Annual and individual patterns in the behavioural cycle of the Manx shearwater, *Puffinus puffinus.*

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Thesis submitted for the degree of Doctor of Philosophy

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Abstract

Recent innovations in the miniaturisation of animal tracking devices have enabled the study of species that are not amenable to direct observation. This has been particularly the case for pelagic seabirds, whose at-sea behaviour would otherwise be very difficult to observe. This thesis investigates patterns in the migration and behavioural cycle of the Manx shearwater (*Puffinus puffinus*) using miniature geolocators. By analysing these data with a range of computational approaches, insights are made into the otherwise cryptic behaviour and ecology of this seabird.

Chapter 1 provides a general introduction to annual cycles in animal behaviour and migration in seabirds. The ecology and behaviour of the Manx shearwater is then outlined, as are recent advances in tracking technology that have enabled the study of otherwise unmeasurable aspects of the ecology of this species.

Chapter 2 first details the core fieldwork and data processing procedures which were used to generate the data used in this thesis. Using a dataset of Manx shearwater migration tracks gathered by geolocation tracking programmes on 5 UK islands, individual consistency, colony-level, annual and sex-differences in the phenology of migrations are investigated.

Chapter 3 provides a detailed analysis of Manx shearwater migration routes. Building on previous work in this area, key differences are identified between colonies and individual birds in wintering area and the overall path along which they migrate.

In chapter 4 an unsupervised classification algorithm is trained to identify behavioural states during the Manx shearwater migration using saltwater immersion data. These behavioural states are used to identify periods of stopover during which a bird pauses its migration to rest or refuel. Areas of sea are identified which are commonly used by Manx shearwaters for stopover behaviour.

In chapter 5 a similar algorithm is used to identify behavioural states during the breeding season using light and saltwater immersion data from archival loggers. These time series of behavioural states are used to estimate the timing of major life history events such as egg laying and incubation, enabling the study of breeding behaviour and ecology in this burrow nesting seabird.

Chapter 6 draws on the results from chapters 2, 3, 4 and 5 to build up a picture of the Manx shearwater annual cycle and then goes on to investigate how the timing of key life history periods impacts on future behavioural events.

Chapter 7 provides a general discussion of the Manx shearwater behavioural cycle in light of the previous chapters, with a focus on inter-colony differences and individual consistency in behaviour, as well as implications of the research for conservation of the species.

You cannot prevent the birds of sadness from passing over your head, but you can prevent their making a nest in your hair.

Chinese proverb.

Between two seas the seabird's wing makes halt,
Wind-weary; while with lifting head he waits
For breath to re-inspire him from the gates
That open still toward sunrise on the vault
High-domed of morning.

Swinburne—*Songs of the Spring Tides.*

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This thesis is dedicated to my sister Ruth, who will always be my squishy.

Author contributions

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

Tim Guilford, Robin Freeman and Chris Perrins contributed their ideas and feedback for all data chapters and during all parts of the preparation of this thesis, including planning, data analysis and fieldwork.

In all chapters Ben Dean equally shared in the fieldwork undertaken and contributed to ideas and feedback during planning and data analysis.

Annette Fayet and Akiko Shoji contributed to the data collection in all chapters and feedback during data analysis.

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Chapter 1

Introduction

1.1 Introduction

The seasonal nature of many ecosystems means that organisms living within them match their behaviour to cyclical events occurring at a range of time scales (McNamara & Houston, 2008; Marra et al., 2015). This leads individuals to carry out different activities during different parts of the year in response to annual fluctuations in ecological conditions. These annual fluctuations may include changes in primary productivity, temperature, and wind conditions (Studds & Marra, 2011; Robson & Barriocanal, 2011; Genovart et al., 2012) or more complex biotic interactions such as interspecific competition and predation pressures (Durant et al., 2012; Bauer & Hoye, 2014). Natural selection has shaped the timing of behaviours such that an organism should be able to capitalize on the conditions that are available at different periods of the annual cycle; for example, hatching date in many bird species occurs just before peaks in food availability (Perrins 1969; Charmantier et al. 2008; McNamara & Houston 2008; Ramírez et al., 2016). For more mobile organisms, these annual cycles frequently exhibit spatially segregated breeding and non-breeding periods (such as overwintering) interspersed with a (sometimes very brief) migratory phase (Mcnamara, Welham, & Houston, 1998; Arizmendi-Mejía, et al., 2013; Hostetler, Sillett, & Marra, 2015). In this thesis, the term migration is used to describe a movement between two phases of an annual cycle which take place in different geographical locations. Whether (and how) animals integrate the behavioural strategies they employ during single breeding and non-breeding events across their annual cycle to maximise survival and reproduction (together, this can be referred to as "fitness") is poorly understood. However, answering these questions is important as such information may be fundamental to understanding the mechanisms framing the development of life-history traits.

These questions may be particularly important to address in long-lived species. Their reproductive events are spread over a long period of time, which is likely to increase the importance of future reproduction, and hence of their own survival, compared to current reproduction. This, combined with their ability to live through many annual cycles, may give them the possibility to learn from their experience and the opportunity to show behavioural plasticity, between different annual cycles as well as among individuals. This, in turn, may have important implications for fitness and population dynamics.

However, addressing these questions is not an easy task. In order to fully understand the annual behavioural strategies an individual employs to maximise its fitness it is vital that more than one stage of the yearly cycle is studied (McNamara & Houston, 2008; Newton, 2011; Hostetler et al., 2015). While studying the breeding behaviour of individuals can be relatively easy, keeping track of an animal and its behaviour during the non-breeding season can be challenging, especially in migratory species. Until recently, many such studies concentrated on a single part of an organism's annual routine; often the breeding season. Fortunately, rapid advances made in tracking and bio-logging technology over the last decade have led to an increase in spatial and behavioural data collected from individuals from a range of species (Ropert-Coudert, & Wilson, 2005; Wakefield, Phillips, & Matthiopoulos, 2009; Tomkiewicz et al., 2010; Guilford et al., 2011; López-López, 2016), and in particular have made it possible to follow individuals throughout their annual cycle (Hostetler, Sillett, & Marra, 2015; Marra, et al., 2015). Additionally, animal-borne loggers or transmitters have made it easier to study single organisms for multiple years, allowing researchers to investigate individual variation across years. These methodological changes have enabled a wider suite of questions to be answered regarding the roles of phenotypic variation (differences between individuals) and the environment on behavioural ecology and population dynamics in longer lived species.

This thesis aims to address several ecological and behavioural questions, with a focus on the role of migration in the behavioural cycle of a long-lived migratory seabird, the Manx shearwater (*Puffinus puffinus*). Using a large dataset obtained from geolocation and saltwater immersion loggers deployed on individuals breeding on multiple colonies encompassing most of the latitudinal range of the species over multiple years, I investigate the behavioural strategies of these birds throughout their entire annual cycle. In particular, I address questions regarding the phenotypic variation among colonies in breeding, migratory and wintering behaviour, the extent to which individual consistency explains temporal and behavioural variation, and the potential interactions between events of the annual cycle.

1.2 Studying seabirds

Burrow nesting seabirds, such as the Manx shearwater studied here, are excellent study species for monitoring individuals over several annual cycles. As long-lived birds which generally breed in the same burrow in consecutive seasons, these species are relatively easy to recapture over an extended period of time. Most seabird species have a non-breeding or wintering area which is geographically distinct from the breeding area, although the distance over which the migrations take place can vary dramatically (Schreiber & Burger, 2002).

Pelagic seabirds are some of the most difficult to observe of all avian groups, spending much of their lives far out at sea, and with many species breeding in relatively inaccessible colonies (Warham, 1990; Warham, 1996). Seabird populations are at risk from a multitude of threats, including fisheries bycatch (Bugoni et al., 2008; Granadeiro et al., 2011; Báez et al., 2014) and competition (Bertrand et al., 2012), plastic pollution (Wilcox, Van Sebille, & Hardesty, 2015), climate variability (Şekercioğlu, Primack, & Wormworth, 2012; Davies et al., 2013; Kowalczyk et al., 2015) and invasive nest predators (Jones et al., 2008). Seabirds are among the most vulnerable animal groups, with 28% species globally threatened (Croxall et al., 2012; Phillips et al., 2016) and with their overall numbers having dropped dramatically in recent years (Paleczny et al., 2015). Many seabird species are migratory, moving large distances during the non-breeding period, sometimes across oceans and hemispheres (Warham, 1990; Shaffer et al., 2006; Egevang & Stenhouse, 2010; Oro, 2014), further complicating their study. Effective species conservation requires, amongst other things, a comprehensive picture of spatial and behavioural ecology, something which tracking technology has recently been able to provide (Wakefield et al., 2009; Wilson & Vandenabeele, 2012; Crossin, et al., 2014). Seabird tracking studies have improved understanding of migration behaviour in a range of species, from the very small – Leach's storm petrels (*Oceanodroma leucorhoa,* Pollet et al., 2014) and little auks (*Alle alle*, Mosbech et al. 2011) - to the very large - wandering albatrosses (*Diomedea exulans,* Weimerskirch et al. 2014) and brown pelicans (*Pelicanus occidentalis*, Walter et al., 2013). In particular, studies using geolocators – miniature, affordable light loggers which can record approximate position for several years - have proved valuable for revealing the long distance movements of a range of seabird species, especially those too small for satellite tracking devices, such as puffins, terns and smaller petrels (Harris et al. 2009; Egevang & Stenhouse 2010; Bogdanova et al. 2011; Guilford et al. 2011b; Klaassen et al. 2011; Mosbech et al. 2011; Nisbet et al. 2011; Rayner et al. 2011; Stenhouse et al. 2011).

