whether observed displacements are real. A practical example of the use of longitude and activity data can be seen in Chapter 3 for the filtering of Hutton´s shearwater data.

Filters here have been applied on their own in order to make a clearer study, however these filters can be used in combination if researchers find it appropriate. On top of this further techniques can be applied to obtain more confidence on retained datapoints like the use of speed filters, Kalman filters, Tremblay *et al.*'s (2009) parsimony method or any other.

My aim here it is to provide the future researcher with an estimate of the error that can be expected to have and the results that could be expected when implementing any of the filtering methods reviewed. To do this I suggest the use of the latitudinal plot as a tool to visualize the error and to decide on a filtering method for each track. I hope this work helps researchers retain more information and gain further knowledge useful for both science and conservation.

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Chapter 3:
Spatial description and phenology of the Hutton's shearwater (*Puffinus huttoni*) winter migration

3.1 Abstract:

In this chapter I use light-level geolocation to describe spatiotemporally the winter migration of adult Hutton's Shearwaters (*Puffinus huttoni*) for the first time. Three migratory itineraries (including the long-time devised circumnavigation of Australia) and three different wintering areas north of Australia have been identified although the former are not necessarily related to the latter. A detailed spatiotemporal characterisation of the different stages of three itineraries has allowed the study of the migratory phenology and to establish relationships between its various stages. This, together with the behavioural characterisation, grant us a better understanding of the function of each stage in the year cycle, time allocation choices and the potential carry-over effects this time-budget can cause. Saltwater immersion data has also been successfully used to sex the birds and to locate the moulting period within the year cycle. The current information of the at-sea life of the species can already serve to assess the level of protection granted by the Australian Marine Protected Areas and conforms a solid base to design further studies and eventual conservation plans.

3.2 Introduction:

Endemic to New Zealand, the Hutton's shearwater (*Puffinus huttoni*) has faced an abrupt population decline as a result of the impact of invasive fauna on the breeding colonies (Cuthbert, 2001; Cuthbert & Davis 2002a). Of the at least ten (natural) colonies discovered in the last quarter of the twentieth century only the two most inaccessible ones remain today (Sherley, 1992). Research and conservation measures have concentrated on the introduced species and the preservation of the two last colonies (Cuthbert & Sommer, 2009). As a result, population numbers today have stopped their decline and are stable but with no increase (BirdLife International, 2014).

No research has yet been conducted on the species while at sea where, like many seabirds, this species might be seriously threatened by overfishing, bycatch and/or ocean pollution (Croxall *et al.*, 2012); of these, only bycatch has been described in the literature (Harrow, 2009). Knowing how important overwinter survival is for the sustainment of population numbers of long-lived seabirds with low reproductive yearly output (Croxall & Rothery, 1991; Cuthbert & Davis, 2002b) the study of the overwinter distribution of this endangered species becomes a priority.

The current degree of knowledge of the at-sea distribution of the species is only good during the breeding season, when the birds are mostly encountered within two hundred kilometres of their colony, between Cook Strait and Banks Peninsula (Halse, 1981; Harrow, 2009). Farther feeding trips south to the Otago peninsula and to the Chatham Islands have also been described although they seem to be infrequent (Harrow 2009). For reference on the geographical features mentioned in this chapter please refer to the maps in Appendix 3.

Agreement on the Hutton's shearwaters location during the breeding season is in marked contrast with the confusion surrounding their distribution overwinter which has persisted for almost half a century. Initially, Imber & Crocket (1970) suggested that the entire population left New Zealand waters after breeding while Serventry (1971) considered them to be a sedentary species like the closely related fluttering shearwater (*Puffinus gavia*). Harrow (1976) added to this by confirming the presence of high numbers of them close to the shore between the mouth of Ure River and Hamuri Bluff during every month of the year.

Sightings in Australia had been made but those individuals were hypothesised to be immature birds (Serventy *et al*., 1971) or attributed to *P. gavia* specimens (Shuntov, 1974). Nowadays, *P. gavia* are considered to be sedentary and to have never been reliably seen around Australia (Halse, 1981; Brooke, 2004). It was Halse (1981), after observing hundreds of individuals a day going south from Point Cloates in late winter, who first proposed those birds to be Hutton's shearwater adults wintering in the Indian Ocean. That same year Warham (1981) proposed Halse's observations to be part of an anticlockwise migration trip around Australia based on several bird recoveries in May from Booby Island in the Torres Strait (Vernon, 1977).

Marchant and Higgins (1990) gathered evidence of several more occurences of Huttons off Queensland coasts from February through to August and found the lack of overlap with Halse's records "confusing". This together with the lack of observations of big flocks crossing the very well invigilated Torres Strait made them dismiss the possibility of an anticlockwise migration. They hypothesized that wintering might happen in the Coral Sea but the return journey would be made reversing the outbound route, not crossing Torres Strait. Marchant & Higgins' (1990) conclusions are the base for currently accepted distribution of the species (Heather & Robertson, 1997; Brooke, 2004; BirdLife International, 2012; Figure 3.1 Left). There have been

more observations outside the described area since (Figure 3.1 Right) but no further discussion has been published on the topic.

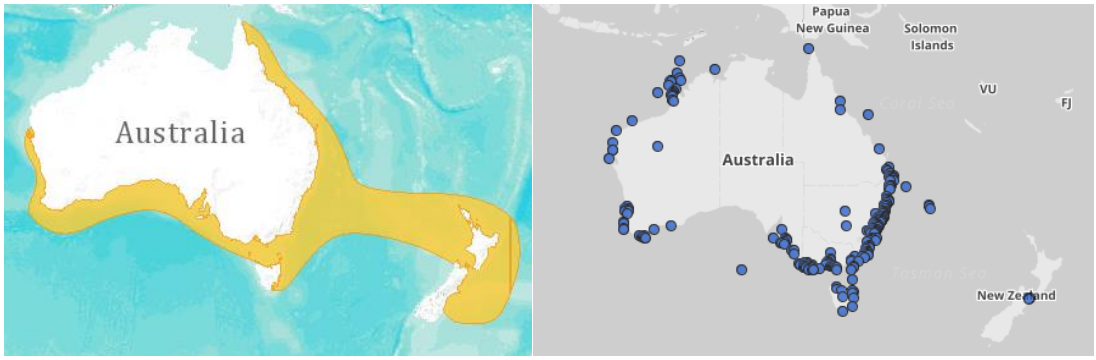


Figure 3.1: **Left**: Current knowledge on the winter distribution of the Hutton's shearwaters as originally proposed by Marchant & Higgins (1990), (From BirdLife International, 2012). **Right:** sightings 1990 – 2014 (ALA, 2014).

In this chapter I will use light-level geolocators to describe for the first time the overwinter migration of the Hutton's shearwater. This description involves the spatiotemporal characterisation of migratory routes, stopovers and wintering grounds as well as description of the birds' behaviours at these areas as estimated from the devices' on-board saltwater immersion data.

The aim of this chapter is to provide useful information for understanding the at-sea life of the species as a first step to assessing the threats it may be facing overwinter, and therefore to start prioritising its conservation needs.

3.3 Materials and Methods

Three main kinds of results were obtained from the GLS devices. Position estimates were analysed to describe the spatiotemporal distribution of the species while Saltwater Immersion Data (SID) was used to estimate behaviours during the migration and to estimate the sex of the individuals. The phenology of the migration was studied using both sources of data.

3.3.1 Deployment of geolocators

All Hutton's shearwaters were tagged at the Kowhai Valley colony (42.24ºS, 173.61ºE), the biggest of the two remaining natural breeding colonies. Birds were captured at their nests by hand although this sometimes involved the use of access hatches in the study burrows. Birds were tagged with BAS Mk-14 geolocators (British Antarctic Survey, Cambridge, UK), recording light intensity maxima every ten minutes and Saltwater Immersion Data (SID) every three seconds (collated into 10 minute bins of accumulated immersion). Devices were attached by two small cable ties (Panduit, USA) to a custom-made Darvic ring, with an all-up mass of 2.1 grams.

In total 23 Hutton's shearwaters were recovered, 17 in 2010 and 6 in 2011. For simplification birds have been given a code that has been used through the text to refer to each individual (Table 3.1). There is currently no information on the number of birds initially tagged neither for their reproductive success. Also there is no device identity data for birds tracked in 2011 nor burrow data for four of them.

Table 3.1: Table showing the code, burrow, Ring Number and device number for each of the birds together with deployment and retrieval dates. Note that code #12 and #13 are both the same individual (ring number 18454) in consecutive years. The same is true for #14 and #15 (ring number 18461).

Bird code	Burrow	Ring Number	GLS Number	Deployment	Retrieval	Year
1	a05	18462	gl9565	13/01/2010	08/12/2010	2010
2	a11	18464	gl3797	13/01/2010	09/12/2010	2010
3	a13	18453	gl9564	13/01/2010	07/12/2010	2010
4	a33	18455	gl9568	13/01/2010	11/12/2010	2010
5	a33	18457	gl9547	13/01/2010	11/12/2010	2010
6	a34	18458	gl9567	13/01/2010	08/12/2010	2010
7	a39	18466	gl3730	13/01/2010	10/12/2010	2010
8	a49	18456	gl9568	13/01/2010	12/12/2010	2010
9	a56	11460	gl9548	13/01/2010	06/12/2010	2010
10	a60	18465	gl3780	14/01/2010	06/12/2010	2010
11	a61	14263	gl3794	13/01/2010	11/12/2010	2010
12	a65	18454	gl9570	13/01/2010	13/12/2010	2010
13	a65	18454	-	13/12/2010	23/12/2011	2011
14	b03	18461	gl9580	13/01/2010	14/12/2010	2010
15	b03	18461	-	15/12/2010	23/12/2011	2011
16	b13	12906	gl3724	13/01/2010	23/12/2010	2010
17	b26	18452	gl9571	13/01/2010	11/12/2010	2010
18	b26	18459	gl9572	13/01/2010	13/12/2010	2010
19	nrB15	12717	gl9579	13/01/2010	23/12/2010	2010
20	-	11487	-	16/12/2010	22/12/2011	2011
21	-	14055	-	18/12/2010	22/12/2011	2011
22	-	19158	-	18/12/2010	22/12/2011	2011
23	-	19167	-	16/12/2010	22/12/2011	2011

3.3.2 Impact of geolocators

In this study I cannot provide with a measurement of the effect the deployment of geolocators could have had on the individuals due to the lack of other data than that extracted from the devices. Studies on other shearwaters have not shown impacts on reproductive success in similar shearwaters (*Puffinus tenuirostris*; Carey, 2011) but more detailed studies have shown impact on the levels of stress hormones for other seabirds (*Uria aalge* and *U. lomvia*; Elliott et al., 2012). Considering that Hutton´s shearwaters are endangered, studies of this kind shall be considered in the future.

3.3.3 Light data analysis and filtering

Light curves were analysed using a threshold-based method to determine the times of sunrises and sunsets. The threshold chosen was of 10 light intensity units combined with a sun elevation angle of -4.5 degrees for birds tagged in 2010 and -3 degrees for birds tagged in 2011. This change in sun elevation angle likely responds to the redeployment of devices, the GLS casing probably darkened during the deployment in 2010 so the sun elevation angle had to compensate for this in the 2011 deployments. Sun elevation angles were calculated using a Hill-Ekstrom calibration performed in the 'Geolight' package (Lisovski & Hahn, 2012) in R (R Core Team, 2012). Filtering around the equinoxes was performed following Filter 5 as described in Chapter 2 of this Thesis. A graphical representation of the filtering process of the 23 individuals can be consulted in Appendix 1.

3.3.4 Determination of itinerary and division of the year into different periods

As latitude estimations are unreliable for most of the migratory periods due to their coincidence with the equinox periods, longitudinal plots (Delmore *et al.*, 2012) have been used here to visualize the birds' migration (see Figure 3.2 for an example). This has allowed us to determine the itinerary around Australia followed by each bird as well as the stage of migration each bird was at.

Longitudinal data are still imprecise (Phillips *et al.*, 2004) but it was chosen for being more accurate than latitudinal data (Fudickar *et al.*, 2012), not being affected by the equinox (Hill & Braun, 2001) and not having a consistent bias (Porter & Smith, 2013, Lisovski *et al.*, 2012). Besides, the migration of the species mainly follows an East-West axis, making longitudinal data a good choice for determining stopovers and migration routes reliably (Guilford *et al.*, 2009). In this species, the need to cross longitudes 113ºE and 153ºE (respectively the westernmost and easternmost points of the Australian continent) to get to the north of

Australia allow us to determine along which side (north or south) of the Australian continent the birds have chosen to travel to get to their wintering areas. These will be generically referred to as the north and the south routes. The combination of routes chosen for the outbound (westbound) and return (eastbound) trips results in four different possible migrations that will be referred to as itineraries from here on. For example, the bird in Figure 3.2 passes longitude 113ºE both on the westwards and the eastwards migration indicating that the bird must have taken the southern route in both trips.

Longitudinal data also allows us to identify stationary periods alternated with fast longitudinal movements (passage periods). The longest of these stationary periods was considered the wintering area when birds were in Australia and the breeding area when in New Zealand. The other stationary periods in between these two areas were considered stopovers (Figure 3.2).

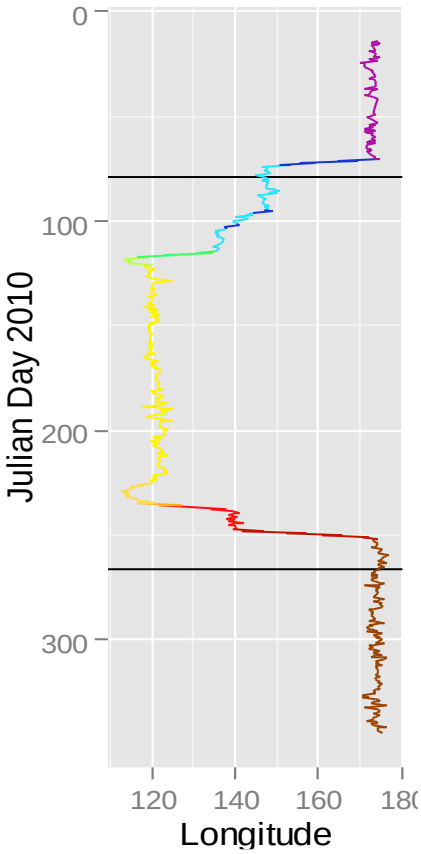


Figure 3.2: Example of a longitudinal plot for an individual's track during a whole year. In such plots longitude is given on the x axis (as it is commonly shown in maps) and date is plotted on the y axis increasing from top to bottom. The plot is coloured according to the consecutive stationary or passage periods the bird is at. Equinox events are marked by horizontal black lines.

3.3.5 Representation of the migration

Due to the equinox effect, latitude data is not available for all birds at all stages of migration. For this reason I have decided to plot joint 2D kernel density estimates over the area map as a way to indicate the likely distribution for the birds at each period of the migration. 'kernels' are represented either by an isoline when depicting the distribution of any individual bird or a continuous polygon in case several birds are included in the same density estimate. In any case these maps are presented together with a longitudinal plot in order to show the differences in spatiotemporal use made of the area by each individual (i.e. whether they use more than one place for stopover and for how long). Only for the stopover in the 2010 westwards migration was it impossible to retain enough latitudinal information to plot a 2D kernel. Instead a 1D kernel using only longitude data is shown. Kernel density estimates were calculated and built using the Geospatial Modelling Environment application (Beyer, 2012).

The parameters used to build the kernel density estimates are a cellsize (resolution) value of 0.5 degrees and a bandwidth value (a measure of the spread) of 1 for stationary periods and of 4 for passage periods. The greater value for the passage periods was chosen due to the greater unreliability associated with times of fast displacement that make it impossible to get a second fix to validate any given location.

3.3.6 Migratory phenology

For the same reasons discussed above only longitudinal data and SID were used to define the migratory phenology. Unless stated otherwise, all analyses undertaken and parameters described in the study of migratory phenology in this chapter are done only using the data gathered by thirteen birds of which I could be certain they followed the main migratory itinerary through the west and south of Australia in 2010 (Figure 3.4). Although, by adopting this method the size of the dataset was reduced, I found it to be the best strategy to avoid

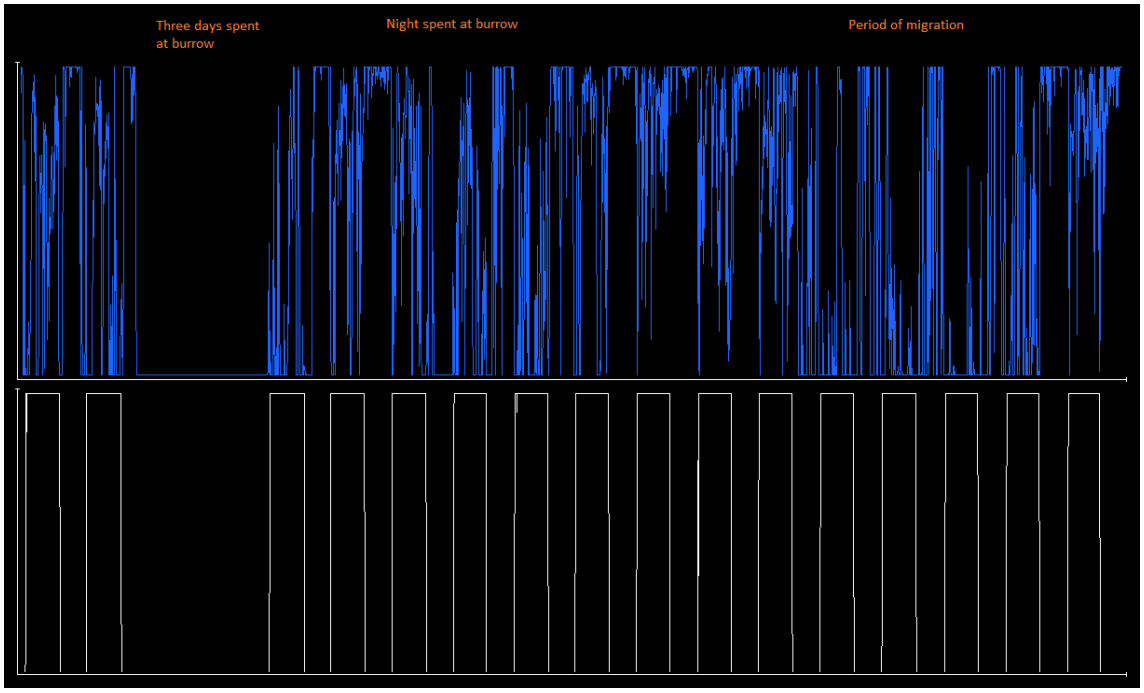
inter-year and inter-route variability that could otherwise confound the analyses. The precise manner in which dates and period lengths were obtained is detailed below. Values for individual birds can be found in Appendix 2:

Last Night at Burrow: Last night with total absence of Saltwater Immersion. See Figure 3.3 Top.
Last Day at Burrow: Last day with total absence of Saltwater Immersion and of Light Data. See Figure 3.3 Top.

Dates for Leaving/Arriving in New Zealand: The possible dates for this event were calculated using two methods: using the days in which birds cross meridian 165 E –where the westernmost tip of New Zealand is– and using the first and last day of low values in Saltwater Immersion Data (Figure 3.3 Top). The comparison of both sets of dates were highly correlated both for the leaving and the arriving date in New Zealand (R^2= 0.9988 and R^2=0.9654 respectively). Finally, the crossing of meridian 165E was used as the estimate due to its simplicity. *The length of the migration period* is considered the period between these two dates.

Arrival into and departure from the Wintering Area. This analysis was only performed for birds following itinerary 1 (see Figure 3.4 below) so the arrival and departure from their wintering areas can be determined by their respective minimal longitude values (usually between 111-113ºE). These values correspond to Cape Cuvier and the islands off Shark bay, the westernmost tip of Australia that birds need to pass while travelling both ways. The number of days between the first and the last crossing of this meridian is referred to as the *total time spent in the wintering area*.

Time spent at stopovers/commuting during migrations: Stopovers and passage periods are identified using the longitudinal plot as explained above.



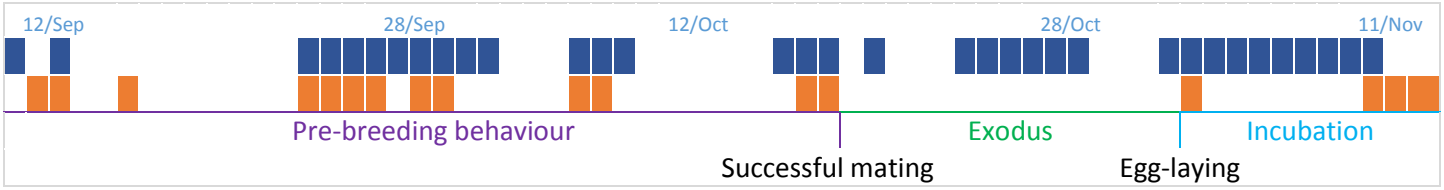


Figure 3.3: Top) Extract of a Hutton's shearwater track over the last days at the colony seen in Saltwater Immersion Data (top, blue) and light data (bottom, white). Presence at the colony and passage behaviour that can be easily identified when both these sources of data are plotted together. **Bottom)** Example of different patterns of night attendance to the colony for males (Bird #4, blue) and females (Bird #5, orange). At first, both birds attend the colony regularly until mating. Then the female departs on a pre-laying exodus while the male keeps attending the colony. Finally, the female lays the egg the male takes the first stint until the female returns for her first incubation shift.

In order to find relevant relationships between the phenological parameters listed above and with the aim to gain a better understanding of the year cycle I undertook several analyses (linear models). These were performed using the *lm* function of the 'lme4' package (Bates *et al.*, 2014) in R (R Core Team, 2012). Individual variation was already accounted for as there was only one data point per individual in each analysis. To minimise the variability that factors

route and year could introduce only 2010 itinerary one birds were included in the analyses. Competing models were chosen using Akaike's Information Criterion (AIC) while p-values were only used to note the significance of the model.

To visualise those models selected, a scatterplot representation including the regression line for the linear model relating the two variables is provided. As itineraries 2 and 3 do not have enough data by themselves to run a reliable model (n = 2 each), their datapoints and regression lines are included in the scatterplot to graphically assess their effect. The same procedure is used to study birds in 2011 (n = 5 for itinerary 1 and n = 1 for Itinerary 2). In all these graphs estimated sex (see below) of the birds is also shown to explore the possible differences between sexes.

3.3.7 Saltwater Immersion Data analysis

The immersion of the logging device in saltwater is measured every three seconds and logged in 10 minute bins for memory saving purposes. This results in values ranging from zero (no time underwater) to 200 (the device was immersed for the whole 10 minute period).

Behaviour estimation:

Behaviours were estimated from Saltwater Immersion Data (SID) assigning a behaviour to each ten minute bin according to its value. A bin with the maximum value of 200 was assigned to an at-sea resting behaviour, a value of 0 was considered flying and all values in between were thought to represent a proxy for foraging (McKnight, 2013).

Flight behaviour is probably the best estimated as these birds do not rest on land except when at the colony and confusion between these two possibilities can be easily ruled out: Visits to

the colony only happen at night when at the breeding area and they mean periods of at least four hours of consecutive dry bins (Figure 3.3 Top).

Resting behaviour can be overestimated as this category could include forage-diving from the surface. This inaccuracy, however, has been proven to be negligible when GLS have been codelpoyed with GPS (Dean *et al.*, 2013) and TDR (Dean, 2012).

The most inaccurate of all is the foraging behaviour as it could include other things different from foraging like transitions between the other two behaviours. For this reason this category has been used as a proxy for searching for food rather than a foraging behaviour estimate. Therefore, although behaviours are referred to as “Foraging”, “Flying” and “Resting” through the text, it is important to appreciate the limitations of this labelling.

Comparison among the three behaviours is carried out using only values occurring during the day as the great intra and inter-individual variability of SID estimates during the night makes it impossible to use extract any information. The times of sunrise and sunset calculated from light data were used to determine the limit between day and night. Behaviour estimates were then quantified as the percentage of daytime or night-time, accounting for day length being different in different periods occurring at different places and times of the year.

Behaviour estimation for the different periods:

To better understand the different periods of the year cycle these were characterised using the behavioural classification described above. To avoid inter-route and inter-year variability only 2010 Itinerary 1 birds were included (n = 13) in the comparison unless indicated otherwise.

Periods were established using longitude data as explained above (Figure 3.2) except for the passage periods and the stationary period of the breeding area that were subject of further division. Passage periods are split into fast and slow migration according to the speed of the shown in each bird's longitudinal plots. At the breeding area birds were divided into breeders (n = 17) and non-breeders (n = 6) depending on whether they showed the night-visit pattern expected of a breeding shearwater (Figure 3.3 Bottom).

Moon effect:

To analyse the effect the moon might have on the night behaviour I related behaviours to the percentage of the moon disk illuminated each day. Calculations for this parameter were carried out using the *moonAngle* function in the 'oce' package (Kelley, 2014) in R. The effect of the moon on the different behaviours was carried out using a Linear Mixed-effects Model including individual and sex as nested random effects. A measure of significance for this analysis was obtained by comparing the model described to a null model including only random effects. A False Discovery Rate p-value correction was applied to compensate for the eighteen models practiced on the moon-effect dataset. Only p-values resulting of the correction will be commented in the text.

Moult:

To identify the moult period the individual daily percentages of time spent on water were calculated from SID for all birds following Itinerary 1. As the values for daily percentages have a great variability for consecutive days LOESS-smoothed curves for each individual bird were used instead of the actual values (smoothing parameter = 0.5). These curves were plotted against the day of the year and against their date of arrival into the wintering area to look for synchrony among individuals. Weekly percentages for the three behaviours estimated were

also plotted from their date of arrival into the wintering area. Fitting of these curves and plotting were carried out in R using the package 'ggplot2' (Wickham, 2009).

Sex estimation

Due to the different functions they perform during the breeding season different sexes are known to have different patterns in the visits to the colony prior to breeding in shearwaters (Brooke, 2004). While females undergo a pre-breeding exodus during which the egg is built, males make frequent visits to the colony ready to make the first incubation stint once the egg is laid (Guilford *et al.*, 2012). Here I use SID values to visualize the patterns of colony attendance at the beginning of the breeding season to recognise these behavioural patterns and sex the birds (Figure 3.3 Bottom).

This method was used successfully by Guilford *et al.* (2012) for Balearic shearwaters (*Puffinus mauretanicus*) and is also appreciable in our dataset. An example for this behavioural pattern of colony attendance can be observed in Figure 3.3 Bottom. Birds skipping breeding do not show any of these behaviours and were consequently not sexed. Estimated sex information for each individual can be found in Appendix 2.

3.4 Results

For clarity, results will be presented using the time of the migration they describe rather than by the method which they were obtained with. First I will review the migration as a whole, then the stay at the wintering area and finally the outbound and return journeys.

3.4.1 Migration as a whole

All tracked individuals overwinter in the tropical seas off the north Australian coasts. In both directions –to and from the wintering area- birds perform migrations characterised by (generally two) short periods of very fast displacement alternated with (generally one) long stopover. The duration of the displacement (or passage) periods is not usually greater than four or five days, however the stopovers range in length from seven to thirty-six days on the outbound trip (westwards migration) and from two to thirty-two on the return trip (eastwards migration).

The trip to or back from the wintering areas north of Australia can be made either by a more direct northern route or by a longer southern route around Australia. Depending on the combination of routes each bird took to and back from its respective wintering area three migration itineraries that encompass all observed migrations can be established (Figure 3.4):

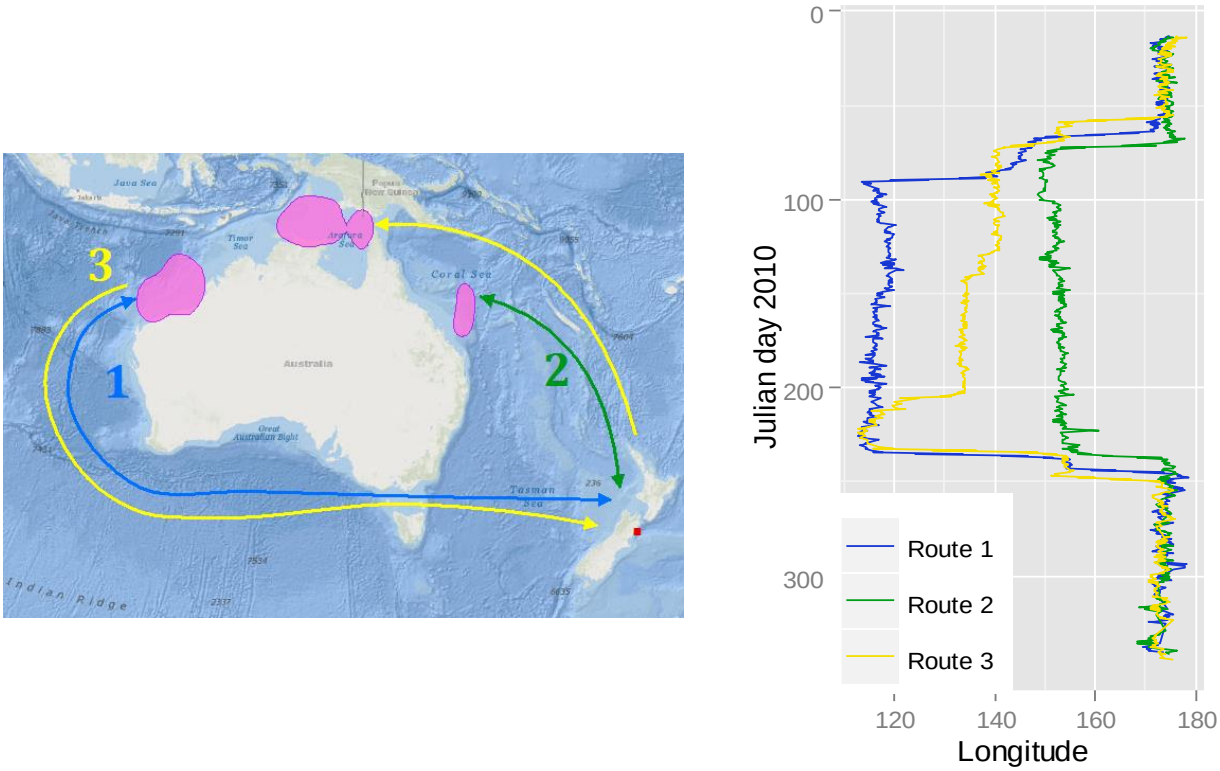


Figure 3.4: Examples of the three routes observed for the Hutton's shearwaters´ migration to their wintering areas north of Australia. **Left:** Map of the area showing a schematic representation of the three observed itineraries: 1 (blue), 2 (green) and 3 (yellow). The colony in New Zealand is marked by a red dot. **Right:** longitudinal plot showing real examples of migration for each of the three routes.

3.4.1.1 Itinerary 1:

This is the most frequent itinerary in the dataset, it is followed by birds #1, #3, #4, #5, #6, #7, #8, #9, #10, #11, #12, #14, #15, #16, #18 in 2010 and #13, #15, #20, #22, #23 in 2011. These birds undertake both their westwards and eastwards migrations via the south and West of Australia. Longitudinal plots of birds following this route are characterised by dipping below 113ºE (longitude of the westernmost tip of the Australian continent) both before and after their period at the wintering area (Figures 3.4 & 3. 5).

The winter migration starts by crossing the Tasman Sea, an event that birds seem to undertake at two different latitudes. There is a southern crossing straight to Tasmania from the south of South Island and a northern crossing that connects the north of New Zealand´s North Island

and the easternmost tip of Australia. Once at the continent these birds follow the coast down to their respective stopover places (Figure 3.5).

On the westwards migration these birds are seen to stop at two distinct stopovers roughly located around longitudes 147ºE and 140ºE. After stopping, birds fly to their wintering areas that for all but one (Bird #9) is located in the Indian Ocean north of Western Australia.

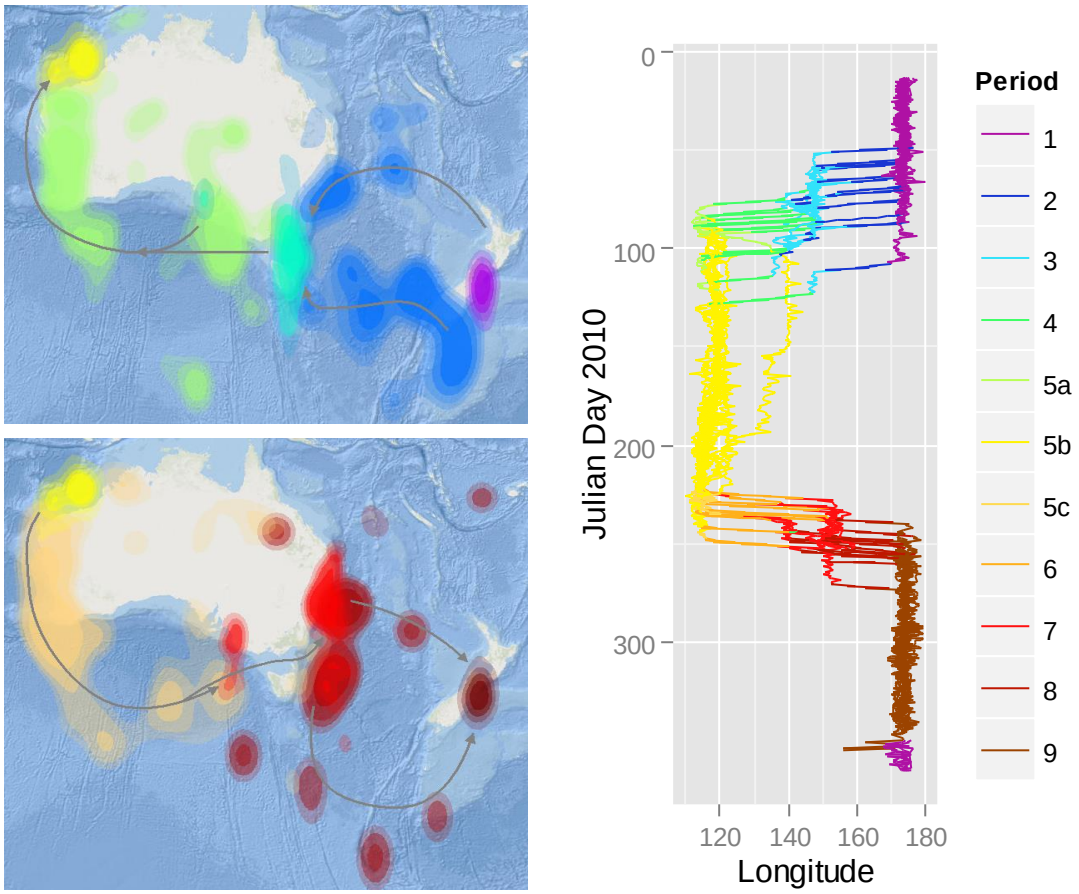


Figure 3.5: Spatial description of each of the periods for all birds following route 1 in 2010. **Top-left**: 20%, 35%, 50% and 65% kernel density estimations for each of the periods of the westwards migration (periods 1, 2, 3, 4 and 5b). **Bottom-left:** Same for the eastwards migration (periods 5b, 6, 7, 8 and 9). **Right:** Longitudinal plot of all birds coloured according to the period they are at. Colour coding of periods is consistent within the figure and follows those depicted in the far-right key. Grey arrows are intended to give a schematic description of the movement of the birds.

On the return journey stopovers are located at longitudes 140ºE and 153ºE. The crossing back of the Tasman Sea is again undertaken at two different latitudes. The northern crossing is analogous to that of the westwards migration, while the southern crossing occurs further south.

3.4.1.2 Itinerary 2:

Birds following this itinerary are Bird #2 in 2010 and Bird #21 in 2011 (Figure 3.6). Both take the northern crossing of the Tasman Sea in both directions of the migration. Both birds stop in the Coral Sea around longitude 153ºE but bird #2 stays to make this its wintering area whilst #21 only uses it as a stopover both in the eastwards and westwards migration. On longitudinal plots this itinerary can be easily recognised as none of the birds approach meridian 113ºE (Figures 3.4, 3.6).

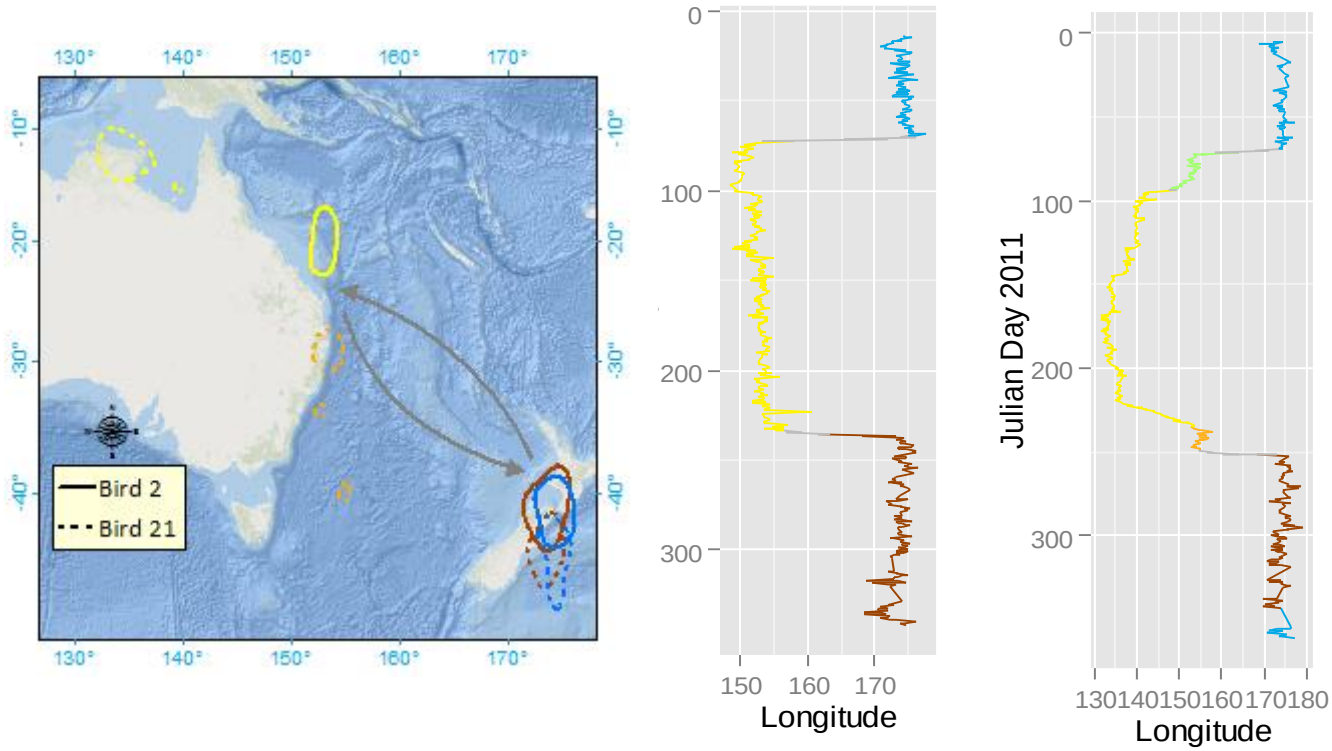


Figure 3.6: Spatiotemporal description of each of the periods for both birds following itinerary 2. **Left:** 35% kernel density estimations for each of the stationary periods recorded for birds #2 in 2010 (solid line) and Bird #21 in 2011 (dashed line). Note that the stopover period around 153ºE on the westbound migration for bird #21 (coloured light green in the longitudinal plot) is not shown due to its proximity to the March Equinox. **Centre:** Longitudinal plot for Bird #2. Different stationary periods are coloured differently. **Right:** Longitudinal plot for Bird #21. Different stationary periods are coloured differently. Colour coding of periods is consistent within the figure. Grey arrows are intended to give a schematic description of the movement of the birds.

3.4.1.3 Itinerary 3:

Two individuals follow this itinerary in 2010, birds #17 and # 19. Birds following this route circumnavigate Australia in an anticlockwise direction (Figures 3.4 & 3.7). These birds take the northern crossing over the Tasman Sea to then endeavour in a series of stationary periods at the Arafura Sea that altogether can be considered their wintering area.

After the wintering area these birds make a stopover at itinerary 1 birds' wintering area. From this point on itineraries 1 and 3 converge, all going back to New Zealand via the southern route.

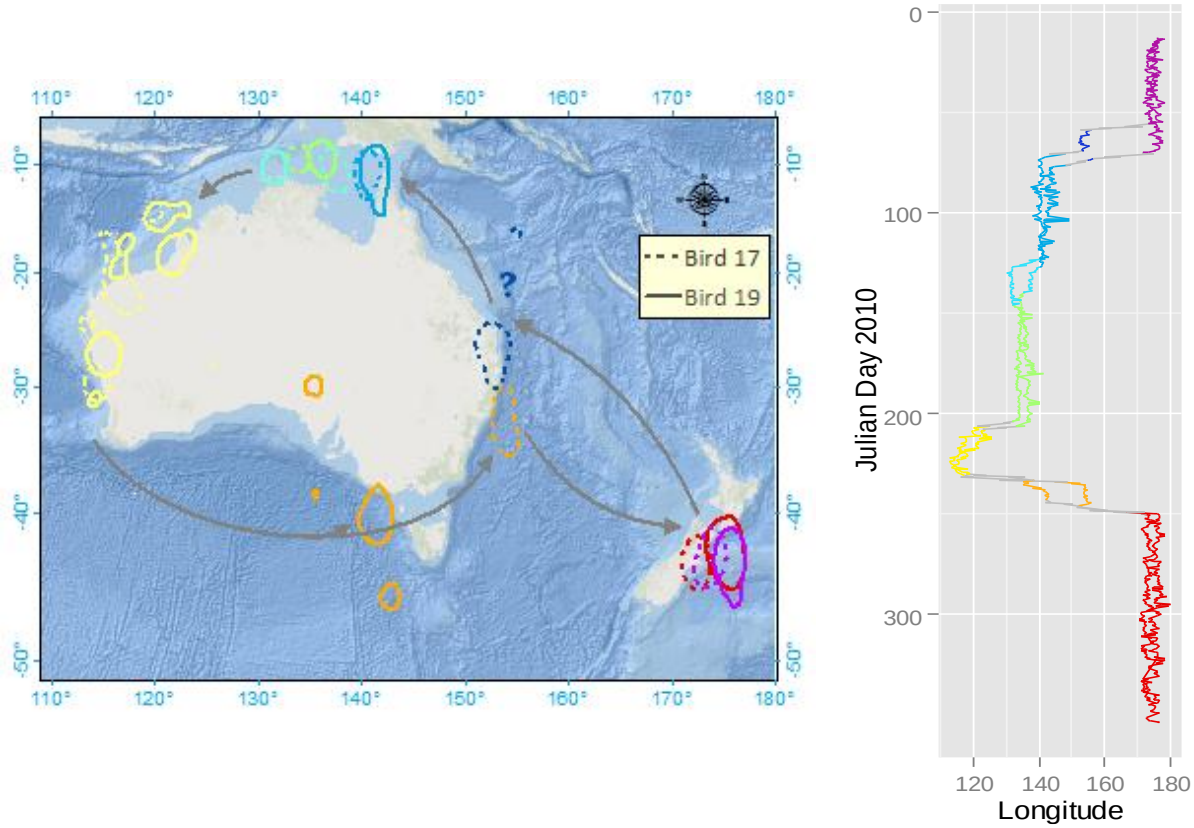


Figure 3.7: Spatiotemporal description of each of the periods for Birds #17 and #19, both following itinerary 3 in 2010. **Left:** 35% kernel density estimations for each of the stopover periods recorded. Note that the stopover period around 153ºE on the westbound migration for bird #17 (coloured dark blue) could not be shown due to its proximity to the March Equinox. **Right:** Longitudinal plot for both birds where different stopover periods are coloured differently. Colour coding of periods is consistent within the figure. Grey arrows are intended to give a schematic description of the movement of the birds.

3.4.1.4 Sex differences

Behavioural sexing of the 21 individual birds tagged resulted in the estimation of eight males and seven females. The remaining 6 could not be identified due to them not showing a recognisable colony-attendance behaviour in SID patterns.

There are no appreciable differences between males and females in their use of space at any of the stationary periods (Figure 3.8). Both sexes stop at the main and secondary stopovers in both directions of the migration (Figures 3.21, 3.28). Both sexes also show the same pattern at the Indian Ocean wintering area (Figure 3.27) and at least one male and one female can be found in each of the three itineraries (Appendix 2).

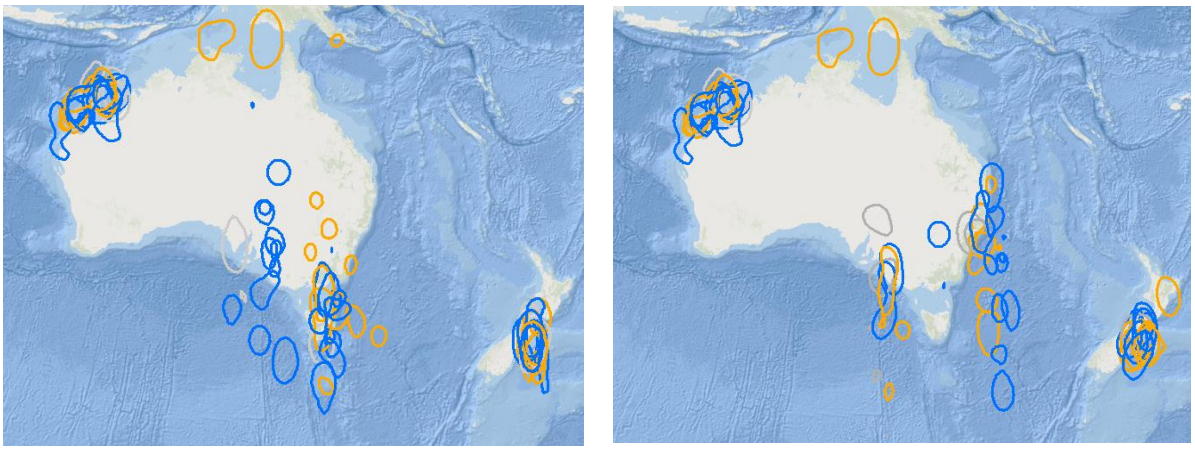


Figure 3.8: Figures showing 35% kernel density contours for the stationary periods of all individuals following itinerary 1 in 2010. Contours are coloured according to the estimated sex of the bird: blue for males, orange for females and grey for birds whom it was impossible to sex. **Right:** Stationary periods for the westbound migration (periods 1, 3 and 5). **Left:** Stationary periods for the eastbound migration (periods 5, 7 and 9).