1.3 Individual variation in behaviour

Variation between individuals within a population is the driving force behind evolution (Senner, Conklin, & Piersma, 2015). This variation is a combination of genetics, development and the environment experienced by an organism, leading to phenotypic differences between individuals. Behavioural variation between individuals has been well documented in many bird species and as such is a fundamental aspect of studies in avian ecology (Dall, Houston, & McNamara, 2004; Dingemanse & Dochtermann, 2013). Variation in behaviour can occur between populations with implications for both conservation and also our understanding of the control of behaviour (genetic or learned). For example: where different populations following different migration routes or destinations (Rayner et al., 2011; Delmore, Fox, & Irwin, 2012; Weimerskirch et al., 2015b); or different annual schedules (Gunnarsson et al., 2006; Conklin, Battley, & Potter, 2013). This underlines the importance of sampling from across the range of a species, which in seabirds ultimately means following individuals from several colonies (Frederiksen et al., 2011; McFarlane Tranquilla et al., 2013; Dean et al., 2015; Corman et al., 2016). Variation in behaviour also occurs within populations: Atlantic puffins (*Fratercula arctica*) breeding in neighbouring burrows on Skomer Island (Wales) migrate to different wintering destinations (Guilford et al., 2011). Ultimately, behavioural variation can have important fitness consequences, which is what natural selection acts upon. Variation in migratory strategies between Wandering albatrosses (*Diomedia exulans*) lead to differences in breeding frequency (Weimerskirch et al., 2015); Atlantic puffins which migrate to the Mediterranean Sea show higher breeding success than birds which do not (Fayet, Freeman, Shoji, Boyle, et al., 2016); and the population stability of breeding of Brünnich's guillemot (*Uria lomvia*) is related to overwintering area (Frederiksen et al., 2016).

Individual consistency in behaviour (sometimes also referred to as individual specialisation) is where an individual animal shows a degree of repeatability in behaviour from one season to the next (Dingemanse & Dochtermann, 2013). Individual behavioural consistency has now been identified in many avian species, including seabirds, and across a range of behaviours: migration routes and destinations (Kubetzki et al., 2009; Phillips et al., 2009; Dias, Granadeiro, & Catry, 2013; Yamamoto et al., 2014), timing of migration (Vardanis et al, 2011; Thorup et al., 2013; Müller et al., 2014) and foraging strategies (Votier et al., 2010; Patrick et al., 2014; Shoji et al., 2014; Ceia & Ramos, 2015). In contrast, individual behavioural plasticity (flexibility in response to extrinsic cues, Dingemanse & Dochtermann, 2013) has also been discovered in a wide range of species, in both breeding and non-breeding behaviours including foraging and migration (Dias et al., 2011). Some species show both behavioural consistency and flexibility in different aspects of their annual cycle (Quillfeldt, Voigt, & Masello, 2010; Stanley et al., 2012). The ability of an individual to adapt its behaviour to varying conditions from one season to the next may have important fitness consequences, especially if current trends in environmental stochasticity continue (Charmantier et al., 2008; Both, 2010; Reed et al., 2010; Fort et al., 2013).

1.4 Carryover effects

With miniaturisation of tracking technology, researchers have been increasingly able to study behaviour in long distance migrants across their whole migration and start to understand more about how migratory and breeding strategies interact (Hedenström et al. 2007; Balbontín et al. 2009; Bowlin et al. 2010; Bogdanova et al. 2011; Guilford et al. 2012; Arizmendi-Mejía et al. 2013; Jessopp et al., 2013; McKinnon, Stanley, & Stutchbury, 2015; Shoji et al., 2015) When an individual's experiences at one part of the annual cycle influence the (non-lethal) outcomes during a subsequent period this can be considered an ecological carryover effect (COE) (Norris, 2005; Harrison et al., 2011; Conklin & Battley 2012; O'Connor et al., 2014). Similarly, migratory carryover effects occur when individual behaviours, or the conditions encountered on migration, impact on the following season (be it the breeding period, non-breeding period, or a separate migration) (Norris & Taylor, 2006; Crossin et al., 2012). Migratory COEs have now been studied in a range of species, including passerine birds (Norris, et al., 2004; Saino et al., 2012; Latta et al., 2015; Paxton & Moore, 2015), sea turtles (Ceriani et al., 2015), amphibians (Green & Bailey, 2015) and mammals (Albon et al., 2016). The focus of many of these studies is how conditions during the non-breeding period and the pre-breeding migration affect subsequent reproductive output or individual fitness (Crossin et al., 2012; Saino et al., 2012 Blomberg, et al., 2014; Clausen, Madsen, & Tombre, 2015). However, some are beginning to focus on COEs across more than two seasons (Latta et al., 2015; Shoji et al., 2015). Inter-seasonal COEs are addressed later in this thesis.

As long-lived species encountering a range of environmental conditions, migratory seabirds are excellent models for studying carryover effects. Their long lifespans increase susceptibility to trade-offs between immediate and lifetime reproductive success and exposure to stochastic environmental impacts during migration may interact with these trade-offs. Despite the increase in seabird tracking studies over the last decade, many questions have yet to be addressed in detail, particularly the effects of breeding and migratory schedules on annual phenology, and what effect individual variation during migration has on fitness. Several studies have used bird-borne loggers (such as geolocators or time-depth recorders) to uncover migration behaviour, breeding phenology and pre-breeding behaviour (Phillips, Silk, & Croxall, 2005; Phillips et al., 2006; Phillips et al., 2007; Yamamoto et al, 2010; Guilford et al. 2012; Linnebjerg et al. 2013; Hedd et al. 2014; Quillfeldt et al., 2014; Dias et al., 2015). Others have investigated individual differences in migration and foraging strategies within species (Catry et al., 2011b, Frederiksen et al., 2011; Fort et al., 2012; McFarlane-Tranquilla et al. 2013; McFarlane Tranquilla et al., 2014; Patrick et al., 2014; Müller et al., 2015) . A some studies have found links between environmental stochasticity encountered during overwintering and subsequent breeding performance (Crossin et al., 2012; Szostek & Becker, 2015). Exposure to stormy winter weather has be found to delay breeding (Harris & Wanless 1996) and increase mortality to different degrees in different age groups (Frederiksen & Daunt 2008).

Increasing numbers of long term tracking datasets have improved our ability to investigate COEs within the seabird annual cycle. Initially these studies have been observational, often using tracking data. Main findings have included: the positive effects of pre-breeding diet and weight on reproductive success (Sorensen et al., 2009; Salton et al., 2015); the effects of migratory strategy on hormone levels (Crossin et al., 2012; Perez, Granadeiro, Dias, & Catry, 2016) and carryover influences between breeding and subsequent wintering behaviour (Bogdanova et al., 2011; Shoji et al., 2015)

These observational studies have identified correlative relationships amongst behaviours and the timing of key events that may be indicative of COEs. However these studies have all evaluated correlations over the course of a single life cycle, and for a single breeding colony. As a result, they are unable to disentangle whether these relationships are due to individual repeatability of timing or behaviour; inter-annual environmental variation simultaneously affecting multiple parts of the life cycle; or the direct impact of an outcome at one stage influencing subsequent periods. These studies have also been unable to determine whether these relationship hold across multiple colonies or are context-specific.

More recently, experimental studies have been combined with tracking, deliberately manipulating the costs incurred by individual birds during breeding (Catry, Dias, Phillips, & Granadeiro, 2013; Schultner et al., 2014; Vincenzi et al., 2015; Fayet, et al., 2016) and quantifying the impacts on subsequent behaviour. By factoring out the effects of individual repeatability and environmental variation, these experimental studies provide robust evidence of the impacts of COEs caused by outcomes during the breeding season. However, due to the inaccessibility of migratory seabirds throughout the rest of their annual cycle, experimental approaches are unable to identify and quantify COEs across much of the annual cycle.

1.5 Manx shearwaters

Shearwaters are medium-sized seabirds in the Procellariidae family, within the order Procellariiformes which also contains other petrels and albatrosses. Shearwater species range in size from around 160g (Bryan’s shearwater, *Puffinus bryani*)(Kawakami et al., 2012) to over 900g (Cory’s shearwater, *Calonectris borealis*) (Granadeiro, 1993). Shearwaters are long-lived birds and many species exhibit long-distance migration between breeding behaviour (Shaffer et al. 2006; González-Solís et al. 2007; Dias et al., 2011; Dias et al. 2010; Guilford et al. 2012).

The Manx shearwater, *Puffinus puffinus*, is one the smaller members of this family (around 400g), and breeds almost entirely around the coast of the UK and Ireland. Current population estimates suggest that more than 90% of the global population breeds here, with a large proportion in just two major areas, those on the Isle of Rum (Inner Hebrides, Scotland) and a group of three closely-spaced islands in Pembrokeshire, Wales (Skomer, Skokholm and Middleholm) (Mitchell et al., 2004). Recent population estimates from Skomer suggest that this population has increased since 1998, by 16% per year, to 316 070 breeding pairs (Perrins et al., 2012).