3.4.1.5 Year differences

Only six devices were recovered for 2011, five of them for birds following itinerary 1 and one of them with itinerary 2. This small number of devices has been enough to see several differences between years that mainly correspond to changes in stopover use and therefore will be discussed later.

3.4.1.6 Phenology

A summary of the phenological parameters studied is shown in tables 2 and 3 below. Data for each individual bird can be consulted in Appendix 2.

Table 3.2: Comparison of mean, median, standard deviation, minimum and maximum values for each of the phenological parameters studied in 2010 and 2011 for the westwards migration and wintering area.

	Last day at burrow	last night at burrow	Leave NZ	Fist arrival in stopover	Leave of last stopover	time spent on stopover(s)	Arrival in Wintering area	Days in Wintering area
Median 2010	30/1	24/2	11/3	9/3	28/3	13.00	1/4	135.00
Mean 2010	30/1	24/2	11/3	13/3	1/4	16.18	4/4	132.12
St. dev. 2010	17.3	12.4	14.8	19.8	14.1	9.5	13.5	16.2
Min. 2010	12/1	2/2	19/2	21/2	11/3	0.00	15/3	93.00
Max. 2010	26/2	18/3	19/4	22/4	3/5	40.00	11/5	158.00
Median 2011	17/1	11/2	21/2	26/2	24/3	21.50	3/4	127.00
Mean 2011	22/1	17/2	26/2	1/3	23/3	21.50	30/3	124.83
St. dev. 2011	22.7	15.2	15.3	15.9	15.5	10.7	10.7	16.3
Max. 2011	29/12	31/1	9/2	11/2	3/3	7.00	10/3	103.00
Min. 2011	1/3	15/3	24/3	28/3	18/4	35.00	10/4	147.00

Table 3.3: Comparison of the mean, median, standard deviation, minimum and maximum values for each of the phenological parameters studied in 2010 and 2011 for the eastwards migration.

	Date leaving Wintering area	Arrival in first stopover	Leave last stopover	time spent in stopovers	Arrival in NZ	1st night at burrow	1st day at burrow
Median 2010	15/8	25/8	5/9	10.50	8/9	11/9	21/9
Mean 2010	14/8	23/8	5/9	13.19	9/9	11/9	21/9
St. Dev. 2010	10	12	9	8.9	7	8.4	9.2
Min. 2010	23/7	26/7	18/8	2.00	27/8	27/8	12/9
Max. 2010	2/9	10/9	28/9	33.00	30/9	1/10	16/10
Median 2011	4/8	8/8	6/9	18.50	8/9	9/9	22/9
Mean 2011	1/8	15/8	3/9	18.83	7/9	10/9	28/9
St. Dev. 2011	12	18	11	11.1	9	7.6	37.6
Max. 2011	10/7	29/7	17/8	3.00	24/8	29/8	9/9
Min. 2011	21/8	9/9	18/9	39.00	21/9	23/9	21/12

The whole migration period, considered since birds cross meridian 165ºE until they cross it again on their way back, lasts 181.1 ± 15.5 days. The median leaving date being the 11/Mar/2010 and the median arriving date the 11/Sep/2010.

The duration of the whole migration period for 2010 Itinerary 1 birds is highly dependent on the leaving date ($p = 2.68x10^{-5}$, Table 3.4, Figure 3.9) but not at all on the arriving date ($p = 0.56$, Table 3.4, Figure 3.10). Sexual segregation in the duration of migration can be seen in the scatterplots for the two variables commented above (Figures 3.9 & 3.10). Males spend on average 23 days more than females on the winter migration ($p = 0.02$, Table 3.4) this is probably due to the relationship of sex and the leaving date ($p = 0.04$, Table 3.6). Birds following other itineraries and birds from 2011 seem to follow the same patterns both for the leaving (Figure 3.9 Right) and the arriving date (Figure 3.9 Left).

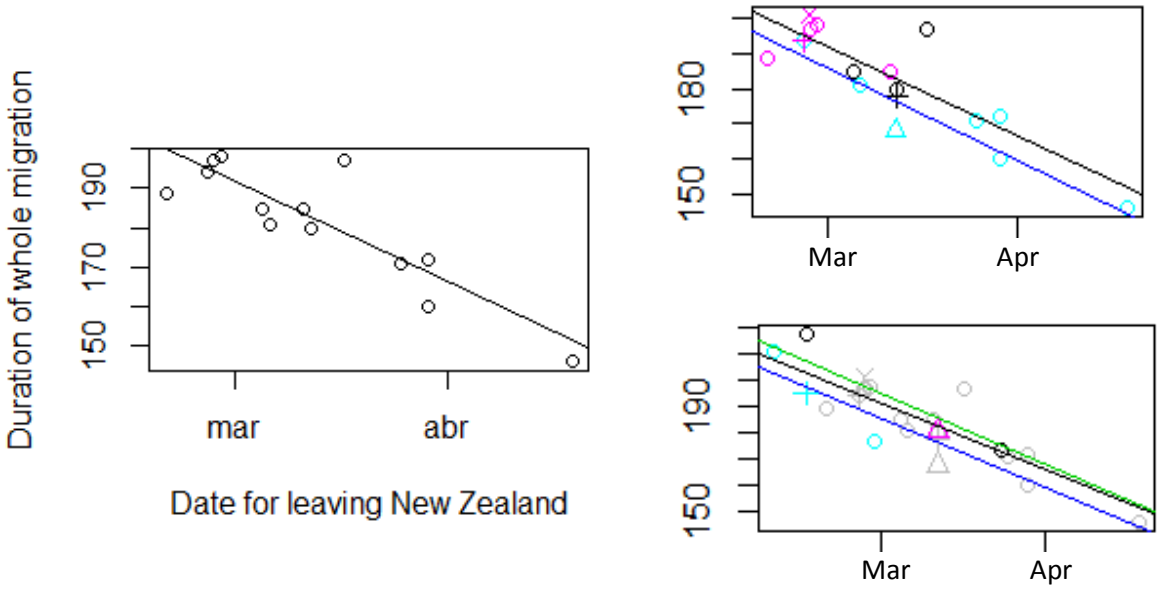


Figure 3.9: Duration of the overwinter migration plotted against the date of leaving New Zealand. **Left)** Including only birds that followed route 1 in 2010. The model fitted is represented by a black line. **Top-Right**) Model including all birds from 2010. Colour indicates estimated sex for the birds: Male (Blue), female (pink) and unknown (black). Shapes indicate the route followed after leaving New Zealand, route 1 (circles), route 2 (triangle), route 3 (plus sign) and a56 (multiplication sign) for which the route could not be initially established whether it was 1 or 3. The resulting model when Routes 2 and 3 are included is coloured blue. **Bottom-Right)** Using the same colour and shape codes the birds from 2011 are plotted together with those from 2010 (coloured grey here for simplicity). The resulting model when 2011 birds are included is coloured green.

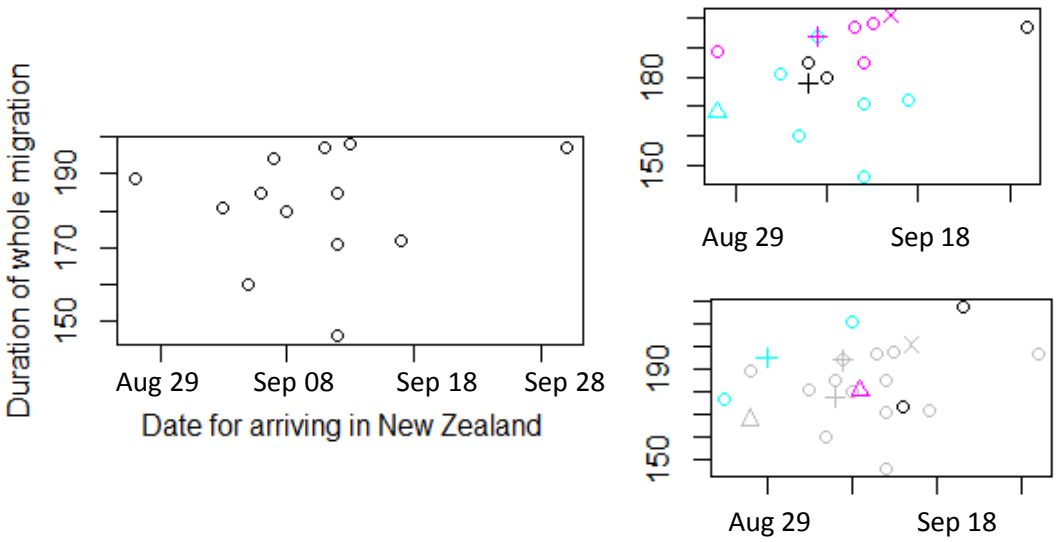


Figure 3.10: Duration of the overwinter migration plotted against the date of arriving in New Zealand after the overwinter migration**. Left)** including only birds that followed route 1 in 2010**. Top-Right)** including all birds from 2010. Colour indicates estimated sex for the birds: Male (Blue), female (pink) and unknown (black). Shapes indicate the route followed after leaving New Zealand, route 1 (circles), route 2 (triangle) and route 3 (plus sign). **Bottom-Right)** Model including all birds using the same colour and shape codes, the birds from 2011 are plotted together with those from 2010 (coloured grey here for simplicity). No model representations are included as none of them explained the duration of the whole migration significantly.

Table 3.4: Table showing the Linear Models (LM) built to explain the duration of whole winter. All variables cannot be included in one model as the dates for arrival and leaving New Zealand necessarily explain 100% of the variance.

Modelled variable	Explanatory variables			p-value	AIC
Whole migration duration	Date for leaving NZ			$p = 2.68 \times 10^{-5}$	100.7
		Date for arrival in NZ		p = 0.56	121.7
			Estimated sex	p = 0.02	114.9
	Date for leaving NZ		Estimated sex	$p = 4.5 \times 10^{-4}$	102
		Date for arrival in NZ	Estimated sex	p = 0.06	116.5

3.4.1.7 Behaviour characterisation of the different types of period

Overall, birds at the breeding area show a much greater flight time and less foraging time than at the wintering area or the stopovers. At the breeding area there is no difference in any behaviours between breeders and non-breeders neither during the day nor during the night (Figure 3.11).

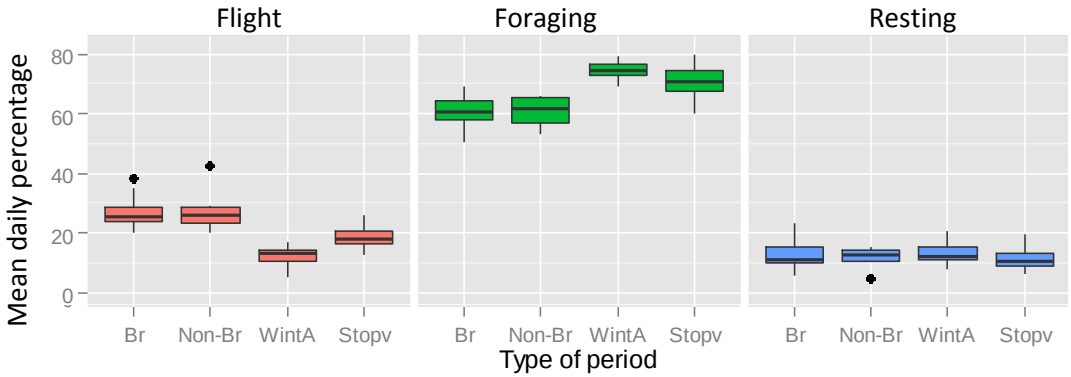


Figure 3.11: Mean individual daytime estimation of Flight, Forage proxy and Resting behaviours for the four different kinds of stationary periods identified: Breeders (*Br*) and non-breeders (*Non-Br*) at the breeding area, and all Itinerary 1 birds at the Wintering Area (*WintA*) and Stopovers (*Stopv*).

Within stationary periods those at the breeding area show a higher flight time and a lower forage time than at the stopovers and wintering area. Within the winter migration birds at the wintering area show a lower percentage flight time and a greater percentage of forage time, although this is not significant (Figure 3.11).

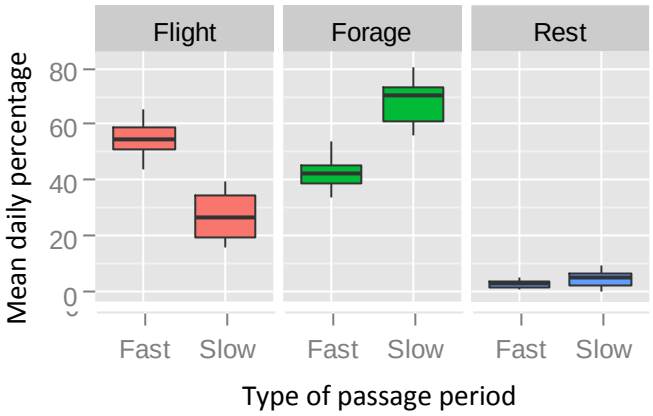


Figure 3.12: Mean daytime estimation of Flight, Forage proxy and resting behaviours at the two different kinds of passage periods observed in longitudinal plots.

The only behaviour that shows a difference between passage and stationary periods is resting behaviour, which is lower in both fast and slow passage periods. Comparison of the two kinds of passage periods show differences both in flight and forage time during daytime.

The high percentage of flight time at night during the fast passage is significantly related to the effect the moon has on this period ($3.6x10^{-10}$, Figure 3.13). Moon also seems to have an effect on the slow passage periods although this is only to decrease the percentage of resting time on moonlit nights ($p = 0.002$, Figure 3.13).

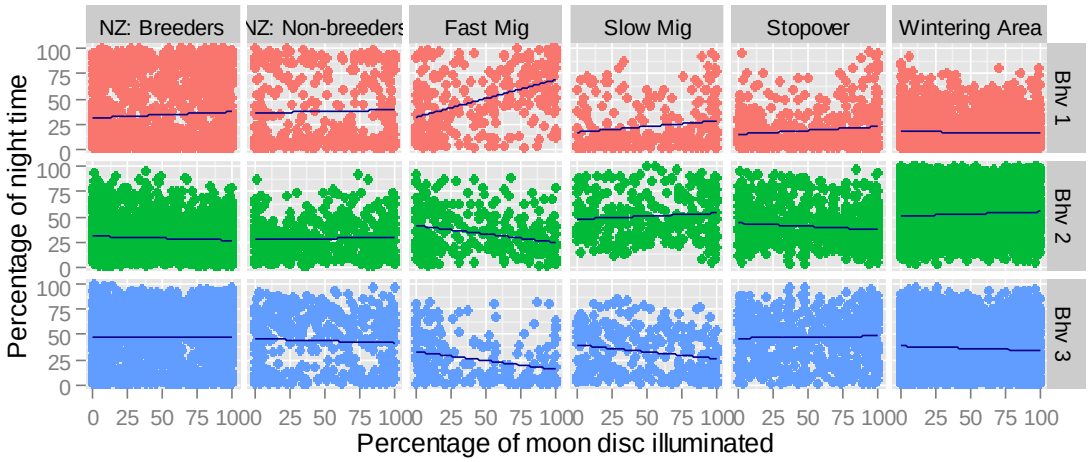


Figure 3.13: Moonlight influence on the Flying (Bhv1), Foraging (Bhv2) and Resting (Bhv3) behaviours for the different kinds of stationary and passage periods identified. Each datapoint corresponds to the percentage of nightime involved in a given behaviour by one individual in one given night. LMM were conducted for all eighteen possible combinations of behaviours and period type and then compared to a null model in order to obtain a measure of significance. Of all of them the only significant relationship after applying a False Discovery Rate correction was Flight behaviour for the fast migration period ($p = 3.6x10^{-10}$), for the breeding birds while at New Zealand ($p = 4.5x10^{-4}$) and resting behaviour for the slow migration period ($p = 0.002$).

Fast passage is not the only period of the year for which moon seems to have an effect on the birds' behaviour. Breeding birds also seem to respond to moon illumination by increasing their night flight time ($p = 4.5x10^{-4}$, Figure 3.13). As non-breeders do not show such a behaviour I assume this is probably the consequence of chick raising duties such as flights between the colony and the feeding areas.

3.4.2 Wintering Areas

There are three distinct wintering areas for the species, all of them north of Australia (Figure 3.14), from west to east: the Indian Ocean north of Western Australia (used by 21 birds), the Arafura Sea (4 birds) and the Coral Sea (1 bird).

In 2010 in the area north of Western Australia most birds shift locations rather synchronously over the season (Figure 3.14); first to the east to a longitude of about 120ºE and in mid to late June to the west until reaching longitudes below 115ºE. Not all birds overwintering in this location do this however; bird 5 stays around longitude 120ºE and birds 8 and 11 go further east after reaching 120E. The three birds wintering at the Arafura Sea first use an area next to Torres Strait at 140ºE and then disperse among several other stopover places until they migrate slowly to the wintering area north of West Australia. For the single bird wintering in the Coral Sea the only longitudinal variation consists of a slow eastwards movement over the whole season (Figure 3.14).

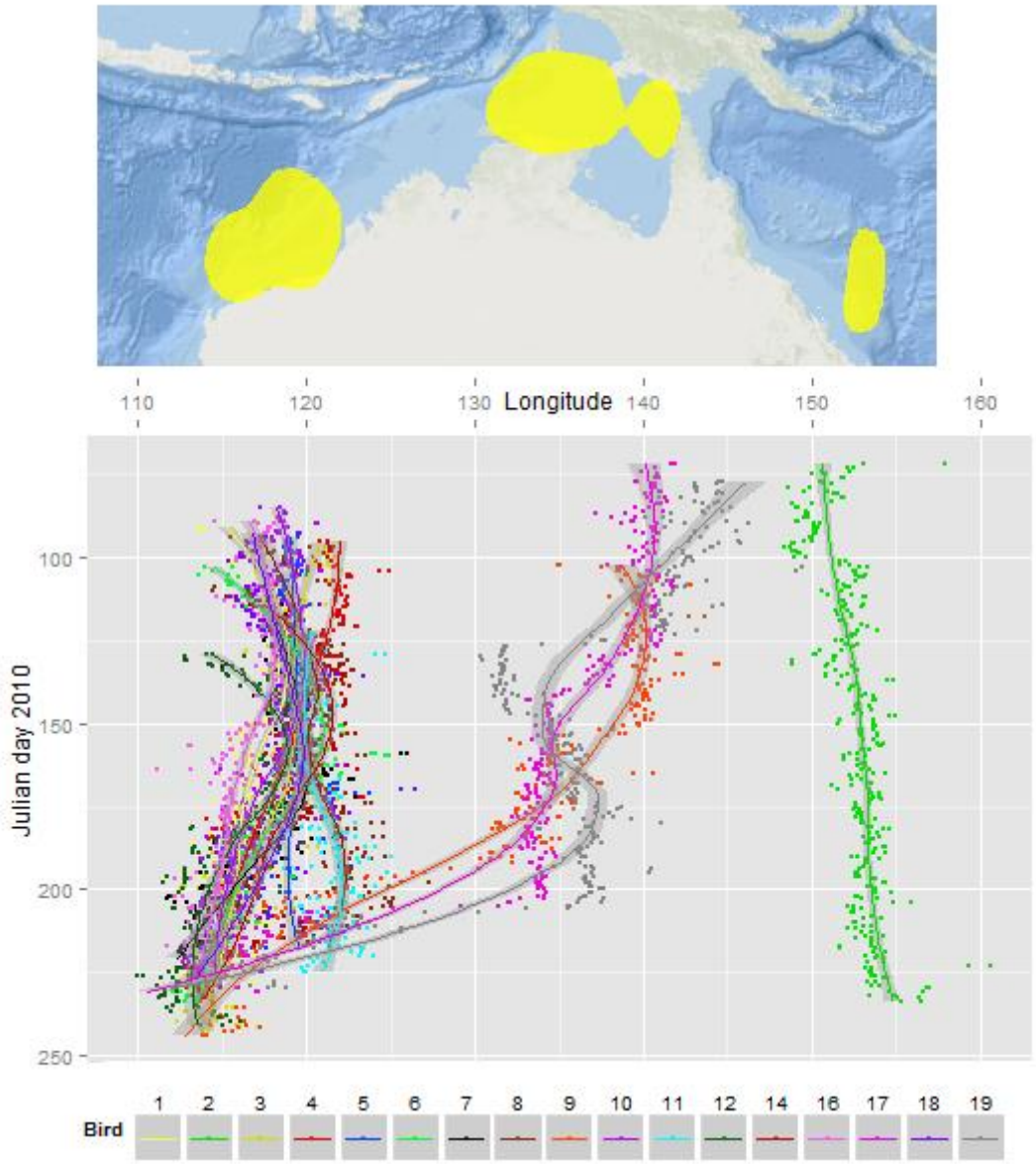


Figure 3.14: Spatiotemporal description of the wintering areas for all birds tracked in 2010. **Top:** three 50% kernel density plots built separately for each of the three areas used during the wintering period. **Bottom:** Longitudinal plot color-coded by bird for all birds in 2010. A LOESS-smoothed line has been added to help visualize patterns for each bird.

In 2011 at the wintering area the locations chosen seem to be the roughly the same as in 2010 for the Indian Ocean and the Arafura Sea. The area used north of Western Australia and even the longitudinal changes within the area observed in 2010 stay constant between years. The single bird wintering in the Arafura Sea (Bird #21) shows successive stationary periods at the same longitudes as birds #9, #17 and #19 used the previous year. No tags were recovered for birds wintering at the Coral Sea in 2011 although Bird #21 uses as stopovers the longitudes previously used by bird #2 as its wintering area both in the outbound and in the return migration (Figure 3.15).