The breeding biology, life history and general ecology of the Manx shearwater has been summarised in detail by Michael Brooke in his book “The Manx Shearwater” (1990). Manx shearwater pairs lay a single egg each breeding season, followed by an incubation period of approximately 50 days. Both sexes incubate the egg and exhibit asynchrony in incubation behaviour. After hatching the chick grows slowly over a period of around 70 days, during which it is fed by both parents (Brooke, 1990). In the breeding season (which runs from mid-March to the end of September) there is a pre-laying period where birds attend the colony during the night and spend time at the breeding burrow (most birds use the same burrow every year), preparing and defending the burrow from competitors (Brooke 1990). After mating, the female Manx shearwater departs from the colony for up to two weeks during which the egg is formed (Brooke 1990; Guilford et al. 2009). Since Brooke's work was published more has been revealed regarding the colony-based breeding behaviour of this species. Differences between male and female provisioning behaviour were uncovered, with females varying the meal size they deliver according to chick begging intensity (Quillfeldt, Masello, & Hamer, 2004), however this behaviour is manipulated by dishonest signals from offspring (evidence of parent-offspring conflict) (Riou, Chastel, & Hamer, 2012). Manx shearwaters are nocturnally active on the breeding colony and as such show a lower probability of visiting the breeding burrow on clear moonlit nights, presumably to limit predations risks (Riou & Hamer, 2008). More recently, the use of bird borne data-loggers has allowed detailed studies of the at-sea foraging behaviour of the Manx shearwater during the breeding season. A maximum directed flight speed of 40km/h was recorded using GPS loggers deployed on the back of breeding birds. After initial work developing attachment methods (Guilford et al. 2008), GPS loggers have been deployed in tandem with leg mounted saltwater immersion loggers and/or time depth recorders (TDR). Combined tracking during different phases of the breeding season has revealed dual foraging behaviour in chick-rearing birds (Shoji et al., 2015); differences in foraging efficiency between adult and immature birds (Fayet et al., 2015); and important multi-colony foraging areas (Dean et al., 2012; Dean et al., 2015). Manx shearwaters are mostly diurnal foragers, feeding both from shallow and deep dives (capable of diving beyond 31m below sea surface) (Shoji et al., 2016). When not visiting the colony at night time, birds rest on the surface of the ocean, often in large conspecific rafts (Wilson et al., 2008).

Manx shearwaters exhibit two phases of long-distance migration. The first begins in early October when birds leave the breeding grounds in the north Atlantic, fly along the west coasts of Europe and Africa, cross the south Atlantic and arrive off the coast of Argentina (Guilford et al., 2009). During the wintering period these birds are entirely pelagic. In February and March, individuals begin the northbound journey back to the breeding colony following a clockwise path along the east coast of South America and the USA before crossing back over the north Atlantic to the UK and Ireland (Guilford et al., 2009). Two geolocation studies have identified migratory stopover behaviour undertaken by these birds on both legs of their migration. This behaviour was initially identified by locations where individuals showed reduced movement and non-flight behaviour over a period of a few days (Guilford et al., 2009). More recently, the distribution of three types of behaviour (resting, foraging and flight) carried out during migration was mapped alongside environmental variables such as sea surface temperature, primary productivity and chlorophyll-α, with resting behaviour more likely in productive waters (Freeman et al., 2013).

Some key carryover effects have been identified in Manx shearwaters. Greater levels of flight behaviour during winter lead to increased likelihood of future breeding failure, and birds which skip breeding one year had improved reproductive success in following years (Shoji, Culina, et al., 2015). Experimentally extending or shortening the breeding period resulted in differences in the timing of migration, the behaviour recorded during wintering and birds experiencing a longer chick-rearing period showed lower breeding success during the subsequent year (Fayet at al., 2016).

1.6 Key themes

By analysing a large, multi-year, multi-colony tracking dataset, this thesis quantifies individual repeatability, and disentangles the importance of repeatability, inter-colony differences, inter-annual environmental variation and carryover effects across the annual cycle of a long lived seabird, the Manx shearwater. I investigate how the migratory behaviour of these birds affects the timing of subsequent events and whether this behaviour is comparable across birds breeding at five colonies around the UK: Rum, Copeland, Ramsey, Skomer and Lundy (figure 1.1). The data used in this study were collected using archival light and saltwater immersion loggers (geolocators or GLS "immersion loggers"). By applying a range of analytical techniques to these data, I estimate positional and behavioural information, and the timing key events during the migration and breeding periods. Chapters two, three and four focus on the pre-breeding and post-breeding migration periods and chapter five investigates phenology and incubation behaviour during the breeding season. Chapter six synthesises the results of the four previous chapters to examine relationships between migratory strategies and breeding phenology.

In chapter two I investigate differences in the timing of key migration events (departure from and arrival at the colony and the wintering area) between breeding colonies, years and individuals, as well as individual consistency in this timing. As the first data chapter of this thesis, this chapter also introduces the methodology for collection and processing of geolocation (GLS) data, and demonstrate the use of these dates to identify key dates during migration as well as to predict the sex of individual shearwaters.

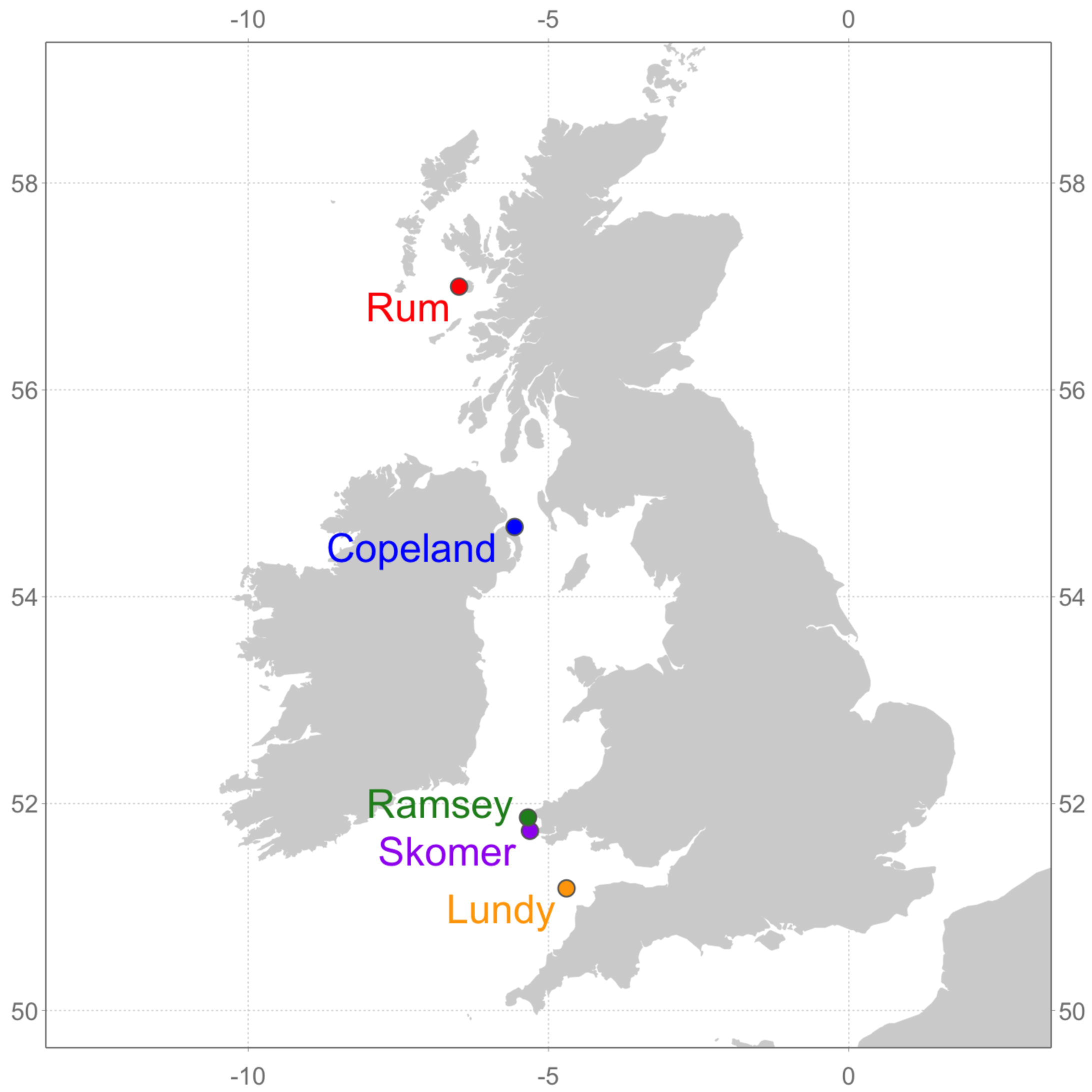

Figure 1.1 Locations of the five breeding colonies of Manx shearwaters studied. The colours used for each colony in this figure are used consistently for figures throughout the thesis.

Chapter three concentrates on spatial analysis of the Manx shearwater migration. I investigate differences in the overall northbound and southbound migration routes and the overwintering location. The most variable part of the Manx shearwater migration is the latter half of the northbound journey (north of the equator), and I identify pronounced individual fidelity in the degree of westerly movement during this part of the migration. I also uncover individual fidelity in overwintering location.