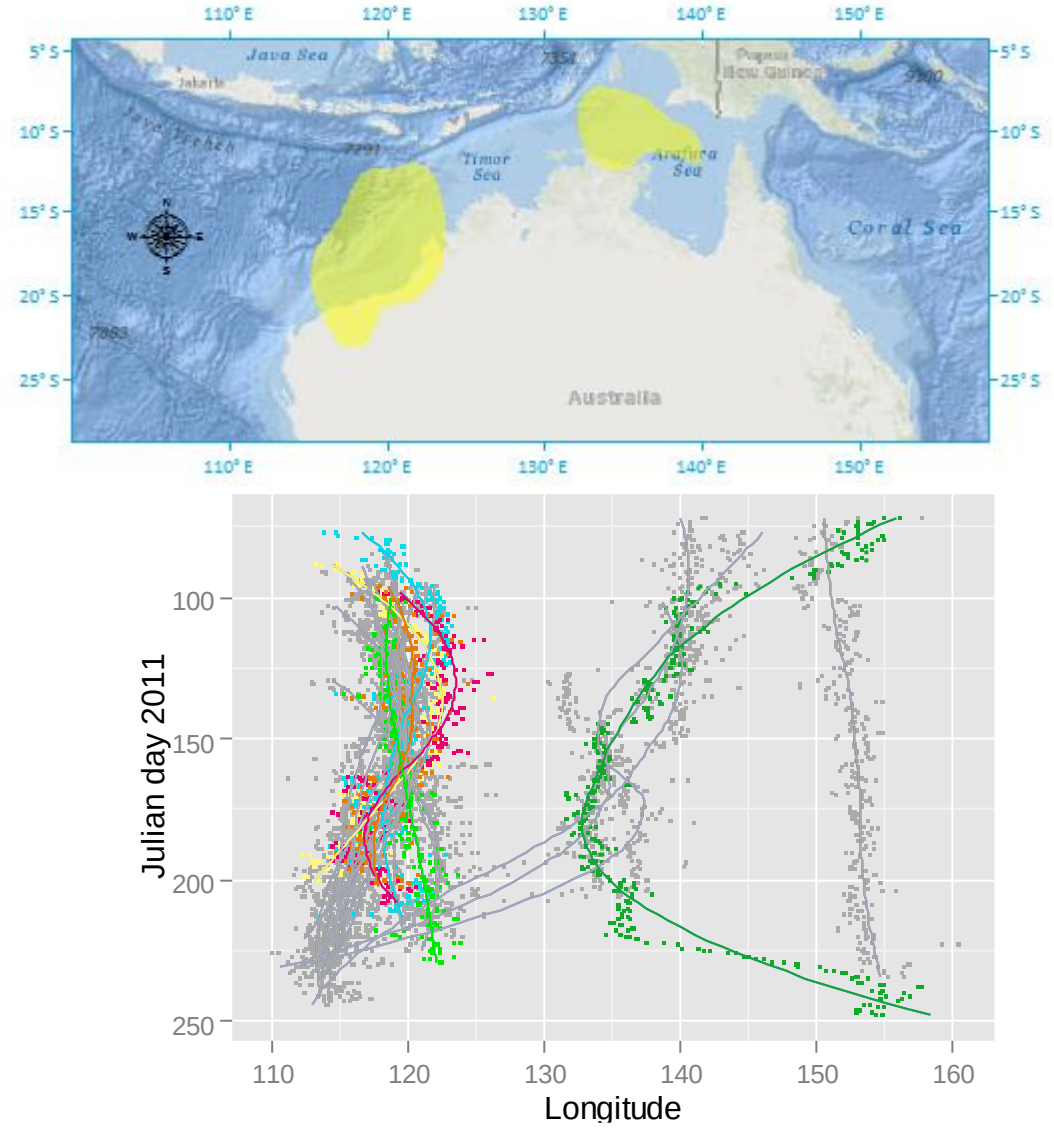


Figure 3.15: Top: Map showing 50% kernel density plots for all six individuals at the wintering area in 2011. **Bottom:** Longitudinal plot color-coded by bird. A LOESS-smoothed curve for each bird has been added to help visualize patterns.

3.4.2.1 *Phenology of the wintering area*

The median arrival date at the wintering area is the first of April 2010 and the mean days spent at wintering area is 130.1 ± 17.3 days. The total time spent at the wintering area depends significantly on the arrival date ($p = 1.08 \times 10^{-5}$; Figure 3.16, Table 3.5) rather than on the departure date for the eastbound migration ($p = 0.26$, Figure 3.17). This is due to the difference between the first and the last arrival into the wintering area being of more than two months (Table 3.3) while all the departures from the wintering area all happen within 23 days (Table 3.5). Sex also seems to have an effect, this is probably due to the males having left the breeding area later.

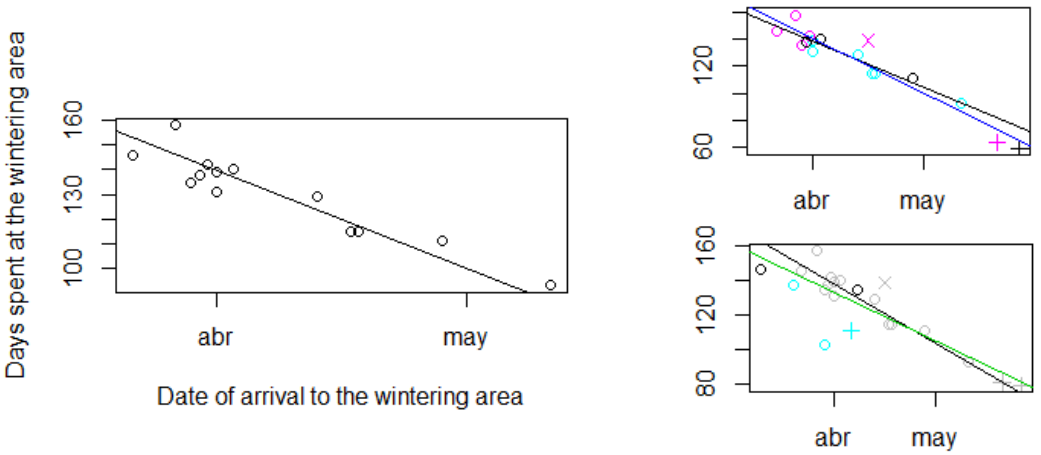


Figure 3.16: Days spent at the wintering area plotted against the date of arrival. **Left)** Including only birds that followed route 1 in 2010. The linear model fitted is represented by a black line. **Top-Right)** including all birds from 2010. Colour indicates estimated sex for the birds: Male (Blue), female (pink) and unknown (black). Shapes indicate the route followed after leaving New Zealand, route 1 (circles), route 2 (triangle), route 3 (plus sign) and Bird #9 (multiplication sign) for which the route could not be initially established whether it was 1 or 3. The resulting model when Routes 2 and 3 are included is coloured blue. **Bottom-Right)** Using the same colour and shape codes the birds from 2011 are plotted together with those from 2010 (coloured grey here for simplicity). The resulting model when 2011 birds are included is coloured green.

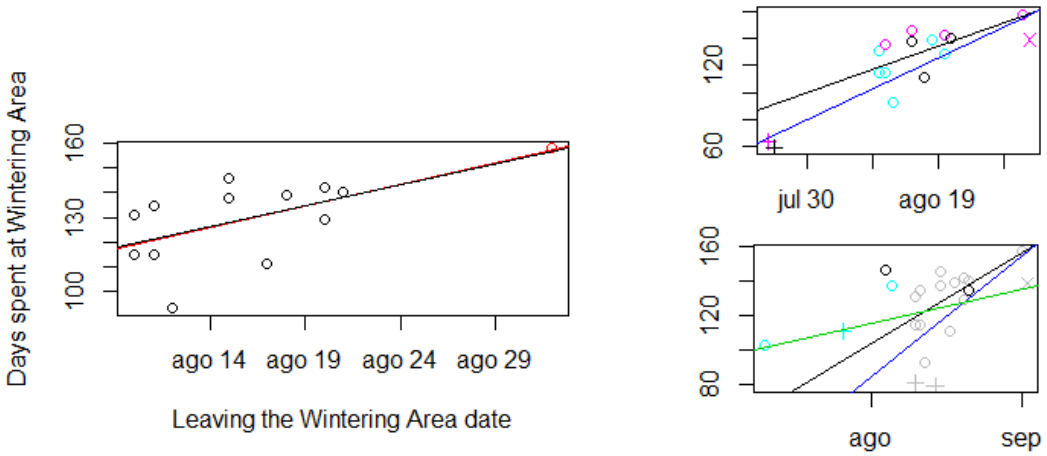


Figure 3.17: Days spent at the wintering area plotted against the date leaving it. **Left)** Including only birds that followed route 1 in 2010. The model fitted to all data-points is represented by a red line while the model considering only those coloured black is represented by a black line. **Top-Right)** including all birds from 2010. Colour indicates estimated sex for the birds: Male (Blue), female (pink) and unknown (black). Shapes indicate the route followed after leaving New Zealand, route 1 (circles), route 2 (triangle), route 3 (plus sign) and Bird #9 (multiplication sign) for which the route could not be initially established whether it was 1 or 3. The resulting model when birds from Route 3 are included is coloured blue. **Bottom-Right)** Using the same colour and shape codes the birds from 2011 are plotted together with those from 2010 (coloured grey here for simplicity). The resulting model when 2011 birds are included is coloured green.

Table 3.5: Table showing the Linear Models (LM) built to explain the duration of the birds' stay at the Wintering Area (WA). All models including the dates for arrival and leaving the WA were not considered as these two variables together explain 100% of the variance.

Modelled variable	Explanatory variables			p-value	AIC
Days at the Wintering Area	Date for arrival in WA			$p = 1.08 \times 10^{-5}$	100.4
		Date for leaving WA		p = 0.26	118.2
			Estimated sex	p = 0.05	118.3
	Date for arrival in WA		Estimated sex	$p = 1.1 \times 10^{-4}$	99.76
		Date for leaving WA	Estimated sex	p = 0.07	118.5

3.4.2.2 Study of estimated behaviours

Comparison of behaviours at the wintering areas cannot show meaningful differences due to the small number of birds wintering at the Arafura Sea or at the Coral Sea and therefore the comparison is made solely for informative purposes (Figure 3.18). During the daytime birds do not show any differences in the behaviour percentages. During night-time there are differences although due to the reduced sample size and great variability displayed it is not clear what the implications of these differences can be.

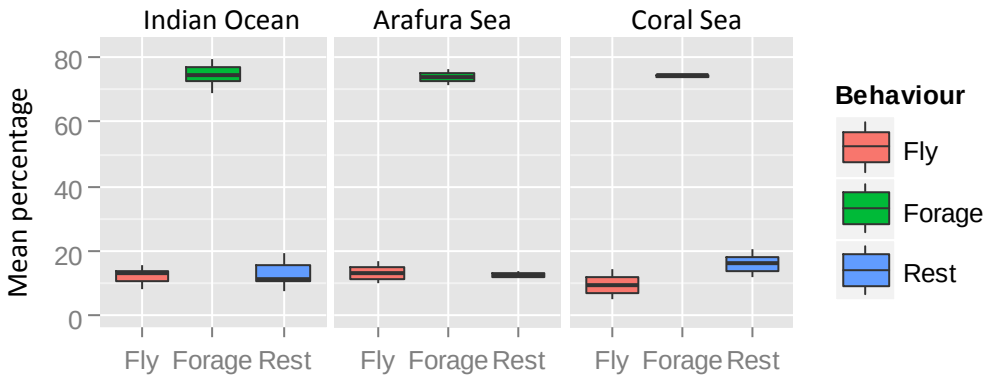


Figure 3.18: Mean daytime individual estimation of Flight, Forage and Rest behaviours for the three different wintering areas.

3.4.2.3 Moult

The daily proportion of saltwater immersion for the whole year reveals that the greatest proportion of immersion happens at the wintering area (Figure 3.19 Left). It seems plausible that this is due to the moult. A rearrangement of the curves shows the moult may be synchronised to the arrival of the birds at the wintering areas (Figure 3.19 Right).

Supporting this, the plotting of the three estimated behaviours for the wintering area shows marked differences between the first and the second half of the period (Figure 3.20). While the second half seems to be constant and consistent with the overall period average (Figure 3.18), the first half shows a discrepancy in the resting and flying behaviour. Resting behaviour

increases at the same time that flight behaviour decreases, both peaking at around the fourth week after arrival at the wintering area (Figure 3.20).

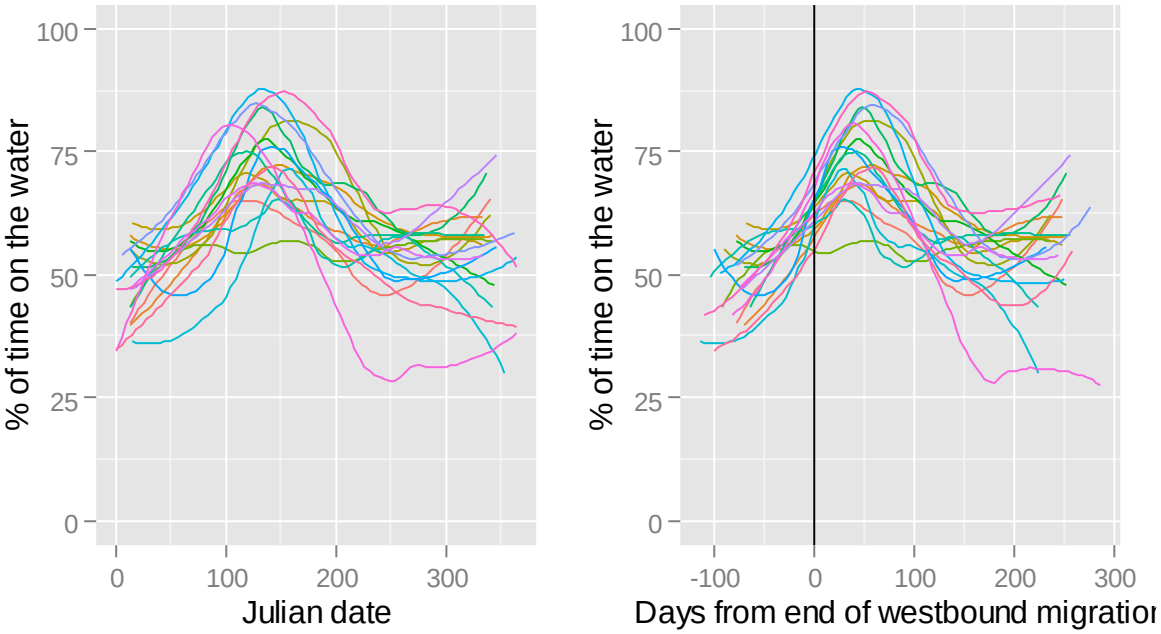


Figure 3.19: LOESS smoothed curves of daily total Saltwater Immersion Data for each individual following itinerary 1. **Left:** Individual curves plotted against the day of the year or Julian date. **Right:** Curves are rearranged according to the day of stopping the westbound migration for each bird (marked by a vertical black line).

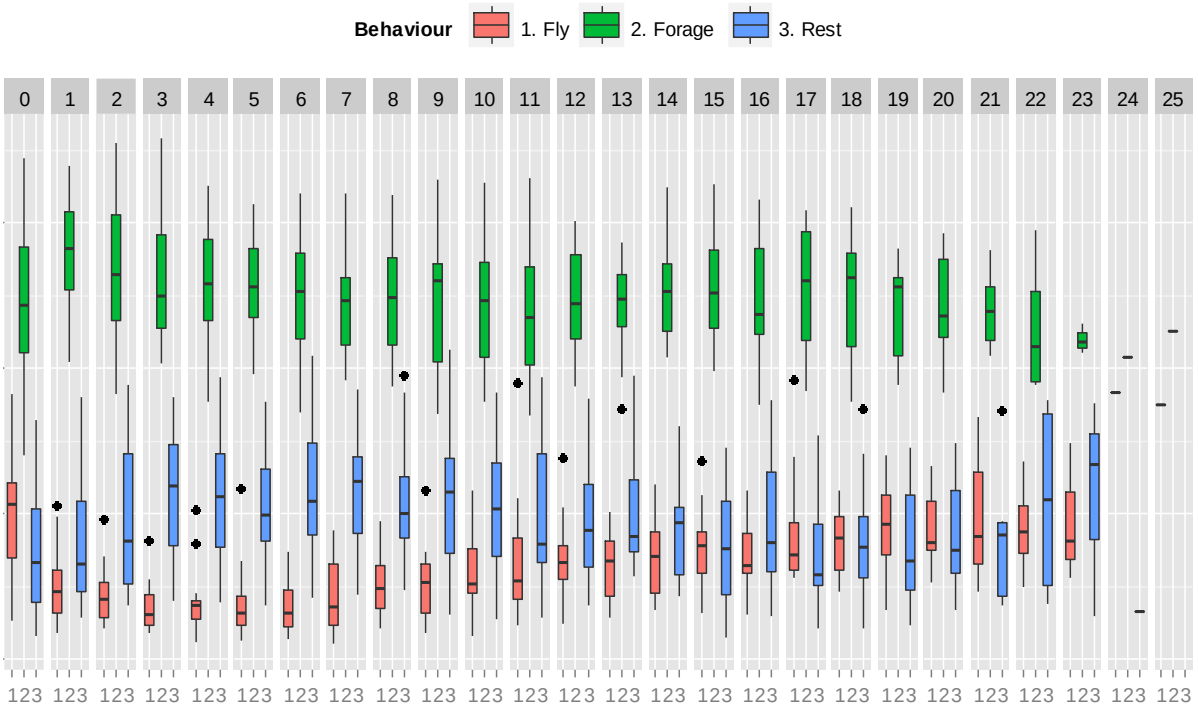


Figure 3.20: Weekly behaviour estimations at the wintering area for all birds following Itinerary 1. Data for all birds was synchronised so each bird started to be considered after their arrival at the wintering area.

3.4.3 Westwards Migration.

Stopovers will not be described and plotted by the itinerary but by route (northern or southern) due to the similarities in stopover locations for birds following the same route. Birds depart from New Zealand from the 19th of February to the 19th of April, with both the mean and median leaving dates on the 11th of March. In order to get to their final destinations in the north of Australia birds follow one of two routes:

Southern route

Birds following this route get to the wintering grounds passing by the south and west of the continent. On their way birds take one to three stopovers where they spend between 7 and 36 days. It is by far the main route, shown by 14 out of the 17 birds tracked in 2010 and by 5 out of 6 tracked in 2011.

In 2010 the main stopover on this route is located around longitude 147ºE as it is also the place where most individuals (all but #14) stop and where more time is spent by all of them (Figure 3.21). Data for early birds and therefore from fixes unaffected by the equinoxes suggest that this stop is located at Bass Strait, between Tasmania and Australia. Latitudes could be different for later dates but the constancy shown in longitude by different birds over two months makes this the most parsimonious option.

Nine birds use several other stopover places west of this main one. Birds #1, #3, #5, #9 and #10 use them as secondary stopover(s) after stopping at 147ºE and before endeavouring on the last flight towards the wintering area (Figure 3.21). For other birds these western stopover longitudes are their main (birds #6, #7, #11) or only (bird #14) stopover. These stopovers are centred around 140E although birds are more disperse than at the main stopover at 147ºE.

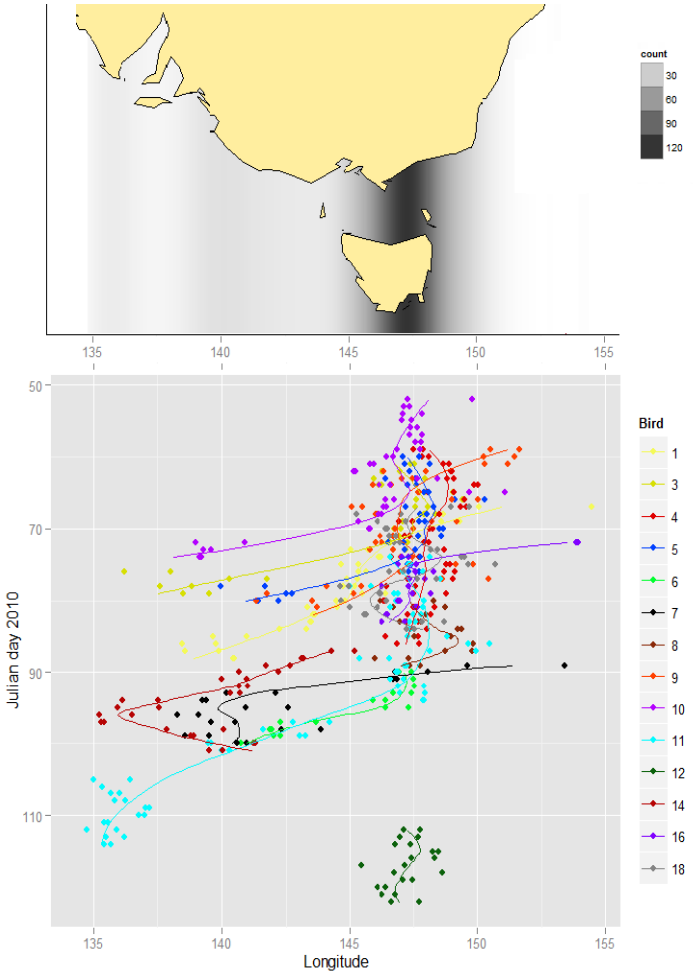


Figure 3.21: Spatiotemporal description of the stopovers taken by each of the birds choosing the southern route on the westwards migration in 2010. **Top:** 1D density plot for the longitudes of all fixes corresponding to this period. The plot is overlaid with a map of Australia for reference. **Bottom:** Longitudinal plot for all birds in the period color-coded by bird. A smoothed line for each bird has been added to help visualize patterns.

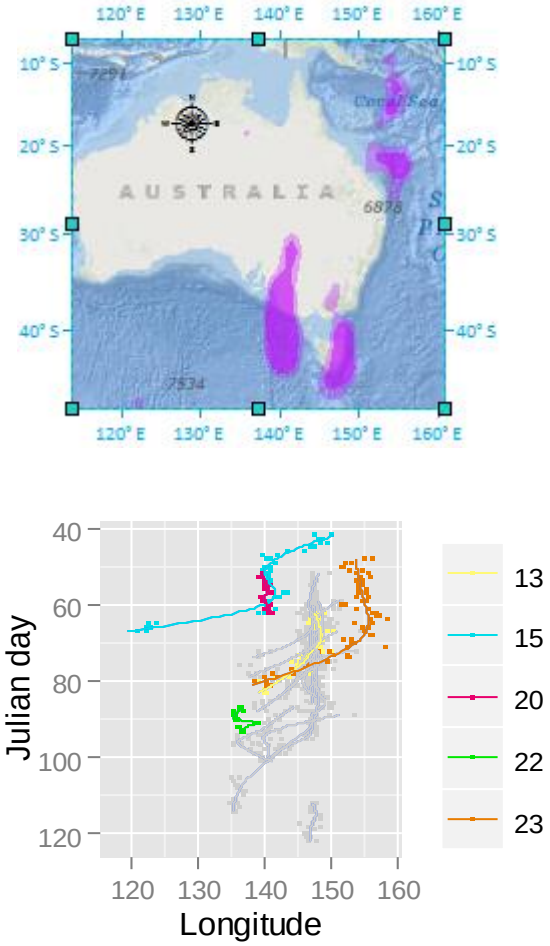


Figure 3.22: **Top:** Map showing 35% and 50% kernel density plots for all five individuals following the southern route on the westwards migration in 2011. **Bottom:** Longitudinal plot color-coded by bird. Birds for 2010 are also plotted and coloured grey in the background. A smoothed line for each bird has been added to help visualize patterns.

In 2011 the two stopover places for the westwards migration remain at 147ºE and 140ºE, however their relative importance is inverted (Figure 3.22). While four of the five birds stop at 140ºE only one stops at 147º, the main stopover of the previous year. Besides, in 2011 we observe two other stopover areas that had not been seen in 2010: one at the Coral Sea (bird #23) and another at the Great Australian Bight, at longitude 123ºE (bird #15).

After the stopovers most birds endeavour on a passage period arriving directly at their final wintering areas except for ten of them (Birds #3, #4, #5, #7, #10, #11, #14 and #18). These birds exhibit a period of slower longitudinal change at the turning of the westernmost tip of Australia and just after passing it (Figure 3.23). This period lasts until the birds arrive in their respective wintering areas. This is true for all of them including bird #9 for which the wintering area is farther east at the Arafura Sea.

Northern route

Only three (#2, #17 and #19) of the seventeen birds for 2010 and one for 2011 (#21) take the northern route on their westwards migration. Only the earliest of the three in 2010 makes a stopover north of Brisbane, lasting 12 days (Figure 3.24).

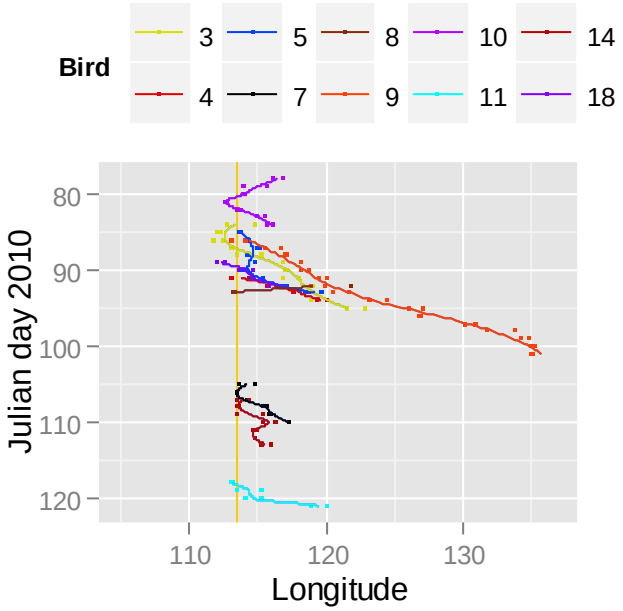


Figure 3.23: Longitudinal plot of the period shown by some birds following itinerary 1 before arriving into the wintering area. The plot is colour-coded by bird. A LOESS-smoothed line for each bird has been added to help visualize patterns. The vertical orange line indicates the westernmost longitude of the Australian continent at 113ºE.

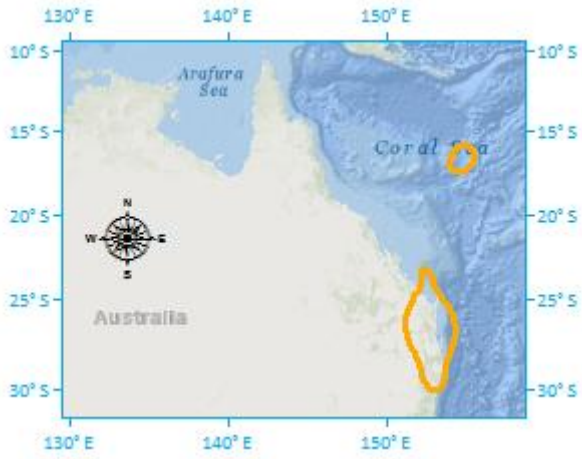


Figure 3.24: 35% kernel density contour plot for the stopover made by bird #17. The only stopover made for the northern route in 2010.

3.4.3.1 *Phenology of the westbound migration*

The date for leaving New Zealand is related to the last night at the burrow (p = 0.043, Table 3.6) and to the sex of the individual (p = 0.044, Table 3.6). The last day at the burrow, however, shows no relationship to the leaving date (p = 0.08, Table 3.6). The average delay between the last night at the colony and leaving New Zealand is ten days.

The mean time spent on the westwards migration for the southern route was 27.31 ± 9.4 days, of which 18.62 ± 8.8 were spent in stopovers and 8.69 ± 3.5 were spent commuting. Out of the thirteen birds studied six made only one stopover, six made two and one made three. The median arriving date at the wintering area was 1/Apr/2010.

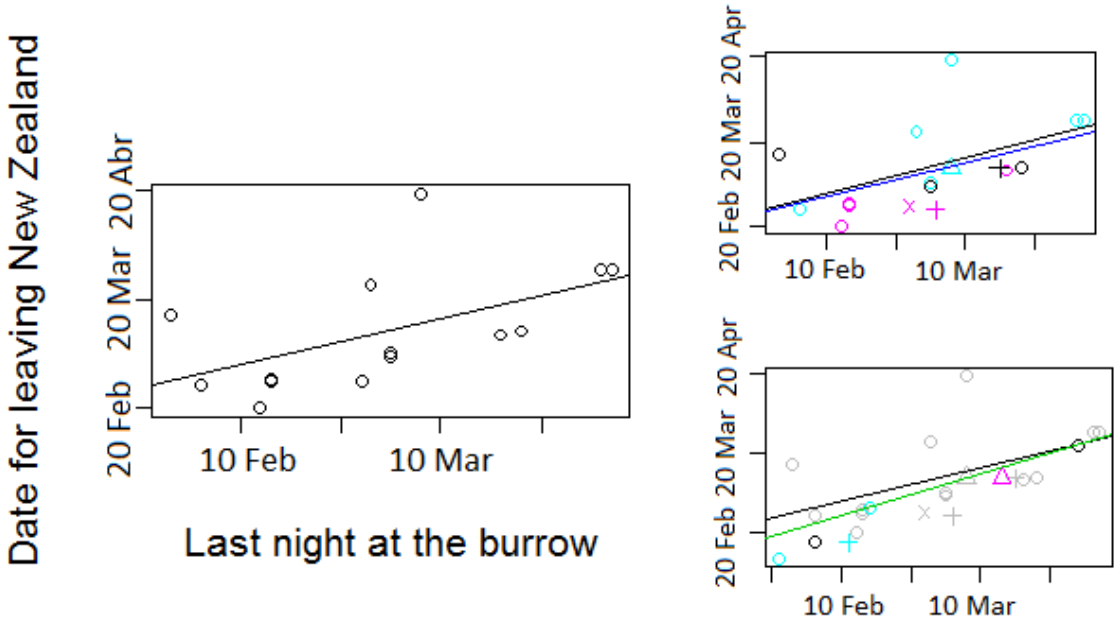


Figure 3.25: Scatterplot of the date for leaving New Zealand plotted against the last night visit to the burrow. **Left)** The black line represents the model fitted. **Top-Right)** Including all birds from 2010. Colour indicates estimated sex for the birds: Male (Blue), female (pink) and unknown (black). Shapes indicate the route followed after leaving New Zealand, route 1 (circles), route 2 (triangle), route 3 (plus sign) and Bird #9 (multiplication sign). The resulting model for 2010, when Routes 2 and 3 are included is coloured blue. **Bottom-Right)** Using the same colour and shape codes the birds from 2011 are plotted together with those from 2010 (coloured grey here for simplicity). The resulting model when 2011 birds are included is coloured green.

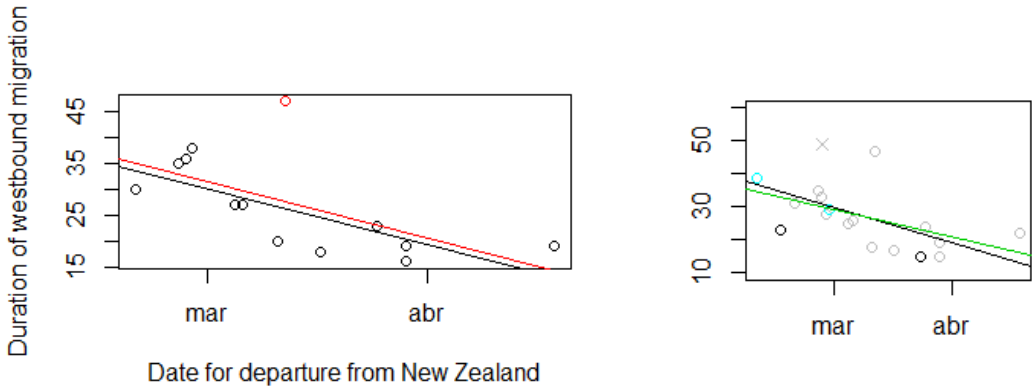


Figure 3.26: Scatterplot of the date for leaving New Zealand plotted against the last night visit to the burrow. **Left)** The black line represents a model fitted using only the datapoints coloured while the red line was fitted using all datapoints, including that coloured red. **Right)** Using the same colour and shape codes the birds from 2011 are plotted together with those from 2010 (coloured grey here for simplicity). The resulting model when 2011 Route 1 birds are included is coloured green.

Table 3.6: Table showing the Linear Models (LM) built to explain date for leaving New Zealand (NZ) and several other parameters of the westbound migration. Competing LM are selected according to the lowest AIC (coloured light blue).

Modelled variable	Explanatory variables			p-value	AIC
Date for leaving New Zealand	Last night at burrow			p = 0.04	118.2
		Last day at burrow		p = 0.08	123.1
			Estimated sex	p = 0.04	117.6
	Last night at burrow		Estimated sex	p = 0.04	116.2
	Last night at burrow	Last day at burrow	Estimated sex	p = 0.08	117.5
Duration of westbound migration	Date for leaving NZ			p = 0.01	76.17
			Estimated sex	p = 0.49	84.08
	Date for leaving NZ		Estimated sex	p = 0.052	77.15
Westwards mig: Days spent at stopovers	Date for leaving NZ			p = 0.03	
Westwards mig: Days spent on passage	Date for leaving NZ			p = 0.55	
Number of stopovers in westbound mig.	Date for leaving NZ			p = 0.28	

The duration of the westwards migration seems to be mainly influenced by the departure date ($p = 0.04$, Table 3.6), such that the last leavers spend the shortest time on migration (Figure 3.26). Reduced migration length seems to be due to a change in stopover time, shorter the later birds left the wintering area ($p = 0.03$, Table 3.6). No effect was detected on the length of passage time ($p = 0.55$) nor on the number of stopovers ($p = 0.28$).

3.4.4 Eastwards migration:

Birds leave the wintering area from the 1st August to 2nd September, with the mean date of departure 16th August. Arrival dates in New Zealand range from the 27th August to 30th September (mean 9th September).

North route.

The northern route is only taken by bird #2 in 2010 with no stopovers.

South route.

In 2010 this route is chosen by all other sixteen birds including Itineraries 1 and 3. The mean time spent on the westwards migration was 24.19 ± 8.7 days, of which 16.92 ± 12.4 were spent in stopovers and 7.92 ± 8.04 were spent commuting. Out of the thirteen birds studied nine made only one stopover, three made two and one made three.

Half of the birds (#1, #3, #5, #8, #9, #11, #16 and #18) instead of departing for the stopover areas straight after wintering showed a period of slow displacement along the west coast of Australia (Figure 3.27). This period is analogous to that seen before the arrival at the wintering area (Figure 3.23) and together are considered the periods of slow displacement.

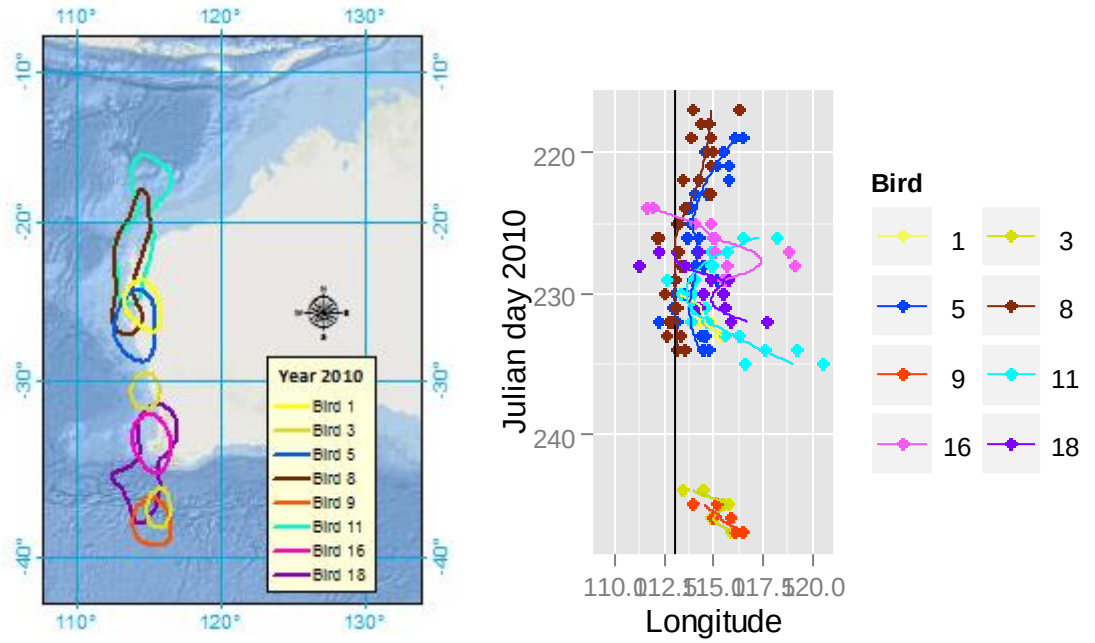


Figure 3.27: Spatiotemporal description of the period after leaving the wintering area and before going on passage. **Right:** 35% contour kernel density plots for each of the birds during the period. **Left:** Longitudinal plot color-coded by bird. A LOESS-smoothed line for each bird has been added to help visualize patterns.

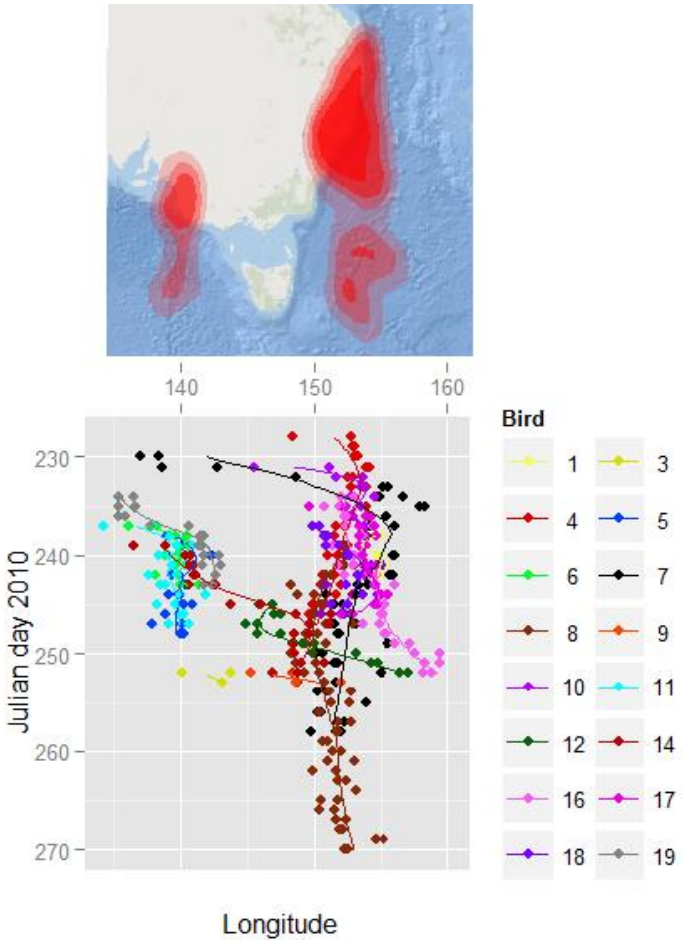


Figure 3.28: Spatiotemporal description of the stopover period for all birds following the southern route on the eastwards migration in 2010. **Top:** 20%, 35%, 50% and 65% kernel density plots for all fixes corresponding to this period. **Bottom:** Longitudinal plot color-coded by bird. A LOESS-smoothed line for each bird has been added to help visualize patterns.

As on the westwards migration, there are two stopover areas (Figure 3.28). The main stopover for the route is located off the south-eastern Australian coast between Brisbane and Sydney (median 153ºE, the easternmost tip of Australia), with a secondary stopover at around 140ºE used only by five birds. Opposite to what happened on the westwards migration, most birds only choose one of the two stopovers (Except for birds #7 and #14 that use both). Furthermore, the secondary stopover, despite being located at the same longitude as in the westwards migration, is much more confined in both time and space. The average time spent at the stopovers in this period is 24 days, ranging from 2 to 32 days.

In 2011 the situation is very similar (Fig. 29); the two main stopover locations are preserved but their relative importance is reversed. In 2011 more than half the birds use both stopovers and 140ºE is the most important stopover by number of birds (all five) and stopover time. The secondary stopover at 153ºE, is only used by three of those birds and for a smaller amount of time. In this year there are also additional stopover areas absent in 2010 such as the area at 123ºE used by birds # 13 and #15 (and also used by #15 on the westwards migration) or the area around 135ºE used by bird #23.

3.4.4.1 Phenology for the eastwards migration

The date of departure from the wintering area is not related to the date of arrival ($p = 0.55$, Table 3.7) nor to sex ($p = 0.15$, table 3.7) but it is to the total time spent in the wintering area ($p = 0.03$, Table 3.7). As in the case of the outbound migration, the duration of the return journey is dependent on the leaving date, in this case from the wintering area ($p = 0.013$, Table 3.7; Figure 3.30) although here there is no significant shortening of the time spent stopovers ($p = 0.13$, Table 3.7) or on passage ($p = 0.99$, Table 3.7).

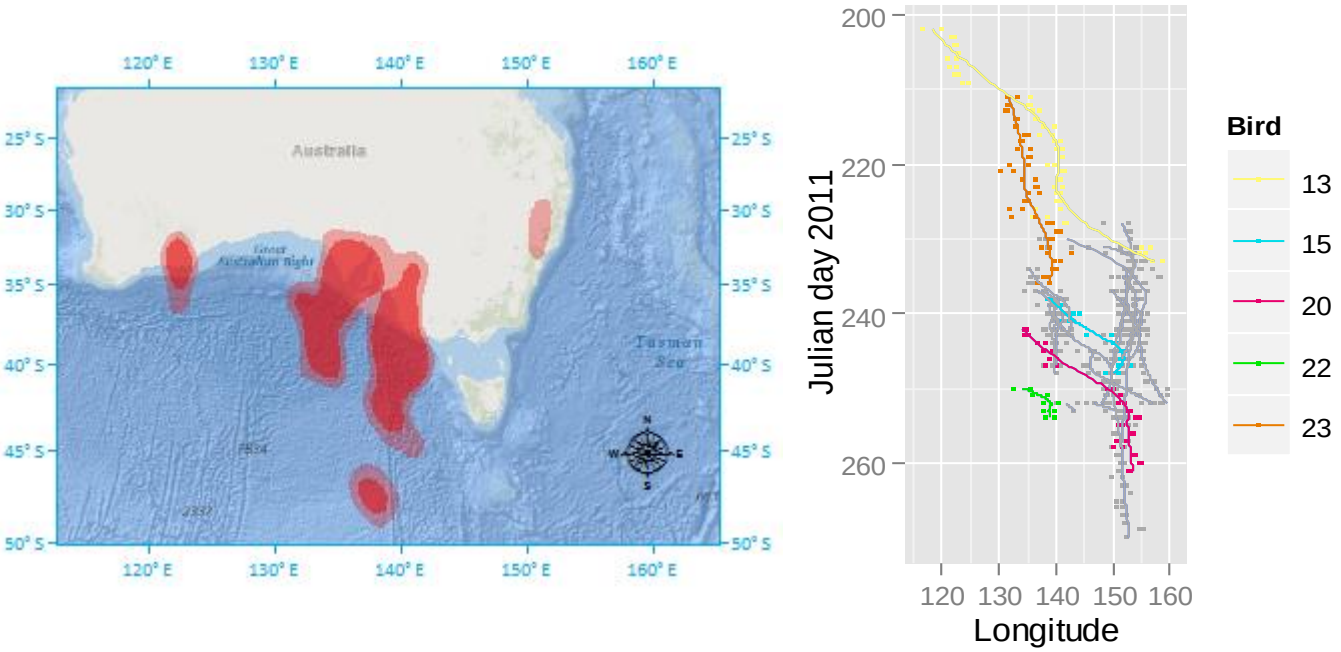


Figure 3.29: **Top:** Map showing 35 and 50% kernel density plots for all five individuals following the southern route on the eastwards migration in 2011. **Bottom:** Longitudinal plot color-coded by bird. A smoothed line for each bird has been added to help visualize patterns.

Table 3.7: Table showing the Linear Models (LM) built to explain date for different parameters of the eastbound migration. Competing LM are selected according to the lowest AIC (coloured light blue).

Modelled variable	Explanatory variable			p-value	AIC
Departure from the Wintering Area	Arrival into the Wint. Area			P = 0.57	100.4
		Total time spent at the Wint. Area		P = 0.03	95.2
			Estimated sex	p = 0.15	98
Duration of eastbound migration	Date for leaving WA			p = 0.013	113.4
		Estimated sex		p = 0.34	120
	Date for leaving WA	Estimated sex		p = 0.09	116.4
Eastwards migration: Days spent at stopovers	Date for leaving WA			p = 0.13	
Eastwards migration: Days spent in passage	Date for leaving WA			p = 0.99	

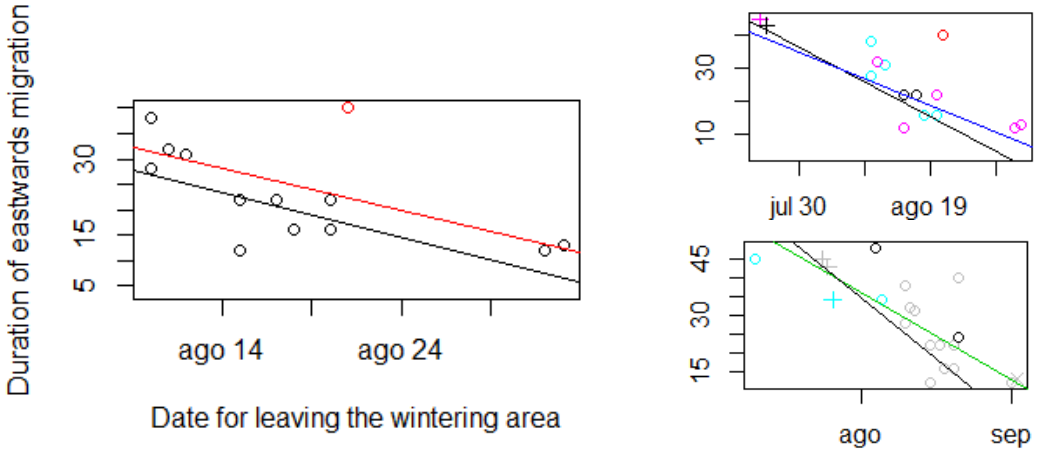


Figure 3.30: Right) The scatterplot on the left shows the fitting of two linear models explaining the duration of the eastwards migration through the date on which the birds crossed meridian 113E for the last time. The red line represents a model using all fourteen datapoints for route 1 while the black line represents a model fitting only the datapoints in black, thus excluding the outlier. **Top-Right**) including all birds from 2010. Colour indicates estimated sex for the birds: Male (Blue), female (pink) and unknown (black). Shapes indicate the route followed after leaving New Zealand, route 1 (circles), route 2 (triangle), route 3 (plus sign) and Bird #9 (multiplication sign) for which the route could not be initially established whether it was 1 or 3. The resulting model when Routes 2 and 3 are included is coloured blue. **Bottom-Right**) Using the same colour and shape codes the birds from 2011 are plotted together with those from 2010 (coloured grey here for simplicity). The resulting model when 2011 birds are included is coloured green.