Stopover or staging behaviour is a key strategy for some migratory birds and this is explored in chapter four. I apply a Gaussian mixture model to the saltwater immersion data to identify predominant behavioural states in order to identify stopover locations during the Manx shearwater migration. Statistical modelling of these locations shows differences in northbound migration stopover behaviour among individuals. Several key locations within the Atlantic Ocean are identified as important stopover sites for birds from all five breeding colonies.

In chapter five the focus moves from the non-breeding to the breeding season. I use immersion data collected from geolocators during breeding to classify daily behaviour, again using a Gaussian mixture model. By recording the date at which birds switch behaviour I identify the timing of major breeding-season events: the first night spent on the breeding colony; start and end of incubation and the date birds leave the breeding colony. I then use these dates to investigate differences in the breeding strategy, in particular incubation, of Manx shearwaters breeding on different colonies.

Using the estimated dates and behaviours across the entire annual cycle obtained in the first four data chapters, chapter six focuses on the annual cycle as a whole and examines relationships between migration strategies and breeding phenology using structural equation modelling, also using an additional dataset of the post-migration weight as a proxy for post-migratory body condition. I look for evidence of inter-seasonal carryover effects by using structural equation models to check for key pathways across the annual behavioural cycle by events in one part of the cycle affected later events, and whether these pathways differ among colonies.

Chapter seven provides a discussion of the main findings within the thesis and the implications of this study with regard to further research and conservation.

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Chapter 2

Timing of migration in the Manx shearwater

2.1 Introduction

Phenology is the study of the timing of annual events in the biological world, such as flowering and seed set in vegetation, or egg laying and migration in birds. The timing of these events may change from one season to the next, dependent on various environmental conditions and the degree of phenotypic plasticity within each species (Walther et al., 2002, Visser & Both, 2005, Buskirk et al., 2012). Studies of phenology across all phyla have become more relevant over the last few decades as scientists recognise the potential effect that long term environmental change may have on the timing of events in an organism's life cycle (Walther et al. 2002, Visser & Both 2005, Saino et al. 2010). For many bird species the timing at which events such as egg laying, fledging and feather moult occur will influence not only breeding success but may also affect survival from one season to the next (McNamara & Houston 2008, Hipfner et al. 2010). Many avian species time breeding to ensure that they are rearing chicks during peak food availability (Charmantier et al. 2008, Conklin & Battley 2012; Davoren et al., 2012; Afán et al., 2015; Lany et al., 2016; Ramírez et al., 2016). In migratory species there are many environmental and biotic factors which can delay or advance departure and arrival dates at both the breeding and non-breeding areas, including the weather conditions along the migration flyway (Felicísimo, Muñoz, & González-Solis, 2008; Both 2010; Klaassen et al. 2011). For species that migrate over large distances, the conditions affecting their breeding phenology could be completely different to those affecting the timing of movements during the non-breeding season (Balbontín et al. 2009, Conklin & Battley 2012). Events during one part of the life cycle (overwintering for example) may have a direct effect on the timing of later phases, even if they happen in geographically separate places (Harrison et al. 2011, Juillet et al. 2012). Despite being the subject of an increasing number of studies, a lot remains to be understood about the phenology of migration in several avian species. Particularly poorly understood is the extent of individual consistency in migratory schedules between years, which may have important implications for behavioural plasticity and adaptability to environmental change. Most previous studies of phenology in migratory seabirds have relied on ringing data (Thorup et al., 2013) or followed individuals for only 2 years (Conklin, Battley, & Potter, 2013) or at a single colony (Yamamoto et al., 2014; Müller et al., 2014). Consequently, these studies have been unable to investigate individual consistency in migratory phenology. Here we use geolocators to investigate the migratory timing of individual Manx shearwaters, a long-distance migratory seabird, from multiple colonies and across a six year period.

Since their development in the 1990s (Afanasyev et al., 2016), and first application to migratory seabirds in the early 2000s (Weimerskirch & Wilson, 2000; Phillips, Silk, & Croxall, 2005), the use of archival light loggers (also known as geolocators) for tracking individual movement has increasingly rapidly among seabird scientists (Bridge et al., 2013). Although location estimates from these devices are not as accurate as GPS or other satellite based location systems, geolocation has many advantages, including small logger size and increased longevity (Phillips et al., 2004) (Phillips et al., 2004; Shaffer et al., 2005). The method has been very successful for recording the long-range movements, especially migration behaviour, of a range of seabird species. This includes terns (Mcknight et al., 2013), gulls (Stenhouse et al., 2011; Bustnes et al., 2013), auks (Gaston et al., 2011; Fayet et al., 2016), small petrels (Pollet et al., 2014), shearwaters

(Hedd et al., 2012; Guilford et al., 2012) and albatrosses (Phillips, Silk, & Croxall, 2005; Weimerskirch et al., 2015).

The Manx shearwater is a migratory seabird, breeding during the northern hemisphere summer and spending the winter (non-breeding period) in the southern Atlantic (Brooke, 1990; Guilford et al. 2009). The two migratory periods in the Manx shearwater annual cycle occur roughly during September-October (outward, southbound migration) and February-April (return, northbound migration) (Guilford et al., 2009). The timing of these two periods could be dependent on a variety of factors including breeding outcome, oceanic conditions (current, weather, wind direction), food availability and intrinsic factors (age, body condition, sex); as has been found in other migratory species (Hedenström et al., 2007; Matyjasiak, 2012; McNamara, Welham, & Houston, 1998). In Manx shearwaters, post-breeding departure (assuming the breeding attempt was successful) occurs once the chick has reached the age (or mass) at which it may be abandoned by both of the adults, with parents always departing the colony before the chick fledges (Brooke, 1990). There may be optimal migratory conditions (for example avoiding autumn storms in the northern hemisphere) which could be missed if departure is delayed, as has been found in Cory's shearwaters (*Calonectris borealis,* Felicísimo et al., 2008). Arrival of adult Manx shearwaters at both the overwintering area and the breeding colony may be timed to take advantage of local peaks in marine resources. In addition, early return to the breeding colony presumably allows a better choice of nest sites and/or mates, time to recover body condition before beginning to breed and a reduced conflict with competitors for burrow space (Brooke, 1990), as is the case in many other migrants (Kokko, 1999; Bêty, Gauthier, &

Giroux, 2003; Gunnarsson et al., 2006). Use of preferential nest sites by older or more dominant birds has also been documented in other seabird species (Velando & Freire, 2001), although it is unclear what would constitute a superior burrow for Manx shearwaters.

This chapter investigates whether the timing of migration in the Manx shearwater varies across years, which may signal the effects environmental change on this species. Individual consistency in the migratory phenology is examined, with implications for behavioural plasticity. For the first time, differences in migratory timing among colonies are investigated and potential drivers discussed. Locations deduced from geolocation data are used to determine the main departure and arrival dates for each phase of the Manx shearwater migration. These data were collected from birds at five different colonies around the UK, with varying population sizes and status (two of the colonies are currently undergoing rapid population expansion since rat eradication, with estimates at 4796 pairs on Ramsey Island (Morgan, 2016) and 1085 on Lundy Island (Brown et al., 2011)). The study took place over six consecutive years from 2006 to 2012 and some individual birds were tracked for three or more years. This unprecedented multi-year, multi-colony dataset is used to investigate in detail the migratory schedule of Manx shearwaters; specifically, the extent of individual consistency in migratory timing, and the effects of colony, year and sex as potential drivers of differences in timing.

2.2 Methods

The overall fieldwork methods used for collection of geolocation (GLS) and salt water immersion data from Manx shearwaters are common to all chapters in this thesis.

2.2.1 Field work methods: bird capture and attachment of devices

Manx shearwaters are burrow-nesting seabirds, which reliably return to the same breeding burrow (or one very close by) each year (Brooke, 1990). This enables long term studies of individual birds. From May 2006 until September 2012 field work took place on five different breeding colonies around the UK coast. The five colonies are: Isle of Rum, Small Isles, Scotland 56°57'36'' -6°29'12''; Lighthouse Island, Copeland Islands, Northern Ireland (hereafter "Copeland") 54°41'23'' -5°31'11''; RSPB Ramsey Island, North Pembrokeshire, Wales 51°51'35'' -5°19'12''; Skomer Island, South Pembrokeshire, Wales -51°44'24'' -5°16'48'' and Lundy Island, Devon, England 51°10'12'' -4°40'47''. Also see figure 1.1 for a map showing all colonies in this study.

Because of differences in the local terrain at each colony, the methods for capturing birds were adapted accordingly. On Rum, Copeland and Skomer access holes were dug into the roof of nest chambers of active burrows and sealed with either an earth plug (Skomer), rock (Rum) or concrete slab (Copeland). If capture was taking place during the night, a set of white pegs or cocktail sticks (or similar) were balanced at the front of each burrow. Every 10-20 minutes the entrance to each burrow would be inspected and if the sticks had been displaced then the nest chamber would be checked for the presence of a bird. On Ramsey and Lundy it was not possible to build access hatches into the burrows, so purse nets were used at night to catch birds at the moment they returned or left the breeding burrow (this method was used by Guilford et al. 2011 for capturing Atlantic puffins, although it is also used for harvesting a number of burrow nesting species). The nets were checked no less frequently than every 5 minutes to ensure that no birds were left entangled for too long.

Once a Manx shearwater was caught, a British Antarctic Survey (BAS, Cambridge) combined geolocator and immersion logger was deployed (after retrieving the previously deployed geolocator if present) on the leg of the bird. The geolocator was attached by cable ties and a small amount of superglue to a pre-shaped darvic leg ring. Depending on the type of logger used, the total mass of the device and attachments was either 1.5g (BAS Mk 13, 14 and 18) or 2.5g (BAS Mk 6, 9, 15 or 19). Figure 2.1 shows a Manx shearwater carrying a BAS Mk 15 geolocator. Usually the bird would also be weighed using a bag and a spring balance and the BTO leg ring number noted before returning it to the breeding burrow. Total handling time was usually less than 10 minutes.

Figure 2.1 BAS MK15 logger attached to a bird's leg using cable ties and a darvic ring. Photo from Skomer 2011.

2.2.2 Summary of data collected and pre-processing techniques

Light and saltwater immersion data were collected from a total of 145 individual Manx shearwaters, with 66 from Skomer, and the remainder from Lundy (n=21), Ramsey (n=11), Copeland (n=33) and Rum (n=14). A total of 275 complete migrations were tracked, 142 of which were from Skomer Island. 40 individual Manx shearwaters were tracked for three or more years. These data have been collected over a period of six years, from July 2006 (the loggers were retrieved in 2007) up until July 2012. Tables 2.1 and 2.2 summarise the numbers of individuals tracked at each colony and in each year. Only complete migration tracks were used in the analyses presented in this thesis.

Table 2.1. Numbers of Manx shearwaters tracked in each year at each colony. The date refers to the year the data were retrieved.

Colony	2007	2008	2009	2010	2011	2012	Number of individual birds	**TOTAL** tracks
Skomer	11	15	26	28	32	28	66	**142**
Copeland		11	12	12	12	13	33	**60**
Ramsey				8	6	4	11	**18**
Lundy				15	13	7	21	**35**
Rum					13	2	14	**15**

Table 2.2 Number of individual Manx shearwaters that were tracked for repeat migrations from each breeding colony.

Colony	2 years	3 years	4 years	5 years	**Total** number of birds with repeat years
Skomer	10	15	8	3	**36**
Copeland	5	4	2	2	**13**
Ramsey	3	3			**6**
Lundy	8	3			**11**
Rum	1				**1**

The migratory timing data presented in this chapter were calculated from the geolocation data alone. The archival loggers used in this study record the light sensor value every 10 minutes. These data can be combined with known times of sunrise and sunset globally, from which day length can be calculated and used to estimate latitude. The timing of midday or midnight is used to gain an estimate of longitude. This gives two estimates of location per day, with a mean error of 186km (± 144 km) (Phillips et al., 2004). All light data were initially decompressed and processed using Decompressor, TransEdit and BirdTracker software (BASTrak, British Antarctic Survey) with a light threshold of 10 and an elevation angle of between -5 and -3 (depending on the logger batch). The locations determined by BirdTracker were subsequently filtered to remove those calculated from noisy transitions. The data were further filtered to remove locations at latitudes greater than 80° (in both hemispheres) as these represent locations where no Manx shearwaters have previously been reported so were deemed highly likely to be erroneous. During the spring and autumn equinoxes, day length is uniform across the globe, leading to increased errors in latitudinal estimates. Locations 7 days on the summer side and 21 days on the winter side of each equinox were labelled for later removal due the asymmetrical levels of uncertainty either side of the equinoxes (higher on the winter side as found by Hill & Braun 2001).

2.2.3 Determination of sex

Manx shearwaters show very little sexual dimorphism, however Guilford et al. 2012 showed that light and saltwater immersion data can be used to determine sex in Balearic shearwaters (*Puffinus mauretanicus*) by examining behaviour in the pre-breeding period. A similar technique is used here to infer the sex of all the individuals in this study. Figure 2.2 shows the raw light curves and saltwater immersion data from two data loggers, which were carried by a breeding pair of shearwaters on Skomer in June 2010. The figure covers the period before an egg is laid.

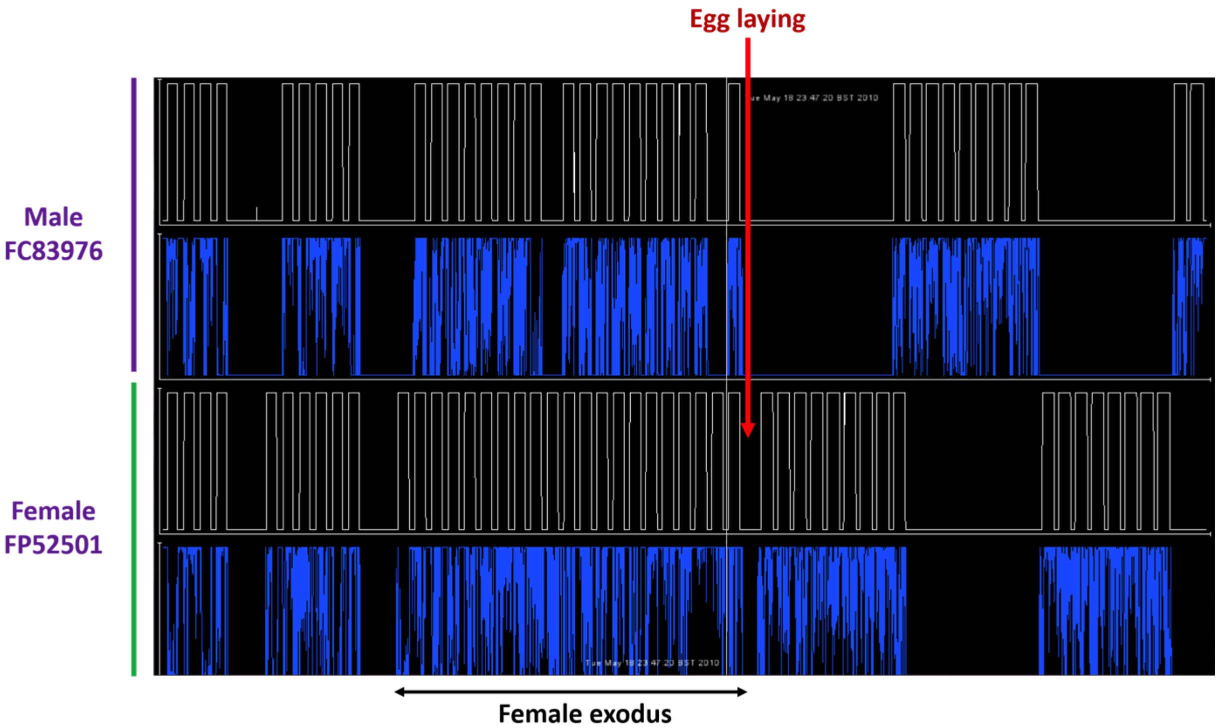

Figure 2.2 Time series showing the light curves (white) and saltwater immersion data (blue) from a pair of birds breeding on Skomer in 2010. The sex of these individuals was assigned by cloacal inspection immediately after egg laying. The female pre-laying exodus period is labelled, during which the male spends more time returning to the breeding colony, visits which appear as interruptions in the light and immersion data. The female does not return to the colony until ready to lay the egg. Egg laying is then followed by a first incubation stint by the male bird; appearing as a sustained period absent of light and saltwater immersion.

Where full days were spent within the breeding burrow there is an absence of saltwater immersion and daylight periods. Female shearwaters spend around 10 days away from the breeding colony post-mating (behaviour referred to as the pre-laying exodus) in order to build the egg (Brooke, 1990; Guilford et al. 2009; Newton, 2011). During that time the male makes more frequent visits to the breeding colony, sometimes staying in the burrow during the day. Using this information, sex can be inferred by looking at attendance in the period of time before the first incubation stint. If this period is characterised by frequent visits to the colony (long dry periods and interruptions to the daylight cycle), the bird is likely male. Conversely, if the bird spent most of its time at sea (indicated by uninterrupted light curves and long periods of saltwater immersion) then the bird is probably female. Data are not needed from both partners, although examining paired patterns reduced uncertainty in some birds. This method was validated by examining the saltwater immersion and light-logger data for 43 birds from Skomer which had been sexed by cloacal inspection. Cloacal inspection took place the morning after an egg laying event, which was determined by daily burrow checks during May and June in 2009, 2010 and 2011. Of the 43 birds with both logger data and cloacal inspection results, sex was inferred from logger data for 31 birds, and for the remaining 12 birds, no sex was inferred due to ambiguity in the pre-laying data. For all 31 of the birds with inferred sex, these concurred with the results of cloacal inspections. This technique was then applied to all birds (from all breeding colonies) where the attendance pattern determined from the logged data was unambiguous.

2.2.4 Statistical analysis

To analyse migratory phenology the dates corresponding to 4 key migration events were determined as follows:

- Departure from/return to the breeding colony: the date at which the bird first crosses the line of -10 degrees longitude on each migration.

- Arrival at/departure from the overwintering location: the date at which the bird is first/last observed within the 80% occupancy kernel around the median overwintering location calculated for each bird, for each year. The extent of the kernel changes depending on the variation within the overwintering location (between 1.1 and 10 decimal degrees in latitude and longitude)

The duration of each migration, and the number of days spent in the overwintering location was calculated using the difference between the departure and return dates.