3.4.4.2 The link with the breeding season

Eight out of thirteen birds in our study visited their burrow at night within one day of arriving in New Zealand. This results in a very significant relationship between the first night at the burrow and the arrival date ($p = 2.3x10^{-8}$, Table 3.8; Figure 3.31). The first day at the burrow, by contrast, is not apparently related to the arrival date ($p = 0.32$, Table 3.8).

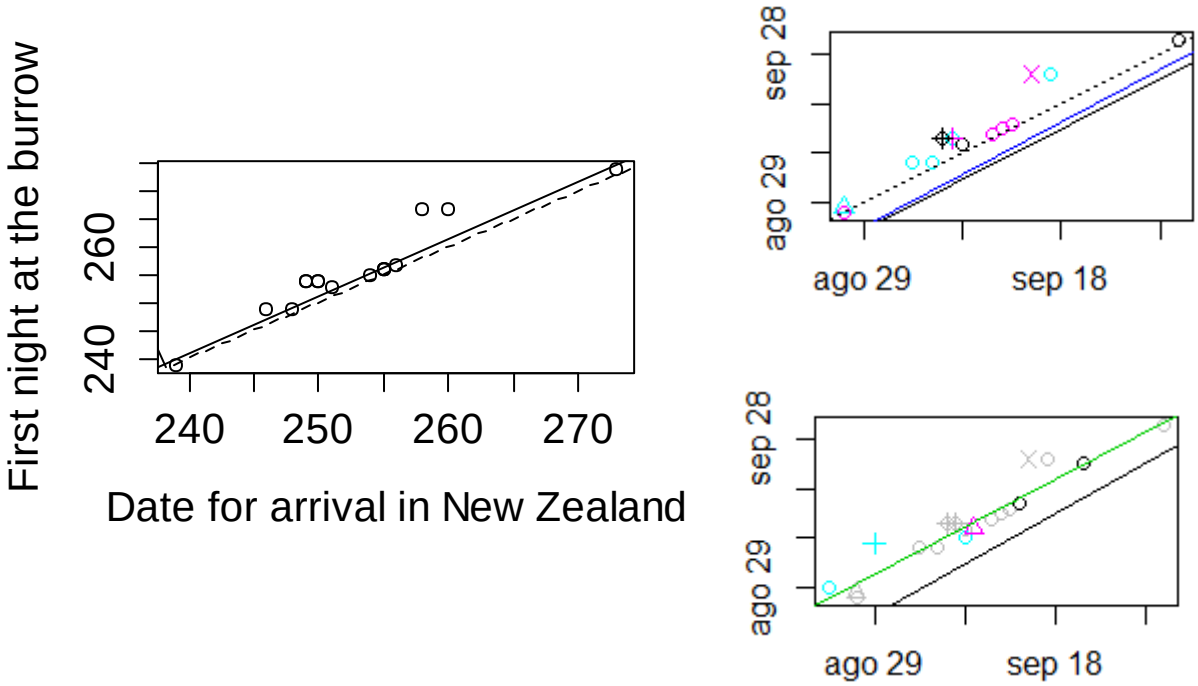


Figure 3.31: First night at burrow plotted against the date for arrival in NZ. **Left)** Including only birds that followed route 1 in 2010. The model fitted is represented by a black line. The dotted line represents the x = y line. **Top-Right)** including all birds from 2010. Colour indicates estimated sex for the birds: Male (Blue), female (pink) and unknown (black). Shapes indicate the route followed after leaving New Zealand, route 1 (circles), route 2 (triangle), route 3 (plus sign) and Bird #9 (multiplication sign) for which the route could not be initially established whether it was 1 or 3. The resulting model when Routes 2 and 3 are included is coloured blue. **Bottom-Right)** Using the same colour and shape codes the birds from 2011 are plotted together with those from 2010 (coloured grey here for simplicity). The resulting model when 2011 birds are included is coloured green.

Table 3.8: Table showing the Linear Models (LM) built to explain the first night and day visits to the colony.

Modelled variable	Tested variables		p-value	AIC
First Night at burrow	Date of Arrival in NZ		$p = 2.3x10^{-8}$	80.5
		Estimated sex	p = 0.73	118.4
	Date of Arrival in NZ	Estimated sex	$p = 2.2x10^{-6}$	84.4
First Day at burrow	Date of Arrival in NZ		p = 0.32	
		Estimated sex	p = 0.19	
	Date of Arrival in NZ	Estimated sex	p = 0.33	

3.4.5 Year to year differences in individuals tagged consecutive years

Both birds tagged in consecutive years follow itinerary 1 in 2010 and 2011. On the westwards migration both individuals choose the same stopover locations chosen on the previous year even though in 2011 migration happens almost two moths earlier (Figures 3.32 & 3.33). The opposite is true for the eastwards migration, where similarities are greater among years than within birds. Both birds show a much greater time spent in stopovers and spend most of it at a stopover in the Great Australian Bight not seen for any bird in the previous year (Figure 3.33 Bottom-left)

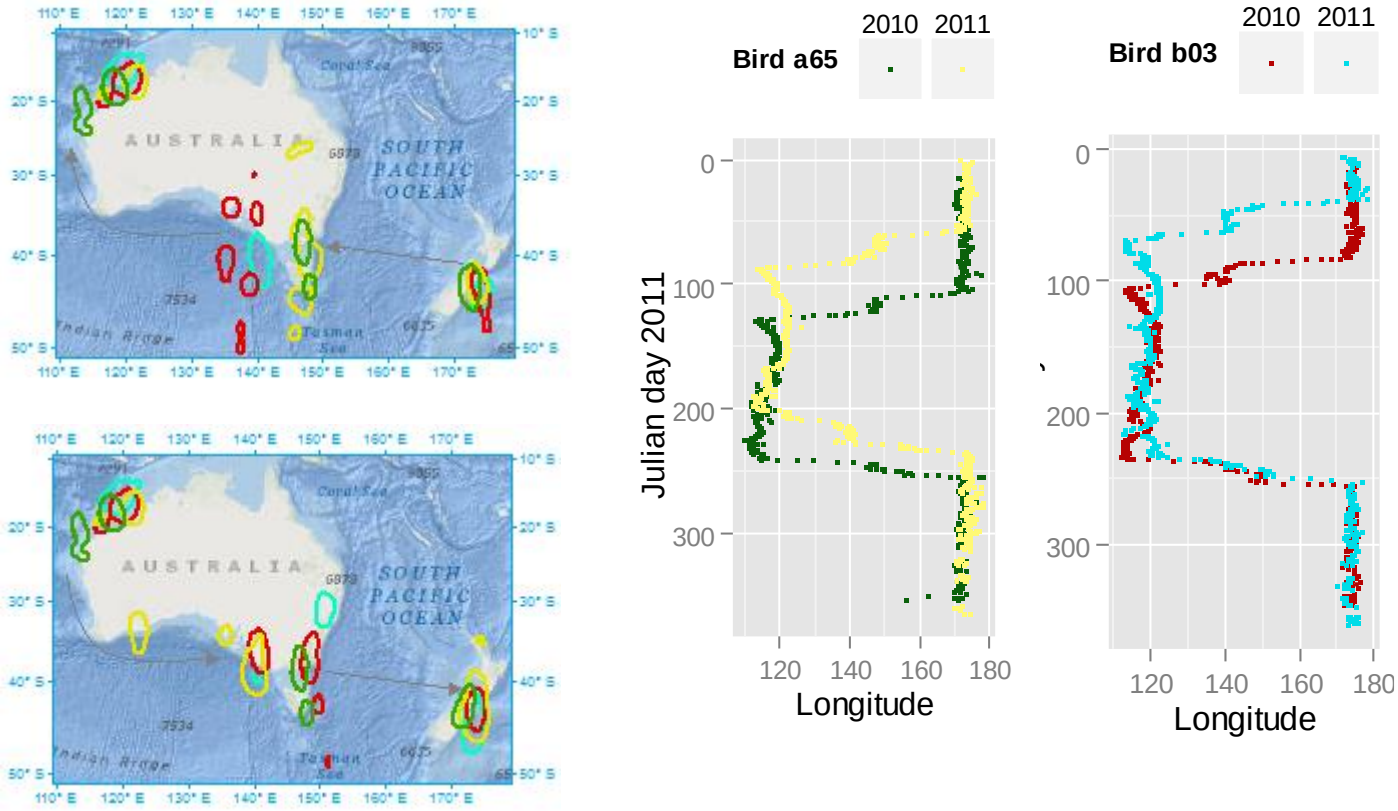


Figure 3.32: **Top-left:** Map showing 35% kernel density plots for both birds tracked in 2010 and 2011 on the stationary periods of the westwards migration. **Bottom-left:** same for the eastwards migration. **Centre:** Plot showing the longitudinal profile for bird a65 during two successive years of tracking (#12 and #13). **Right:** Plot showing the longitudinal profile for bird b03 during two consecutive years of tracking (#14 and #15).

There are no obvious simmilarities between years in the movements within the wintering area for both birds tracked in both years (Figure 3.33).

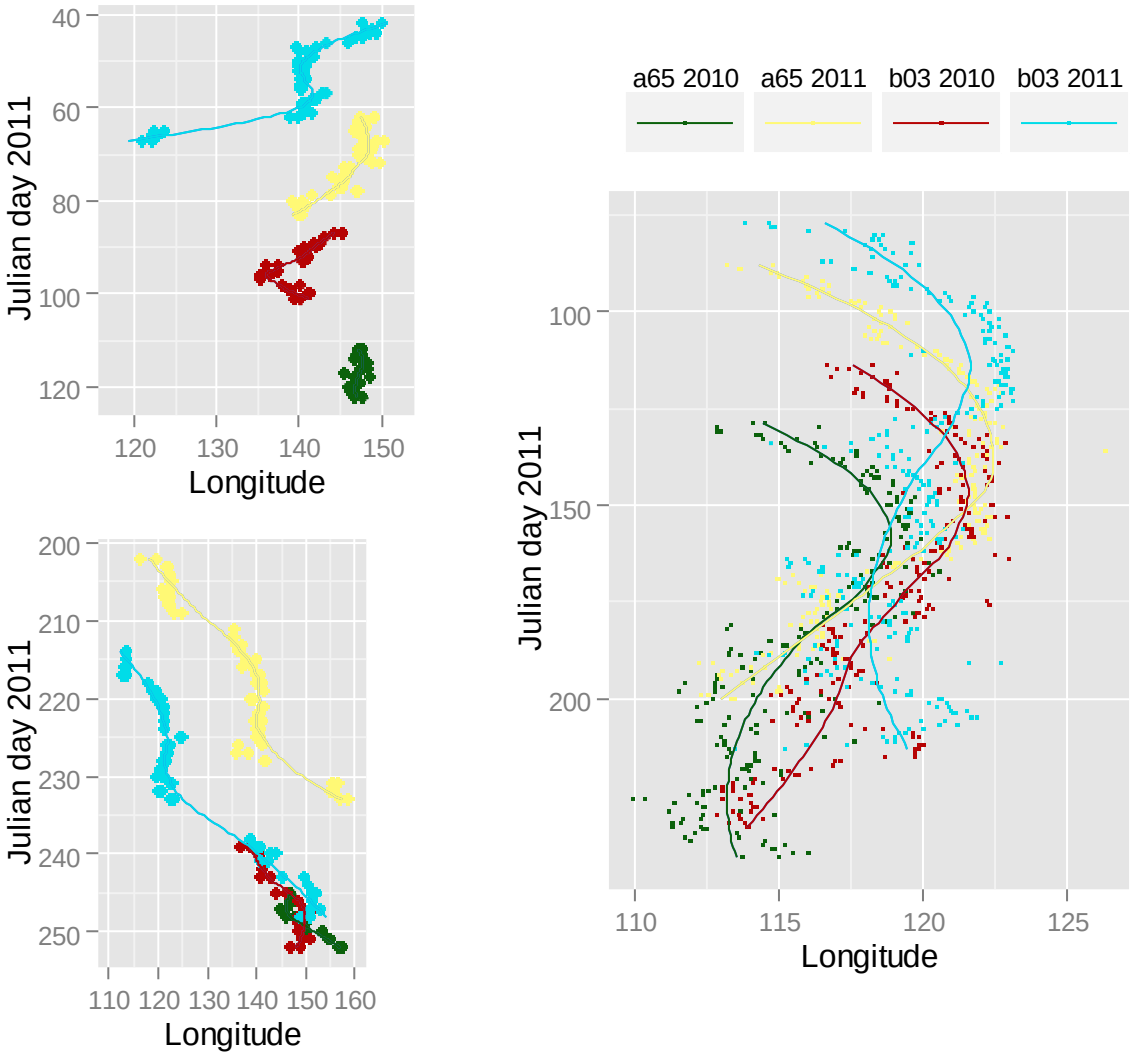


Figure 3.33: Plot showing the longitudinal profile for several periods of the migration of bird a65 in 2010 (#12, green) and in 2011 (#13, yellow) and for bird b03 in 2010 (#14, red) and 2011 (#15, blue). **Top-left:** Longitudinal plot for the westwards migration. **Right:** Longitudinal plot for the wintering area. **Bottom-left:** Longitudinal plot for the eastwards migration.

3.5 Discussion

3.5.1 Wintering areas of the Hutton's shearwater

All Hutton's tracked spend most of their wintering time at three different areas off the north-Australian coast. This finding solves the long-standing question over the breeding adults' overwinter location (Harrow, 1976; Marchant & Higgins, 1990) and explains the presence of Hutton's Shearwaters sighted north of Australia (Halse, 1981).

The mismatch between the current observations and published knowledge of the species (Figure 3.1 Left) is probably due to several reasons. First, northern Australia being scarcely inhabited together with the birds not coming too close to the coast (Halse, 1981) has probably resulted in fewer sightings than for example in the more populated southwest Australia (Figures 3.5, 3.22 & 3.29). Also the birds' behaviour has probably contributed to making them inconspicuous as at the wintering areas shearwaters have only been seen flocking in small groups if at all (Halse, 1981). Second, the lack of a review accounting for sightings since Marchant & Higgins (1990) has kept recent observations out of the literature (ALA, 2014, Figure 3.1 Right).

These data fail to explain those individuals washed up on Australian shores during the breeding season (Warham, 1981) and those observed in New Zealand overwinter (Harrow, 1976). Given the current results it seems unlikely those observations correspond to breeding adults so I hypothesize that these birds may be juveniles.

The extent and location of the wintering areas and the individual movement patterns within are consistent in the two years of study for the two main wintering locations in the Indian Ocean and the Arafura Sea. For the area in the Coral Sea we can only speculate as no tracked birds in 2011 overwintered there although birds #21 and #23 used the area as a stopover in

their respective migrations (Figures 3.15 & 3.22). Wintering areas are consistent for the two individuals observed in consecutive years (Figure 3.32).

Movement patterns within the wintering areas are shared among birds and between years. In the area north of Western Australia most birds show a slow displacement in longitude with the same pattern. Birds show firstly an eastwards displacement followed by a much slower westwards movement until leaving the wintering area (Figures 3.14 & 3.15).

When wintering at the Arafura Sea birds do not stay within one discrete area but switch place two or three times over the course of the wintering period (Figures 3.14 & 3.15). The locations chosen are shared by different individuals of the three different routes and both years, with the most used ones located at 140ºE, 133ºE and 137ºE (Figure 3.15). At these locations birds do not show broad movements within the areas as at the Indian Ocean but a very high fidelity to the longitudes of stay maybe pointing towards the presence of more localised resources birds

The wintering area in the Coral Sea is comparatively smaller than the other two. This area is only used by one bird during the whole winter in 2010 (Figure 3.14) although it is also used as a stopover for two other birds in 2011 (Figure 3.15).

The explanations for these consistent within-area movements among individuals in different years could be due to the birds following shifting areas of high productivity. Supporting this is the remarkable similarity between both birds following itinerary 3 after their arrival into their wintering area at the Arafura Sea (Figure 3.7). Both of them undertake the following changes in location within a day of each other even when they are several degrees apart. This is probably due to them following the same environmental changes through their route.

More years of tracking and further studies involving remote sensing data of productivity and wind would be needed to test this and explore the environmental drivers of detailed migratory movements.

The moult occurs during the first half of the birds' stay at the wintering area (Figure 3.20), a common strategy with many other long-distance migrants (Bridge, 2006; Ramos et al., 2009). Its aim is to avoid this period to overlap with the migration or the breeding season and at the same time make use of high-productivity waters to feed easily during this costly process (Newton, 2011). The duration of the moult would be of at least twelve weeks, in line with other small *procellariiformes* (Bridge, 2006). During this time birds never lose the ability to fly although the time spent in flight is greatly reduced compared to other periods of the year or to the second half of the time spent at the same wintering area (Figure 3.20). The start of the moult is synchronised with the arrival at the wintering area rather than it happening at a fixed time of the year (Figure 3.19). This ability to regulate and to prioritise metabolic processes associated with migration or with moult has already been reported in many bird species including seabirds (Lindström *et al.*, 1994; Kemper *et al.*, 2008; Newton, 2008).

3.5.2 Itineraries

Hutton's Shearwaters follow at least three distinct itineraries on their overwinter migration, with itinerary 1 being the most common of them. Itineraries 2 and 3 are much less frequent although they must not be rare as we see each twice despite our small sample size. Reasons behind itinerary and route choice remain elusive for a number of reasons. First, the relationship between route choice and Wintering Area is not exclusive as both the Indian Ocean and the Arafura Sea wintering areas are accessed by both routes. Second, birds following itinerary 3 pass through the three wintering destinations in an anti-clockwise

migration and birds #9 and #21 both overwinter at the Arafura Sea coming from itineraries 1 and 2 respectively (Figures 3.14 & 3.15). In fact this coincidence suggests the possibility of a not yet observed itinerary 4 with birds completing a clockwise migration. This could happen if a bird took the southern route to winter in Arafura Sea as bird #9 does (Figure 3.14) and returned to New Zealand via the Northern Route as bird #21 does (Figure 3.15).

Also, it is much shorter to get to all three wintering areas via the northern route and yet the southern route is the overwhelmingly the most chosen option. This is especially puzzling when considering those birds wintering north of Western Australia. For them using the northern route would mean a minimum distance of 7,952 Km, whilst doing it via the southern route means 10,565 Km (using the northern crossing of the Tasman sea) or 8,924 Km (for those taking the southern crossing) (Figure 3.5).

Route choice does not seem to be influenced by the latitude chosen to cross the Tasman Sea as birds choosing itinerary 1 take both the northern and the southern crossings to Brisbane and to Tasmania (Figure 3.5). Phenology does not seem to be a reason either as birds choosing the northern route do not seem to leave for migration later than southern route ones nor arrive earlier for breeding (Figures 3.16 & 3.31). There does not seem to be a sex effect either, as we can see both males and females taking both routes (Appendix 2). We cannot rule out the possibility that the itinerary may be idiosyncratic, maybe as a result of individual learning during the juvenile stage (Guilford *et al.*, 2011), as both birds tracked for consecutive years show fidelity to their itinerary.

The crossing of the Tasman Sea in both directions is undertaken via (at least) two different paths (Figure 3.5). The reasons behind the choice are also unknown and I can only speculate.

The northern crossing means the closest distance between Australia and New Zealand. This would also explain why its position is the same for the eastwards and westwards migration (Figure 3.5). Also I speculate whether the presence of Lord Howe islands on the way could be used as waypoints on their passage. Especially as this archipelago includes Ball's pyramid, a 1,800 feet high stack in the middle of the Tasman Sea.

The southern route is located much more southern on the return migration compared to the outbound trip (Figure 3.5). I speculate this could be due to the birds following different favourable winds at these two different times of the year as longer routes are not necessarily the more costly energetically (González-Solís *et al.*, 2009). Again, further studies involving environmental data would be needed to confirm or dismiss these hypothesis.

3.5.3 Stopovers

Stopovers are a key part of the migration for birds following the southern route. From behaviour estimates we can deduce these areas serve as resting and refuelling place for the migrating birds (Figure 3.11). Behaviour percentages are similar to other stationary periods and show the second highest foraging percentage after the wintering areas. Stopovers also show an intermediate flying percentage between the wintering and the breeding area. Lower values than at breeding area are probably a consequence of their function as central-place foragers when in New Zealand and higher values than at the wintering area may indicate fewer or more dispersed resources at the stopovers. Further analyses involving environmental data or productivity proxies (i.e. SST or Chlorophyll a) would be needed to explore this hypothesis further.

All birds following the southern route use at least one stopover in each direction of migration (Appendix 2). The most important stopover overall is located at 140ºE off the coast from Mount Gambier as it is used on both directions of the migration on both years (Figures 3.21, 3.22, 3.28 & 3.29). The eastern end of Bass Strait (147ºE) is also a very important stopover area as it is used in both years and it is the main stopover in 2010 for the westwards migration (Figure 3.21). For the 2010 eastbound migration the main stopover is located off the south eastern coast of Australia between Brisbane and Sydney (153ºE; Figure 3.28). Both areas are also used in 2011 but they are of relatively less importance compared to the stopover off Mount Gambier (Figures 3.22 & 3.29).

A relatively small sample size precludes testing whether flexibility in stopover choice is due to inter-year variability in environmental conditions or to individual idiosyncrasy. The greater within-year than within-individual similarity for the two birds tagged in consecutive years and the appearance of new stopover areas in these individuals would point towards the flexibility hypothesis. However this could still be due to intra-year environmental changes as migration in 2011 is retarded with respect to 2010 (Tables 3 & 4). Once more, these hypotheses would require detailed environmental data for testing.

Duration of stopovers is linked to the date of leaving the breeding area ($p = 0.03$, Table 3.6) in the westwards migration. This is probably a consequence of the birds leaving over more than two months as they are constrained by the breeding season ($p = 0.04$, Table 3.5) although it could also be due to a foreseeable (maybe seasonal) depletion of food resources at the stopover areas or to a change in favourable environmental conditions for migration. This is not the case of the return migration ($p = 0.13$, Table 3.7) for which all birds flee the wintering area within the short time-span of two weeks (Appendix 2).