The relative importance of each of the potential drivers of differences in migration phenology (individual consistency, colony, year, sex) was analysed by linear mixed-effects modelling, with year and colony as fixed effects and individual as a random effect. Because the explanatory variable for individual was entirely nested within the colony variable (each individual only ever bred on one colony), this structure was represented by a nested random effect of individual within colony. In order to determine which of these factors explained variation in each response variable, a series of candidate models (listed in table 2.3) were defined, and the model that best fitted the data whilst controlling for model complexity (as judged using the Akaike information criterion, AIC) was taken as the base model. As well as reporting the best model as judged by AIC, the statistical significance of each of the component terms was assessed by F-tests comparing the base model with models either adding or removing the variable of interest. This approach was adopted so that the F-tests always evaluated candidate terms by comparison with the best fitting model, rather than the full model, since otherwise the full model could contain non-significant terms which would nevertheless absorb explanatory power, weakening the statistical power of the tests. In most cases however, the full model was selected as the best model by AIC.

Table 2.3 Summary of the 3 different models used to determine which factors described most of the variation within each response variable. The best model was selected using AIC, and for most variables was model 3.

Model name	Fixed factors	Random factors
Null		BIRD (nested in colony)
One	COLONY	BIRD (nested in colony)
Two	YEAR	BIRD (nested in colony)
Three	COLONY + YEAR	BIRD (nested in colony)

An additional candidate model including a regression terms representing all interactions between the year and colony variables was considered, but this model comprised 29 more fixed effects terms. Due to the very large number of predictors (in combination with the nested mixed-effects structure) this model failed to converge, so was excluded. Marginal and conditional R-squared estimates (from Nakagawa & Schielzeth, 2013) were also calculated for the AIC-selected model for each response variable, in order to partition the variance explained by the random and fixed factors. Because sex was not determined for all birds, the effect of sex was evaluated by refitting the best model from the full dataset to the subset of data with identified sexes (231 migrations out of 275) and comparing this against a model including an additional fixed effect for sex. In order to test individual consistency in the timing of migration, repeatability analyses were conducted for each response variable, using the method defined by Nakagawa & Schielzeth, 2010. All models were fitted in R 3.1.2 using the following packages: `lme4` (fitting linear mixed effects model), `MuMIn` (AIC), `lmerTest` (significance tests for model comparisons) and `rptR` (repeatability analysis).

2.3 Results

A general summary of the median migration departure and arrival dates and mean migration durations for each year and colony can be found in tables 2.4 and 2.5. These summarise the data from all 143 individuals (275 separate migrations).

Table 2.4. Summary of mean departure and return dates and migration duration from each year for shearwaters from five breeding colonies. The year on the left hand side of the year column shows the year that southbound migration took place and those on the right of the year column show the year that northbound migration took place.

	Southbound migration			Northbound migration			
YEAR	Departure colony	Duration (days)	Arrival overwintering	Departure overwintering	Duration (days)	Return colony	N=
2006/2007	20 Sep	34	23 Oct	11 Mar	35	15 Apr	11
2007/2008	19 Sep	27	16 Oct	20 Mar	28	18 Apr	26
2008/2009	21 Sep	29	20 Oct	13 Mar	33	15 Apr	38
2009/2010	11 Sep	32	13 Oct	8 Mar	38	15 Apr	63
2010/2011	8 Sep	36	14 Oct	9 Mar	40	18 Apr	76
2011/2012	5 Sep	37	14 Oct	5 Mar	38	12 Apr	54

Table 2.5. Summary of mean departure and return dates and migration duration for Manx shearwaters from five UK colonies tracked in multiple years. Colonies are ordered by decreasing latitude.

	Southbound migration			Northbound migration				
COLONY	Departure colony	Duration (days)	Arrival overwinter	Departure overwinter	Duration (days)	Arrival colony	N =	No. of years
RUM	27 Sep	40	23 Oct	14 Mar	41	24 Apr	15	2
COPELAND	26 Sep	31	9 Nov	6 Mar	40	22 Apr	60	5
RAMSEY	17 Sep	37	10 Nov	12 Mar	44	25 Apr	18	3
SKOMER	25 Sep	33	2 Nov	10 Mar	41	25 Apr	140	6
LUNDY	4 Sep	32	9 Oct	21 Feb	36	21 Mar	35	3

2.3.1 Individual migratory phenology

A significant degree of individual repeatability in timing was detected for all the key migration dates calculated from light based locations (table 2.6), except for the duration of northbound migration which although still marginally significant, shows the lowest proportion of repeatability. This indicates that variation in the date at which birds depart and return from migration is greater between individuals, than within each individuals' multiple migrations (figures 2.3 and 2.4).

Table 2.6. Results of linear mixed effects modelling testing the effects of breeding colony and year on each of the seven response variables, and from repeatability analysis of individual consistency. Statistically significant results (at the p<0.05 level) are highlighted in grey.

Response Variable	Colony (fixed effect)	p	Year (fixed effect)	p	R2 model	R2 fixed effects	R2 random effects	Individual repeatability (standard error)	p
Breeding departure	F_4=3.77	0.006	F_4=5.12	<0.001	0.50	0.15	0.35	0.398 (0.08)	<0.001
Overwinter arrival	F_4=3.24	0.014	F_4=5.29	<0.001	0.46	0.11	0.35	0.424 (0.08)	<0.001
Southbound duration	F_4=1.94	0.107	F_4=1.35	0.244	0.30	0.05	0.26	0.305 (0.08)	<0.001
Overwinter duration	F_4=1.42	0.231	F_4=4.99	<0.001	0.55	0.07	0.48	0.497 (0.08)	<0.001
Overwinter departure	F_4=1.34	0.260	F_4=2.23	0.055	0.86	0.04	0.83	0.318 (0.08)	0.001
Breeding return	F_4=12.04	<0.001	F_4=1.86	0.103	0.56	0.21	0.34	0.547 (0.07)	0.001
Northbound duration	F_4=6.82	<0.001	F_4=3.22	0.008	0.25	0.13	0.12	0.133 (0.08)	0.044

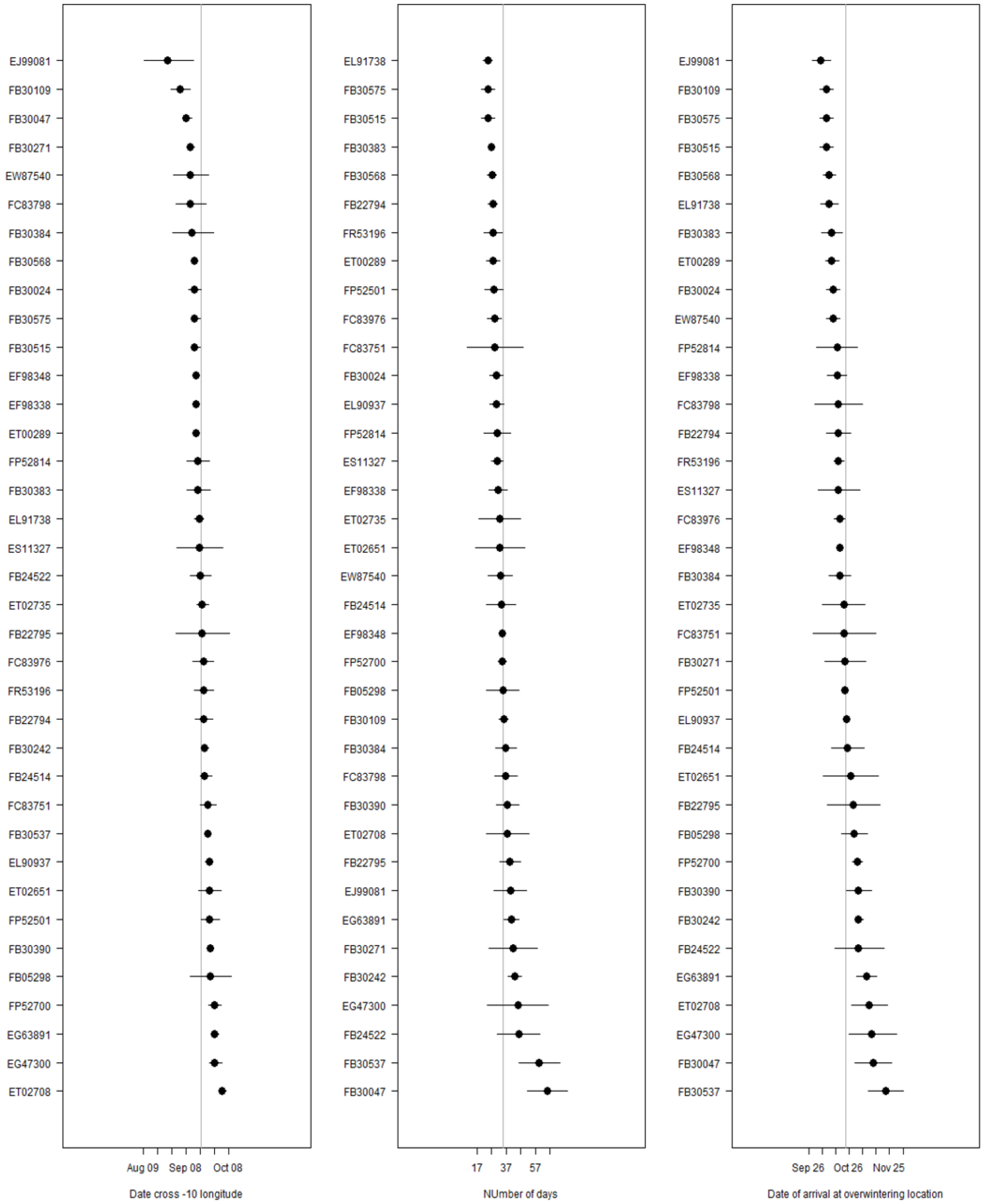

Figure 2.3. Timing of key events in the southbound migration of individual Manx shearwaters. From left to right: Date crossed the -10° longitude (leaving the UK), duration of migration, date arrived at the mean overwintering location. Each row represents one bird (here, n=37 birds with three or more repeat migrations), the black dot is the mean date, lines show the 95% confidence intervals. The vertical line shows the mean for the whole data set.

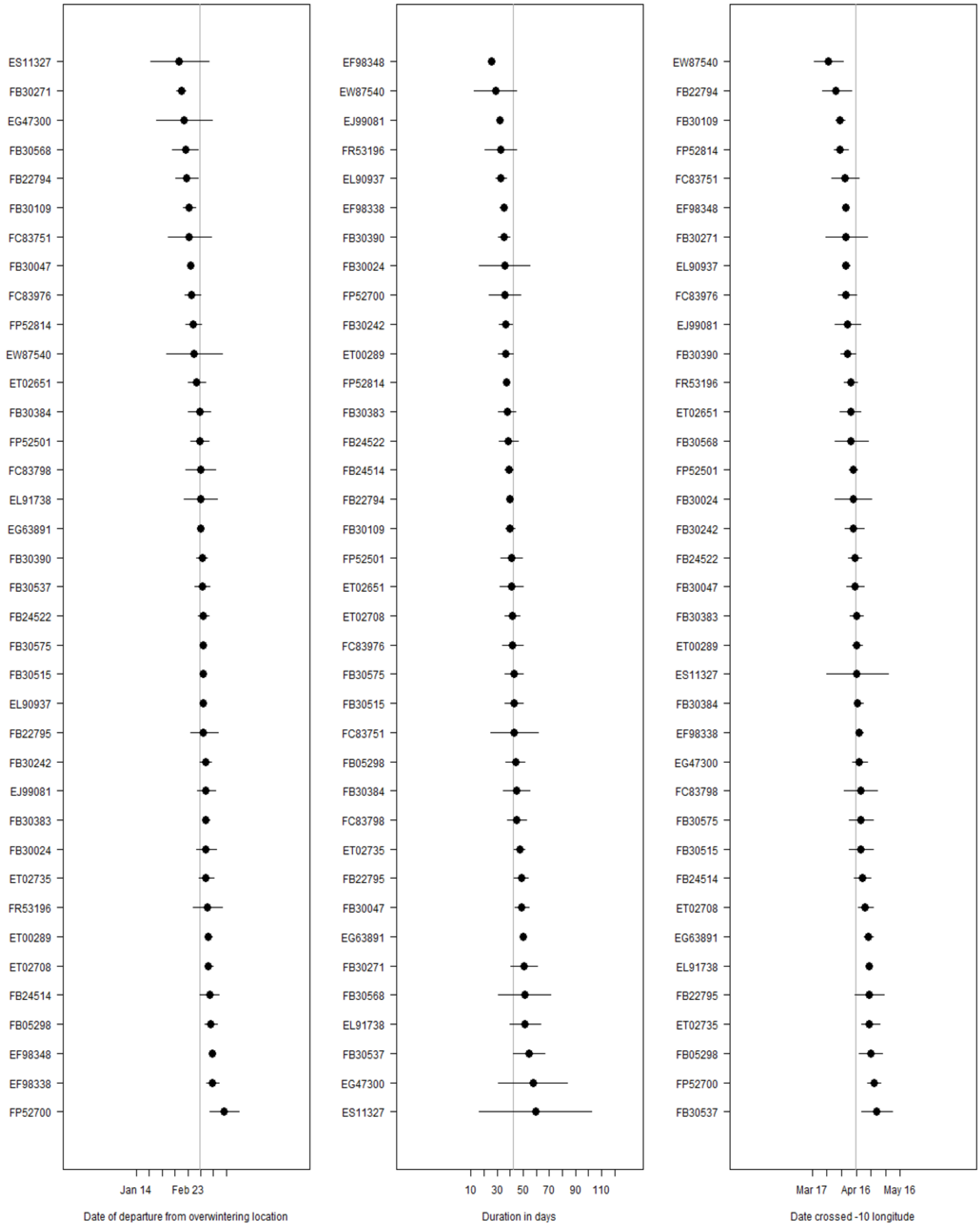

Figure 2.4. Timing of key events in the northbound migration of individual Manx shearwaters. From left to right: Date of departure from the mean overwintering location, duration of migration, date crossed the -10 °longitude on return to UK. Each row represents one bird (here, n=37 birds with three or more repeat migrations), the black dot is the mean date, lines show the 95% confidence intervals. The vertical line shows the mean for the whole data set.

2.3.2 Colony differences in migratory phenology

There were significant differences between colonies in the mean dates of crossing the -10° longitude line on departure from the breeding colonies, arrival at the wintering grounds, the date of return to the UK (again passing the -10° longitude line, from west to east) and the time spent on the northbound (or return) migration – see table 2.6 for the statistical results. Figures 2.5 and 2.6 summarise the southbound migration data and figures 2.7 and 2.8 the northbound migration, showing the mean dates for birds from each colony and the variation in the data. Birds from Lundy also appeared to be consistently earlier than those from all the other colonies in the return date to the breeding colony (average difference of -20.1 days), and also had a shorter northbound migratory duration (figure 2.8). Additionally, birds breeding on Rum appeared to be generally later (average difference of +6.5 days) than the overall population median.

2.3.3 Effect of year on migration phenology

Yearly differences in the mean dates of crossing the -10° longitude line on departure from the breeding colony, arrival at the wintering grounds, the amount of time spent overwintering before departure back to the northern hemisphere were significant (table 2.6). There were also significant yearly differences in the duration of the return migration. Figures 2.9 and 2.10 show the yearly distribution of dates and durations for the southbound (2.9) and northbound (2.10) migrations. There were no overall patterns across the years, although data collected in years ending in 2011 and 2012 appeared to be slightly earlier in timing.

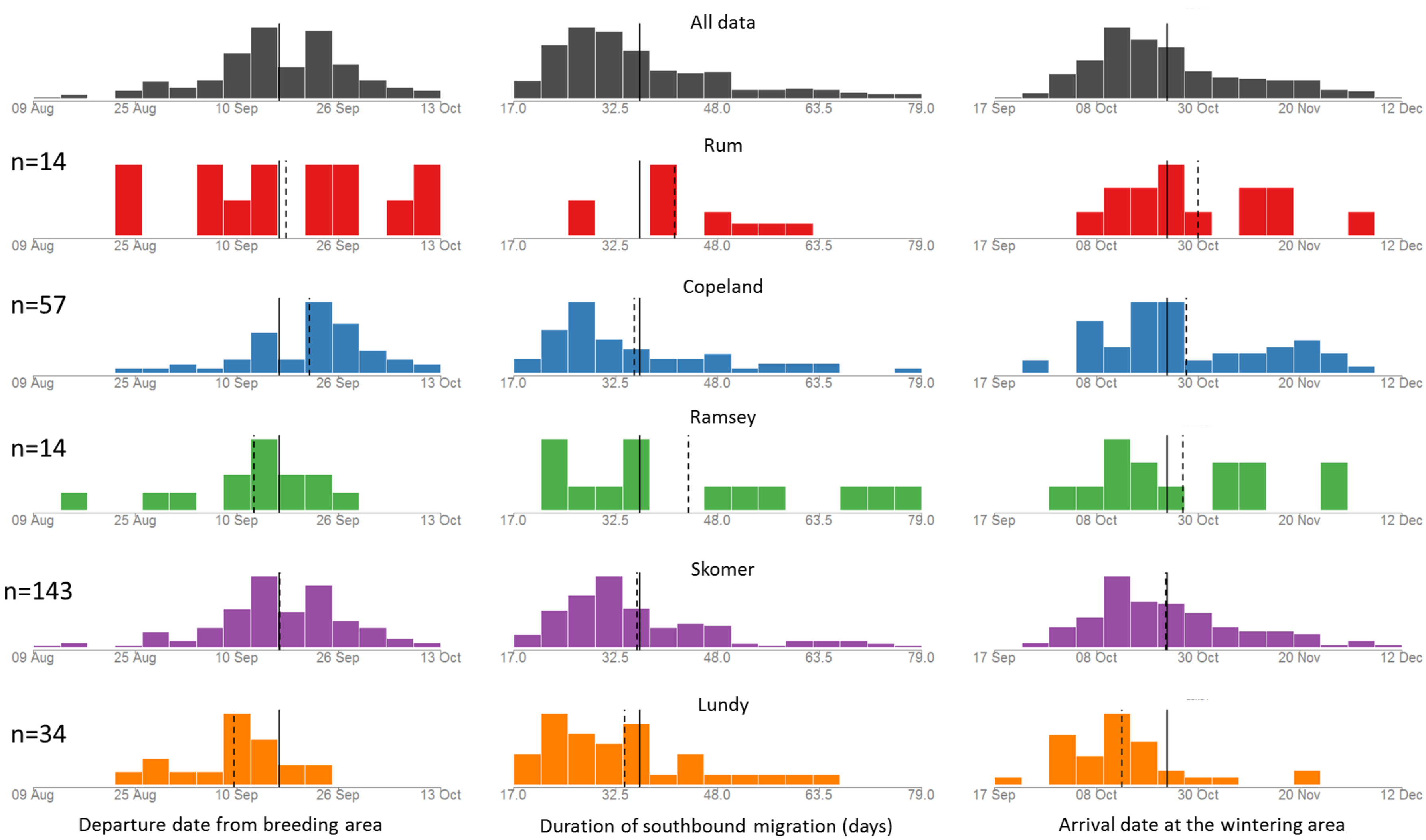

Figure 2.5. Timing of key events in the southbound migration from different colonies. The top plot in each column shows the data from all colonies together. The colonies are plotted in order of latitude, Rum-Lundy (from top to bottom). The solid vertical line shows the median for the whole data set, the dashed line the median for that colony.