3.5.4 Passage periods

These are periods of great longitudinal variation that birds use to move between stationary areas in unidirectional displacement –at least as far as the limited resolution of the dataset allows us to see. Behaviour estimate percentages show that these periods are characterised by a very low resting behaviour always below 5% in daily average (Figure 3.12).

During fast migration birds engage in flight during more than half of the day (Figure 3.12) and a varying percentage of the night depending on the moonlight available (Figure 3.13). This, together with the great longitudinal change that defines these periods, suggests these passages are intended to maximise time in flight even during the night, perhaps making use of favourable wind conditions. Fast flight behaviour at night has been observed in Cory's shearwaters (*Calonectris diomedea*; Dias *et al.*, 2012) and assessed with GPS in the closely related Manx Shearwaters (*Puffinus*; Guilford *et al.*, 2008).

None of this is the case for slow passage periods. Despite resting behaviour also being very low, flight behaviour for this period is not different from that of the stationary periods in the breeding season (Figures 3.11 & 3.12). Night behaviours are influenced by the moon in slow migration however only the resting behaviour is affected in a significant way (Figure 3.13).

The differences between these two kinds of passage periods are limited to behaviour or speed but these behaviours are also spatially segregated, with fast migration is shown only in the southern half of the Australian continent and slow migration found only to the north and west of it. The reason behind this could be that the northern half of Australia is in the 'horse latitudes' for most of the austral winter. Horse latitudes are high pressure belts that impede wind and cause winter to be the dry season in the north of the continent (Pidwirny, 2006). This lack of winds in winter would not allow shearwaters to shear-soar and probably oblige them to use a greater proportion of flapping flight. This would be at a time more costly (Furness &

Bryant, 1996; Amélineau *et al.*, 2014) and slower, explaining the lower flight time and the higher foraging time with respect to the fast passage periods. This different strategies could also explain why the vast majority of Hutton's shearwaters tracked chose the southern route to the wintering area despite its longer distance. Once more, detailed analyses on wind and productivity data would help us step out of the speculative grounds.

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Chapter 4:
General conclusions

4.1 General conclusions

Light-level geolocation (GLS) has been used widely for more than two decades to study many different aspects of migration, behaviour and breeding ecology in fish (Skomal *et al.*, 2009), reptiles (Fuller *et al.,* 2008), mammals (DeLong *et al.,* 1992) and birds (Croxall *et al.*, 2005). In Chapter 2 of this thesis I have tried to contribute to the potential of this method by describing a filtering procedure that allows mitigation of one of the greatest problems with geolocation, latitudinal unreliability around the equinox. This filter retains a greater amount of fixes that can now be used to better describe the events happening during the equinox period, which in many species is generally an important time for migration period.

It is likely that the use of GLS technology declines as miniaturization allows the more precise GPS technology to equal light level geolocation in coming years in fix frequency, size, weight and –eventually– price. However, this will not undermine the usefulness of the filtering method I introduce for two reasons. First, this technological redundancy is still several years away and, second, this method can be applied *a posteriori* making it a useful tool for the analysis of previously gathered data. Especially in a climate-change context it is likely that this technique may become useful for future researchers revisiting archived data. For example, trying to find baselines with which to compare future data. I hope this method allows present and future researchers to rescue the greatest amount of information possible from their datasets.

GLS technology is still not obsolete and this thesis is an example of its usefulness in shedding light onto many different aspects of the annual cycle of the endangered Hutton's shearwater. These include the identification of wintering and stopover areas and behaviour within them, the moulting period, the use of moonlit nights for migration and the relationships between the

different stages of the migration. At the same time results found here have given rise to several new questions concerning the migratory ecology of the species.

First, from a conservation perspective, it is a priority to assess at-sea risks such as by-catch or pollution (Croxall *et al.*, 2012) that Hutton's shearwaters can be subject to during the winter migration. The spatiotemporal description of the overwinter locations made in this thesis could be used in a similar way to Gaston *et al.* (2013), who quantified the overlap of Thick-Billed Murre (*Uria lomvia*) distribution with oil developments. For the same purpose, it could be important to study the birds overwinter locations' overlap with Australian Marine Protected Areas (MPAs). Given the consistency in stopover and wintering locations among birds and between years, protection using MPAs might be a very effective conservation measure for the species (Camphuysen *et al.*, 2012) and shall be taken into account in marine conservation planning.

It is also a priority from the research point of view to try to establish which environmental variables are responsible for the wintering distribution of Hutton's shearwaters. Remote sensed measurements of productivity could help explain not only wintering area choice but also the movement patterns within them (Figure 3.14, 3.15). The same applies to stopovers and the relative shift in importance seen between the two years of this study (Figures 3.21, 3.22). Remote sensed wind data might be used to help explain the causes behind the existence of the two different crossings of the Tasman Sea or at least explain why the southern crossing occurs at different latitudes in the two directions of the migration (Figure 3.5). Other questions would need the concourse of wind and productivity data to determine which is responsible for the pattern observed. For example, what are the causes behind changes in location of birds wintering in the Arafura Sea that happen within a day of each other even when birds are not in the same location (Figure 3.7).

Use of environmental data in future studies would also be interesting in order to further study the mechanisms underlying itinerary and route choice. None of the parameters measured in this thesis have managed to explain the puzzling multi-wintering-area and multi-itinerary migration of the Hutton's shearwater. To answer these questions it will also be necessary to increase the sample size for itineraries 2 and 3 to achieve a meaningful spatial, phenological and behavioural comparison among itineraries. This comparison together with the study of environmental conditions will be key in unravelling the causes behind this very interesting migration.

Another interesting topic for further study involves the relationships between migration and the breeding season as the peculiarities of this species could lead to being affected by important carry-over effects. Firstly, previous work has described how the breeding season of the Hutton's shearwaters is longer than that of the closely related Manx Shearwater (*Puffinus puffinus*) due to the conditions imposed by such a remote breeding location (Cuthbert & Davis, 2002). Secondly, in this thesis we have seen how the almost synchronous arrival back at the breeding area (Fig 3.10, Table 3.4) makes the early stages of the migration have a great influence (The duration of the whole migration depends on the date for leaving New Zealand (Fig 3.9, Table 3.4) and the duration of stay at the wintering area depends on the date of arrival there (Fig 3.16, Table 3.5)) in turn dictated by the breeding season through the date of leaving for New Zealand (Table 3.6). And thirdly, once at the wintering area, more than half of the time is spent undergoing a costly and handicapping moult, leaving on average a month (Subtracting 12 weeks from mean time spent at wintering area in Table 3.2) for individuals to recover condition and undertake the metabolic and anatomical changes necessary for the return migration (Newton, 2011). In this tight-schedule scenario the delay of the breeding season by late winter snows (Harrow, 1976; Cuthbert & Davis, 2002), or the effect of other

environmental variables still unknown to us, could potentially have a carry-over effect that has not been yet accounted for. Given the current endangered status of Hutton's shearwaters I think it is important to study this possibility and its potential effect in population numbers.

4.2 Final remarks

I hope my findings here have started filling in the knowledge gap on the life of Hutton's shearwaters at sea. Hopefully, my conclusions are useful ground on which to base further research into the many aspects of the biology or the conservation of the Hutton's shearwater that it has not been possible to answer here. In addition, the new methodology I have proposed for filtering of GLS data should aid all researchers who are currently using this technology, increasing the accuracy and potential of this data source.

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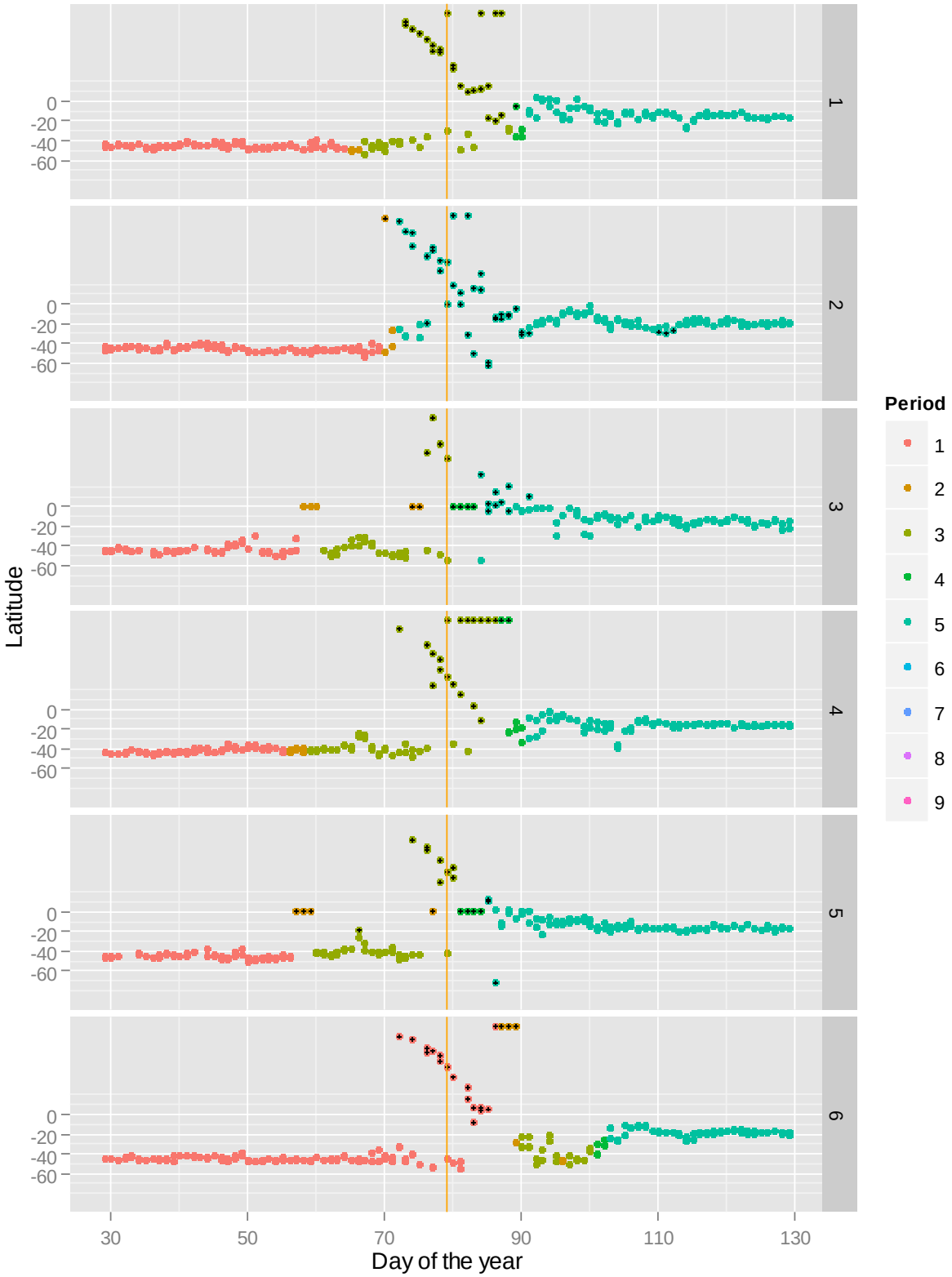
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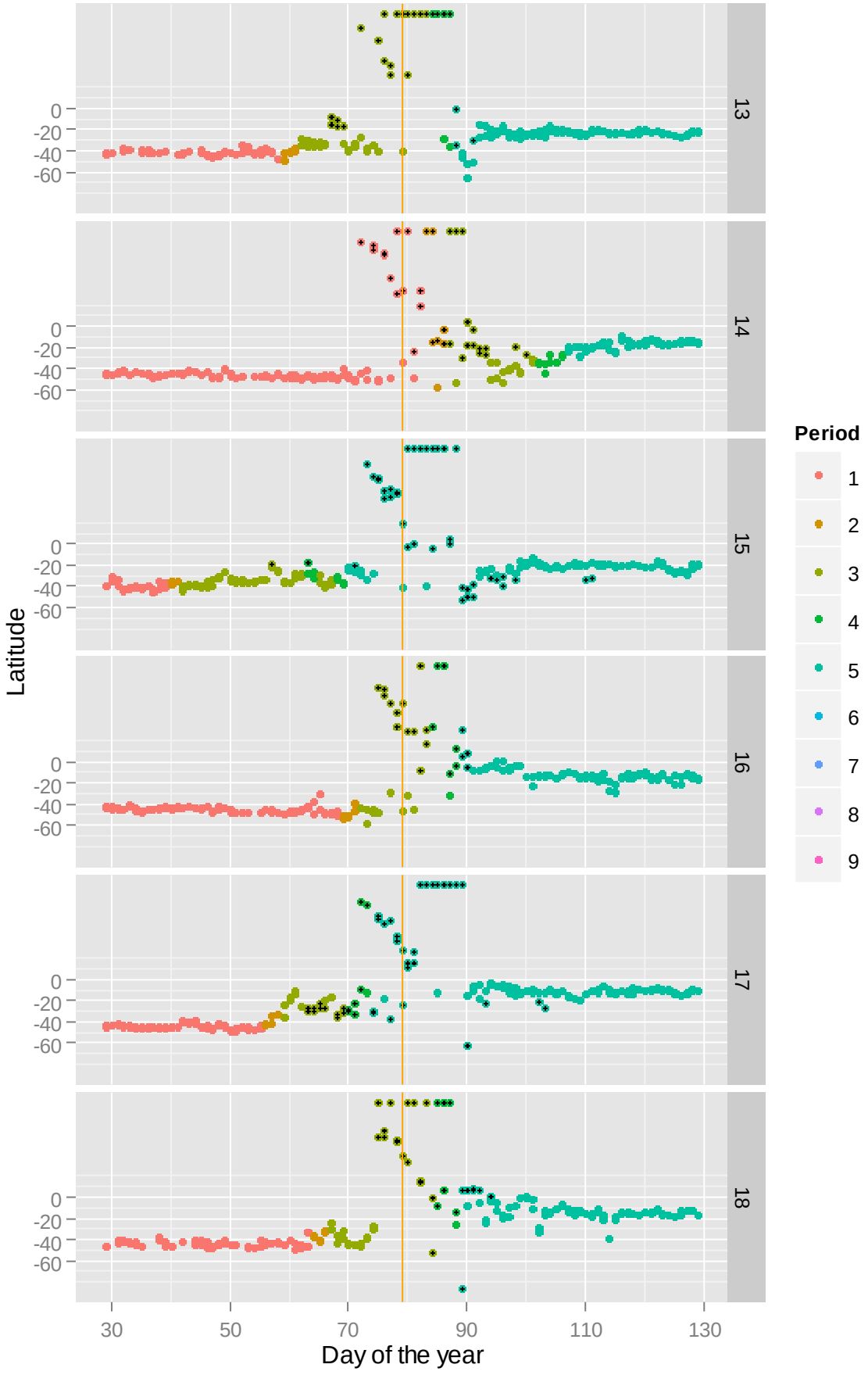
Appendices

5.1 Appendix 1

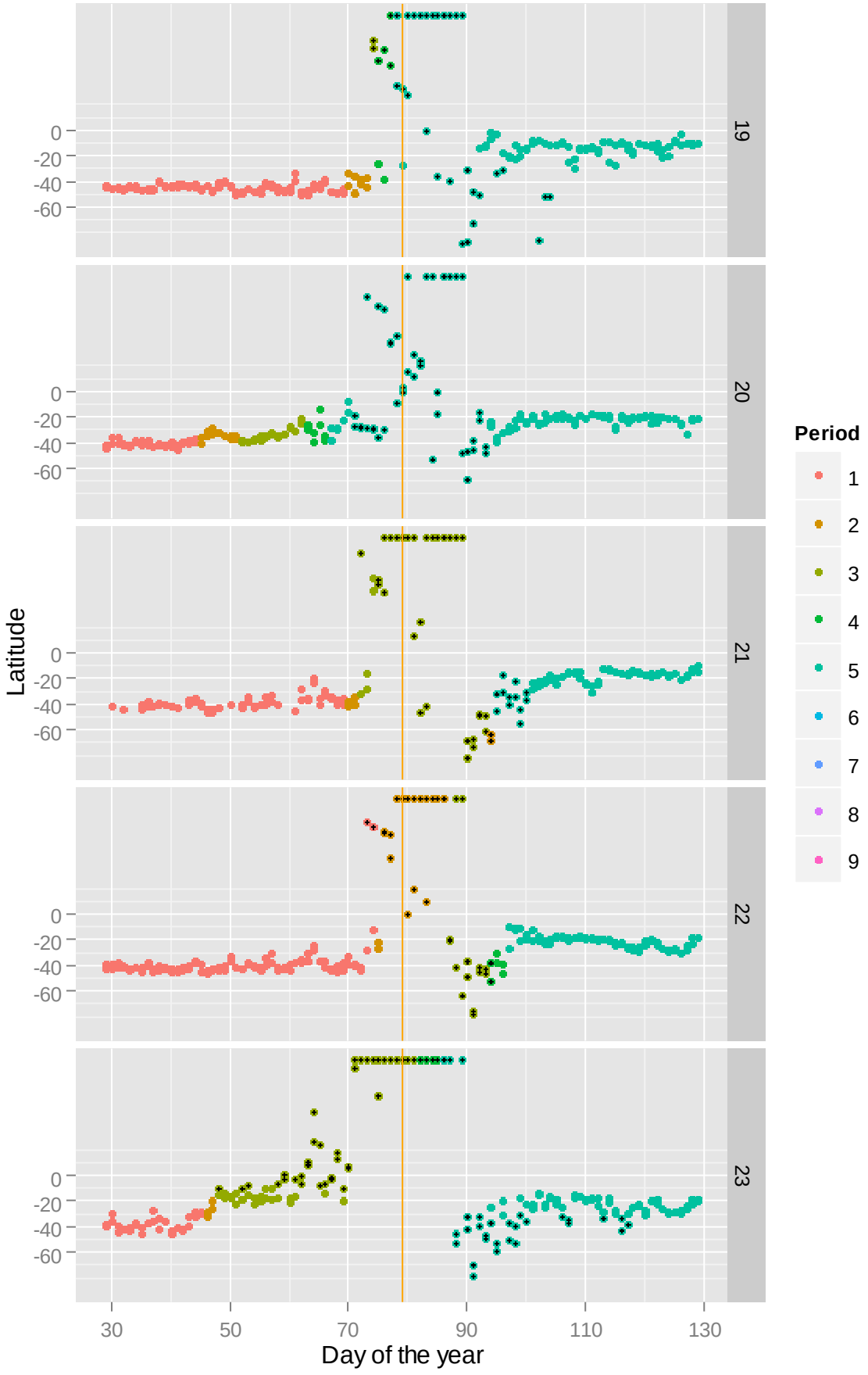
In this Appendix is shown a graphical representation of the application of Filter 5 from Chapter 2 to all 23 Hutton's shearwaters studied in Chapter 3. Filtered-out datapoints are marked with a black "+" sign. In order to apply this filtering method the itinerary chosen by the individuals together with knowledge of the period of migration in which they were in at each day of the year (both extracted from longitude data) were considered. Period abbreviations for the figure: 1) Wintering area before migration. 2) Westwards crossing of the Tasman Sea. 3) Stopover in the westwards migration. 4) Passage into the wintering area. 5) Wintering area. 6) Passage out of the Wintering Area. 7) Stopover in the eastwards migration. 8) Eastwards crossing of the Tasman Sea. 9) Wintering area after migration. Not all birds show all of the periods described. Bird coding is consistent with that of Table 3.1 and Appendix 2.

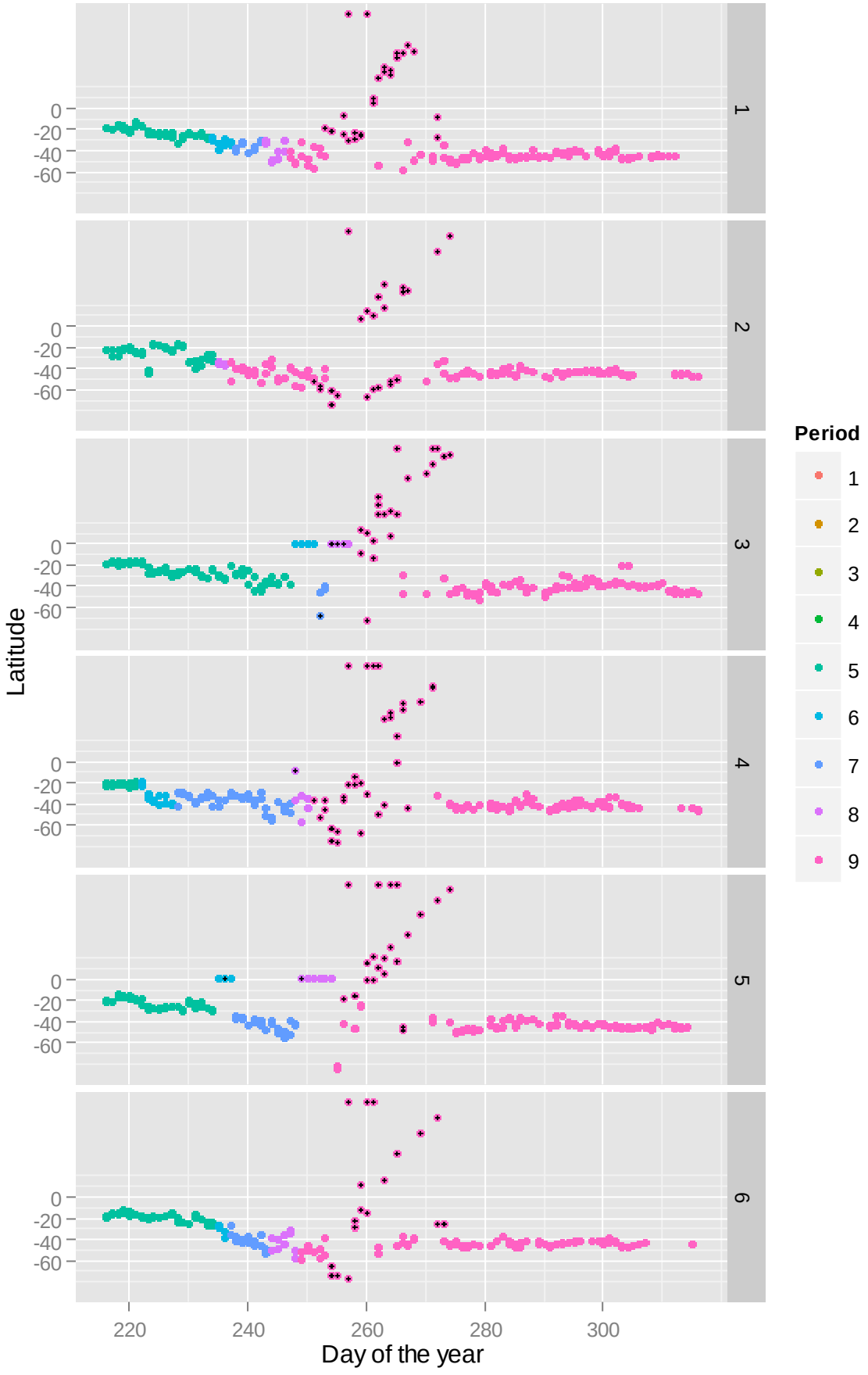

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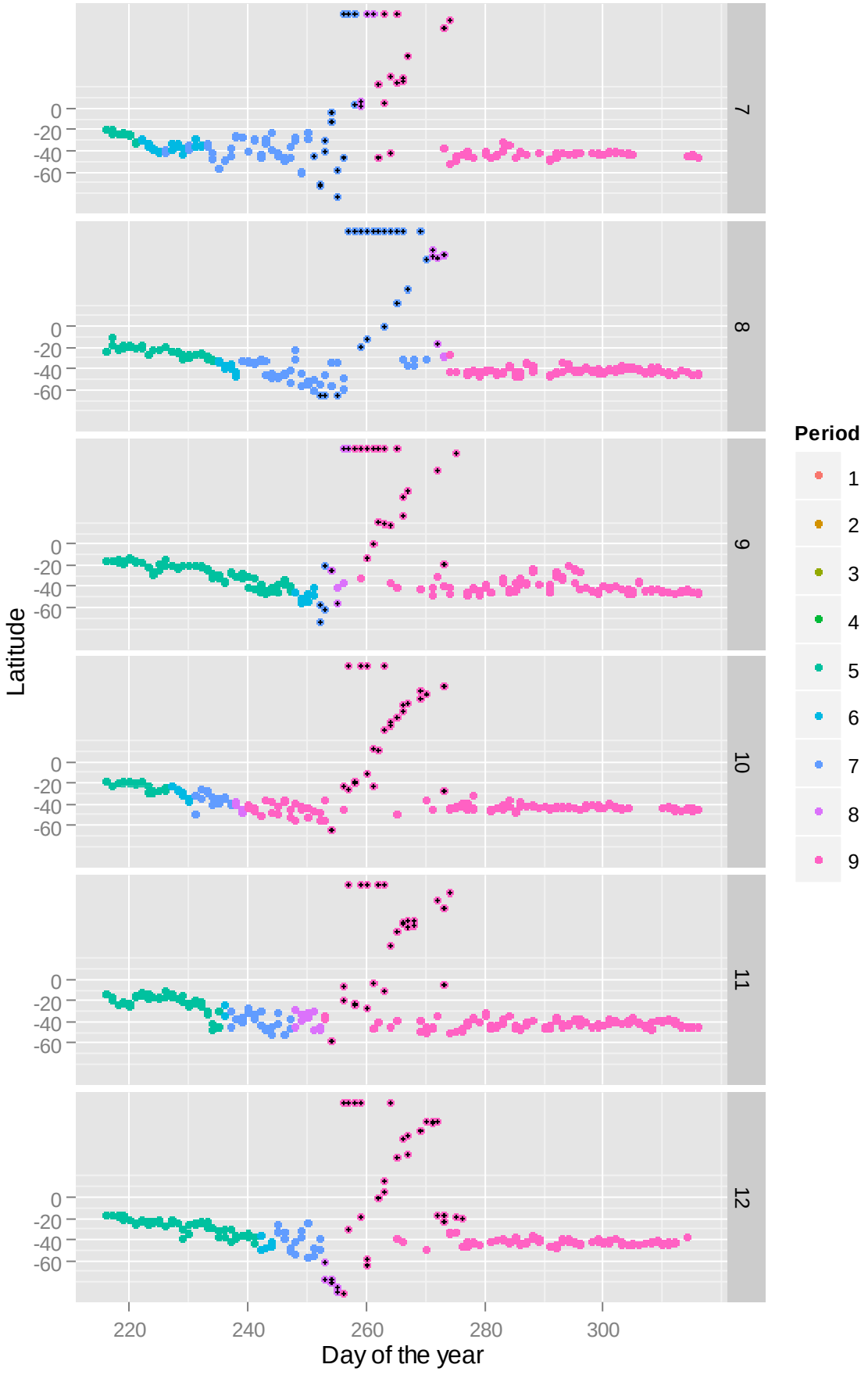

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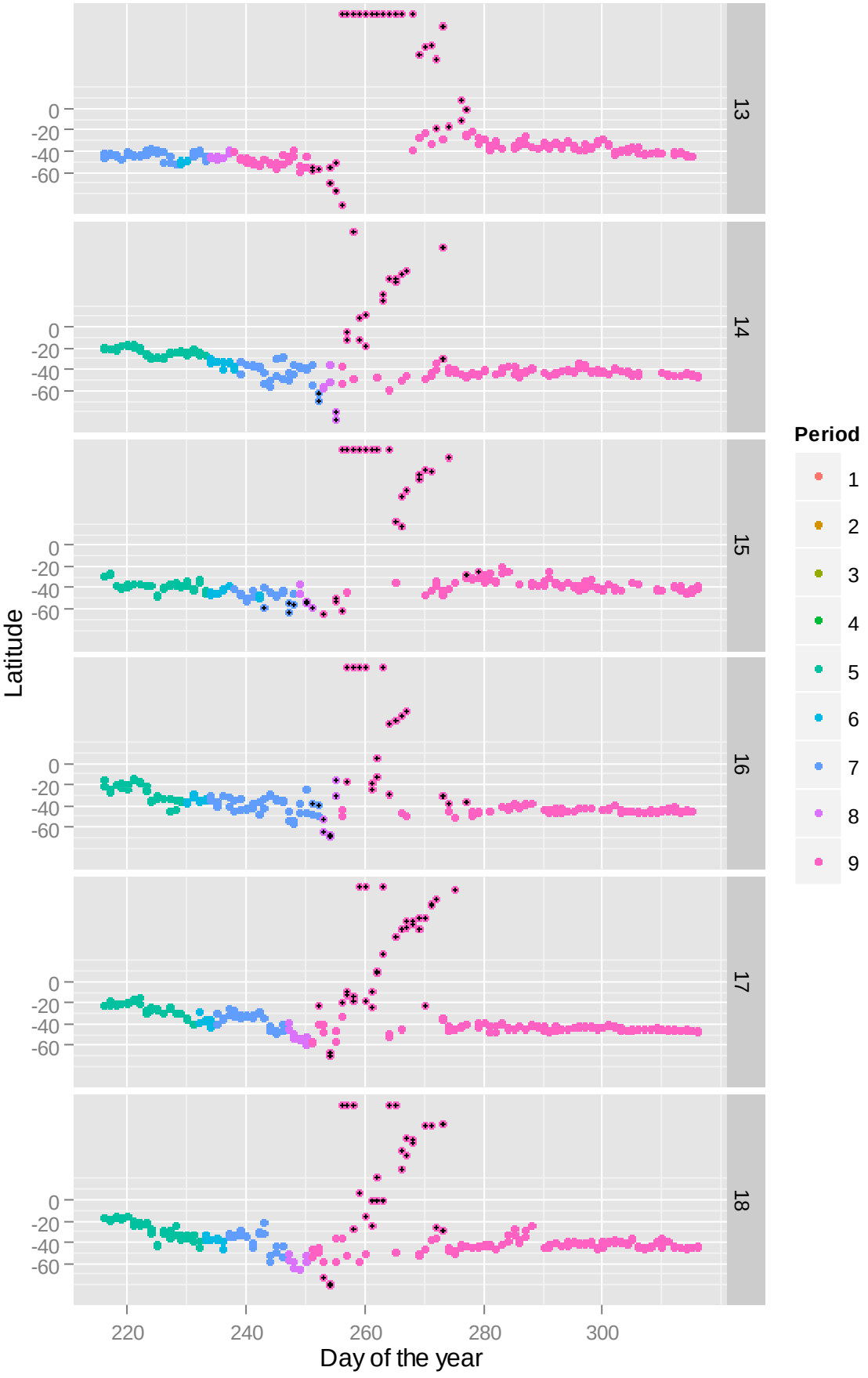

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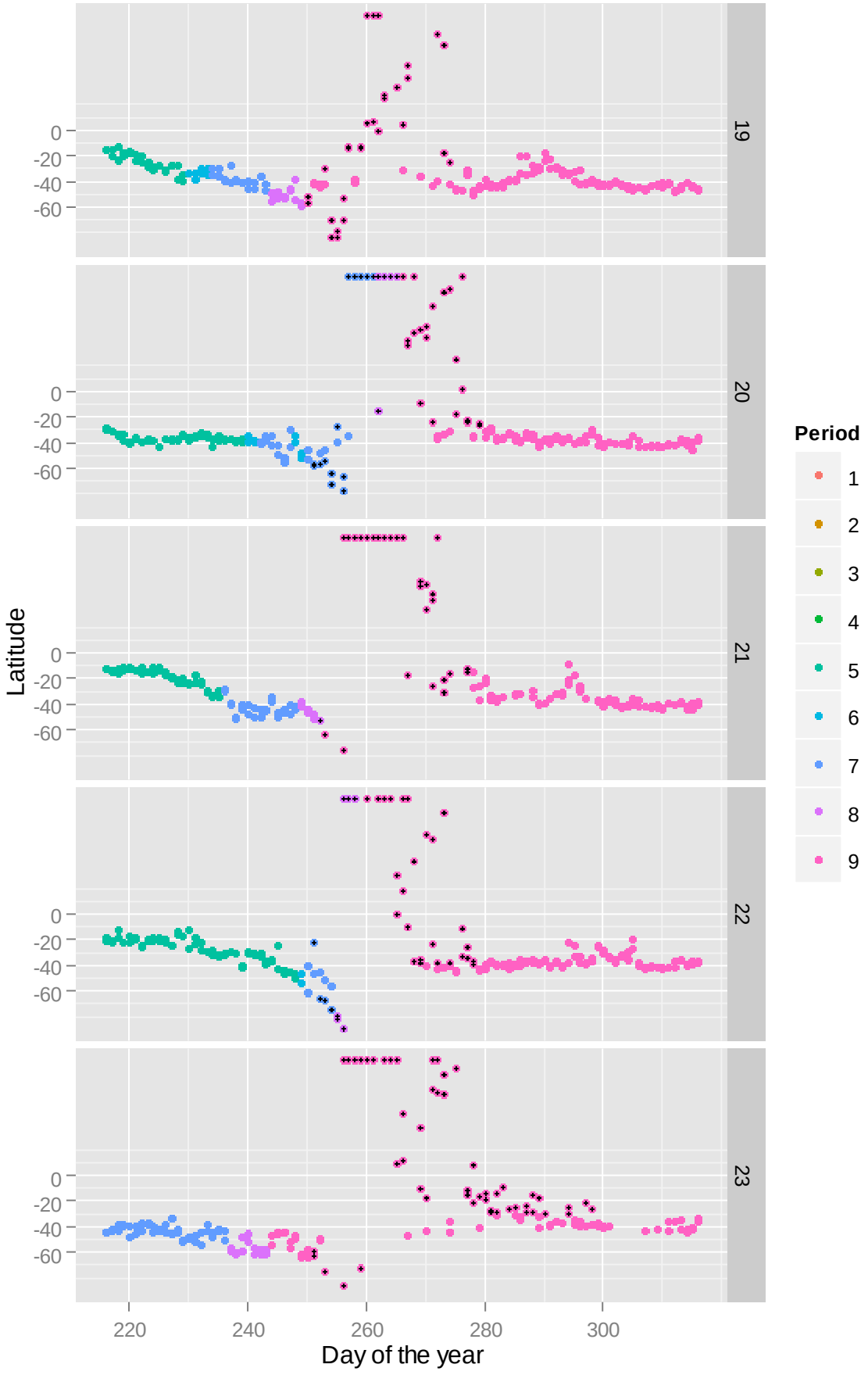
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5.2 Appendix 2

Table 1: Dates obtained as explained in the Materials and Methods section for the analysis on phenology. Dates for the westbound/outbound migration trip.

Bird code	Year	Sex	Itinerary	Last day at burrow	last night at burrow	Leave NZ	Arrival at stopover	Leaving stopover	Arrival in Wintering Area	Days in Wintering Area
1	2010	M	1	12/1	24/2	6/3	9/3	30/3	1/4	139
2	2010	M	2	12/1	27/2	12/3			17/3	158
3	2010	F	1	12/2	12/2	27/2	1/3	21/3	27/3	158
4	2010	M	1	25/1	5/2	25/2	28/2	28/3	1/4	131
5	2010	F	1	12/2	12/2	26/2	2/3	22/3	31/3	142
6	2010	M	1	12/1	17/3	29/3	31/3	11/4	13/4	129
7	2010	M	1	30/1	18/3	29/3	31/3	11/4	17/4	115
8	2010	-	1	12/1	2/2	17/3	20/3	31/3	3/4	140
9	2010	F	1	12/2	21/2	26/2	28/2	23/3	16/4	139
10	2010	F	1	13/1	11/2	19/2	21/2	16/3	22/3	146
11	2010	-	1	21/2	9/3	12/3	16/3	25/4	28/4	111
12	2010	M	1	10/2	27/2	19/4	22/4	3/5	11/5	93
14	2010	M	1	22/2	22/2	25/3	31/3	12/4	18/4	115
16	2010	F	1	26/2	7/3	11/3	12/3	25/3	29/3	135
17	2010	F	3	12/1	25/2	25/2	28/2	11/3	15/3	130
18	2010	-	1	21/2	24/2	5/3	6/3	26/3	30/3	138
19	2010	-	3	12/1	6/3	12/3			20/3	127
13	2011	M	1	13/2	13/2	28/2	3/3	25/3	29/3	103
15	2011	M	1	18/1	31/1	9/2	11/2	4/3	20/3	138
20	2011	-	1	29/12	5/2	15/2	21/2	3/3	10/3	147
21	2011	F	2	1/3	4/3	12/3	14/3	18/4	10/4	119
22	2011	-	1	30/12	15/3	24/3	28/3	4/4	8/4	135
23	2011	M	1	16/1	10/2	15/2	17/2	23/3	10/4	107

Table 2: Dates obtained as explained in the Materials and Methods section for the analysis on phenology. Dates for the eastbound/return migration trip.

Bird code	*Year*	*Sex*	*Itinerary*	*Leave Wintering Area*	*Arrival in stopover*	*Leave from stopover*	*Arrival in NZ*	*1st night at burrow*	*1st day at burrow*
1	2010	M	1	18/8	26/8	31/8	3/9	6/9	12/9
2	2010	M	2	22/8			27/8	28/8	13/9
3	2010	F	1	1/9	9/9	11/9	13/9	14/9	15/9
4	2010	M	1	10/8	20/8	5/9	7/9	11/9	25/9
5	2010	F	1	20/8	26/8	6/9	11/9	12/9	25/9
6	2010	M	1	20/8	25/8	1/9	5/9	6/9	13/9
7	2010	M	1	10/8	21/8	16/9	17/9	24/9	25/9
8	2010	-	1	21/8	26/8	28/9	30/9	1/10	3/10
9	2010	F	1	2/9	10/9	12/9	15/9	24/9	25/9
10	2010	F	1	15/8	19/8	26/8	27/8	27/8	12/9
11	2010	-	1	17/8	26/8	5/9	8/9	10/9	12/9
12	2010	M	1	12/8	2/9	10/9	12/9	13/9	18/9
14	2010	M	1	11/8	2/9	10/9	12/9	13/9	18/9
16	2010	F	1	11/8	22/8	10/9	12/9	13/9	25/9
17	2010	F	3	20/8	26/7	20/8	7/9	11/9	5/10
18	2010	-	1	15/8	24/8	4/9	6/9	11/9	16/10
19	2010	-	3	19/8	28/7	18/8	6/9	11/9	21/9
13	2011	M	1	10/7	30/7	17/8	24/8	29/8	10/9
15	2011	M	1	5/8	29/7	6/9	8/9	8/9	9/9
20	2011	-	1	4/8	7/9	18/9	21/9	23/9	21/12
21	2011	F	2	7/8	18/8	6/9	9/9	10/9	11/9
22	2011	-	1	21/8	9/9	12/9	14/9	15/9	15/9
23	2011	M	1	26/7	29/7	21/8	29/8	7/9	11/9

5.3 Appendix 3

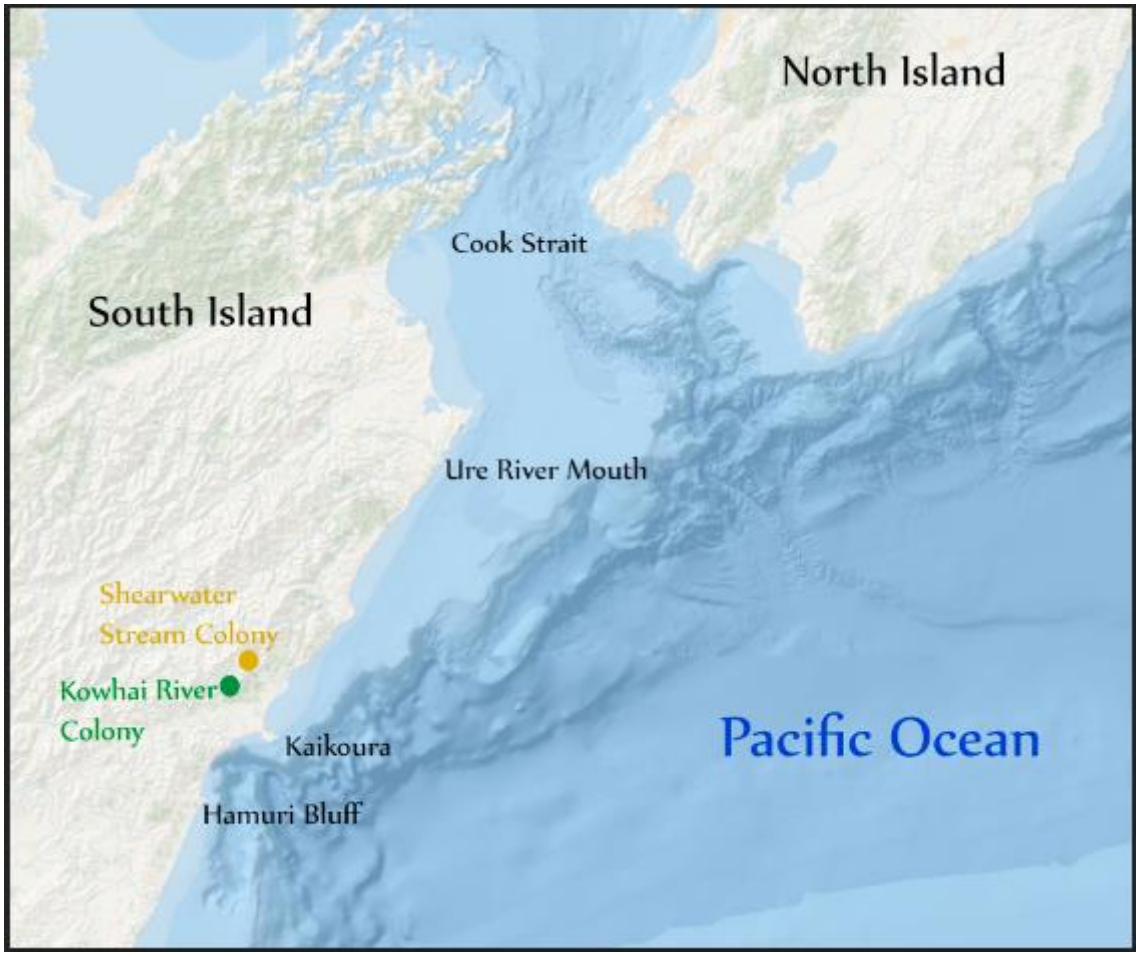


Figure 1: Geographical Features of New Zealand around the two remaining natural breeding colonies (Kowhai River and Shearwater stream).



Figure 2: Geographical Features of New Zealand mentioned in the main text of the thesis

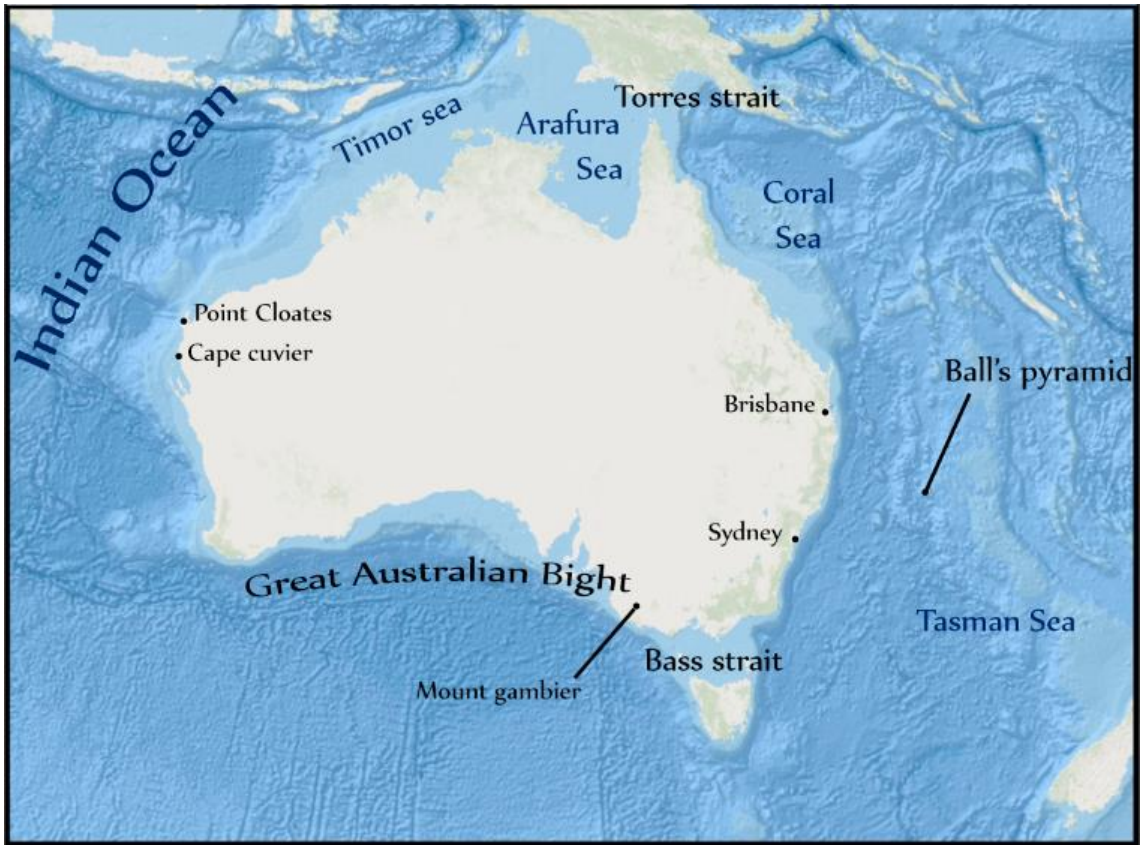


Figure 3: Geographical features of Australia mentioned in the main text of the thesis