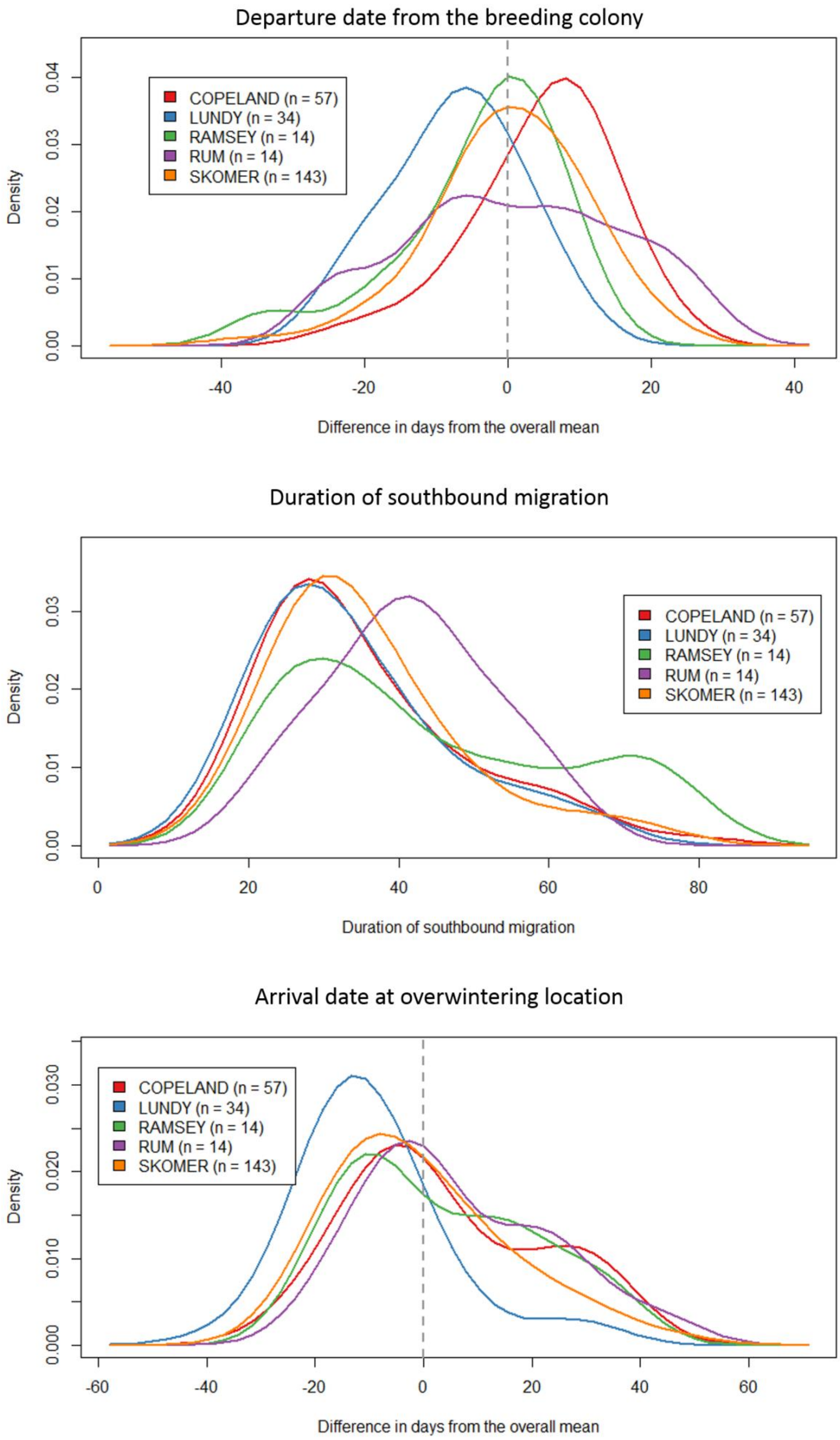

Figure 2.6. Cross-colony comparison of the southbound migration timing in Manx shearwaters from five different breeding colonies. Dotted line shows mean for the whole dataset and the curves show the distribution of each colony around the overall mean.

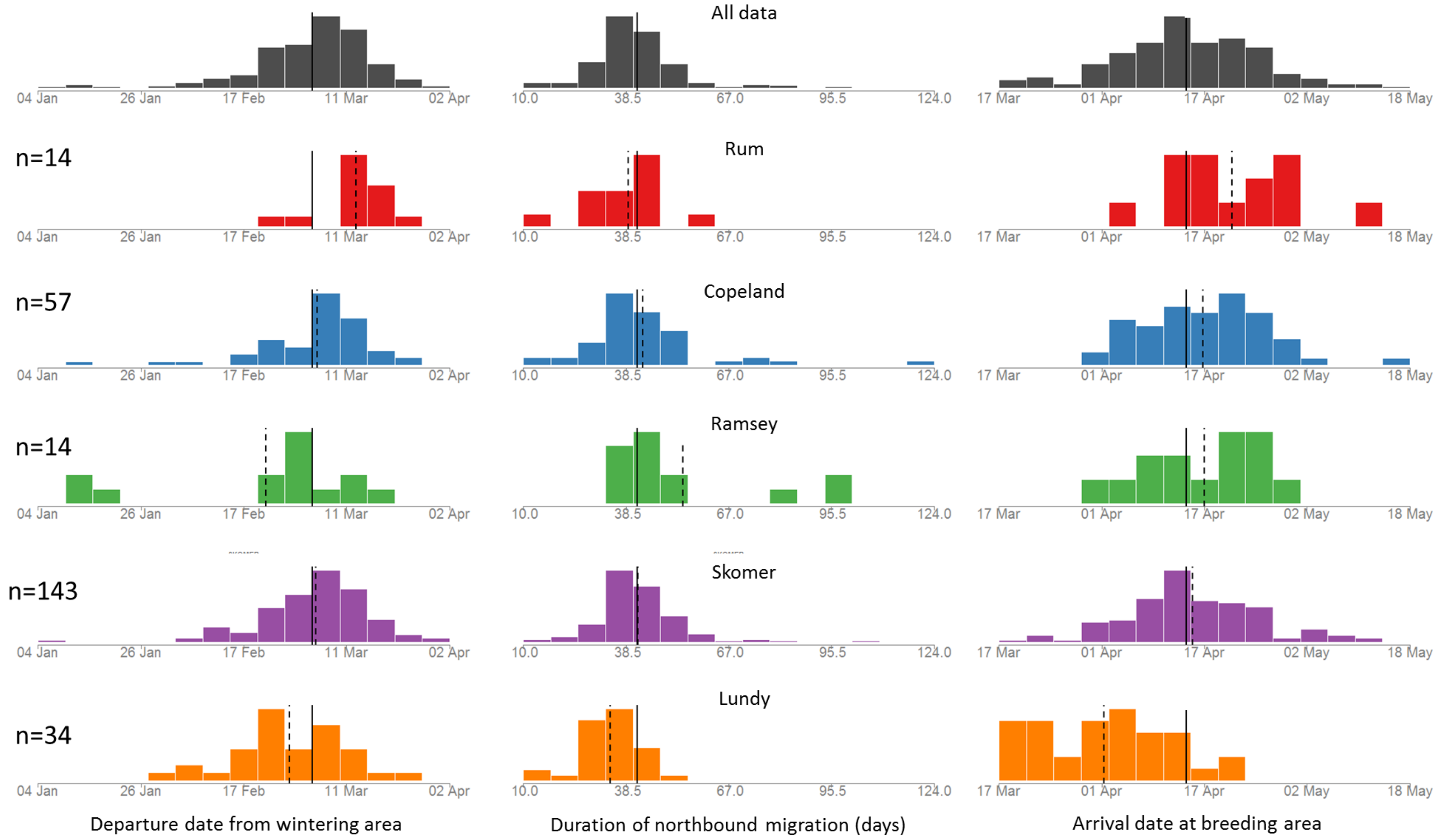

Figure 2.7. Timing of key events in the northbound migration from different colonies. The top plot in each column shows the data from all colonies together. The colonies are plotted in order of latitude, Rum-Lundy (from top to bottom). The solid vertical line shows the median for the whole data set, the dashed line the median for that colony.

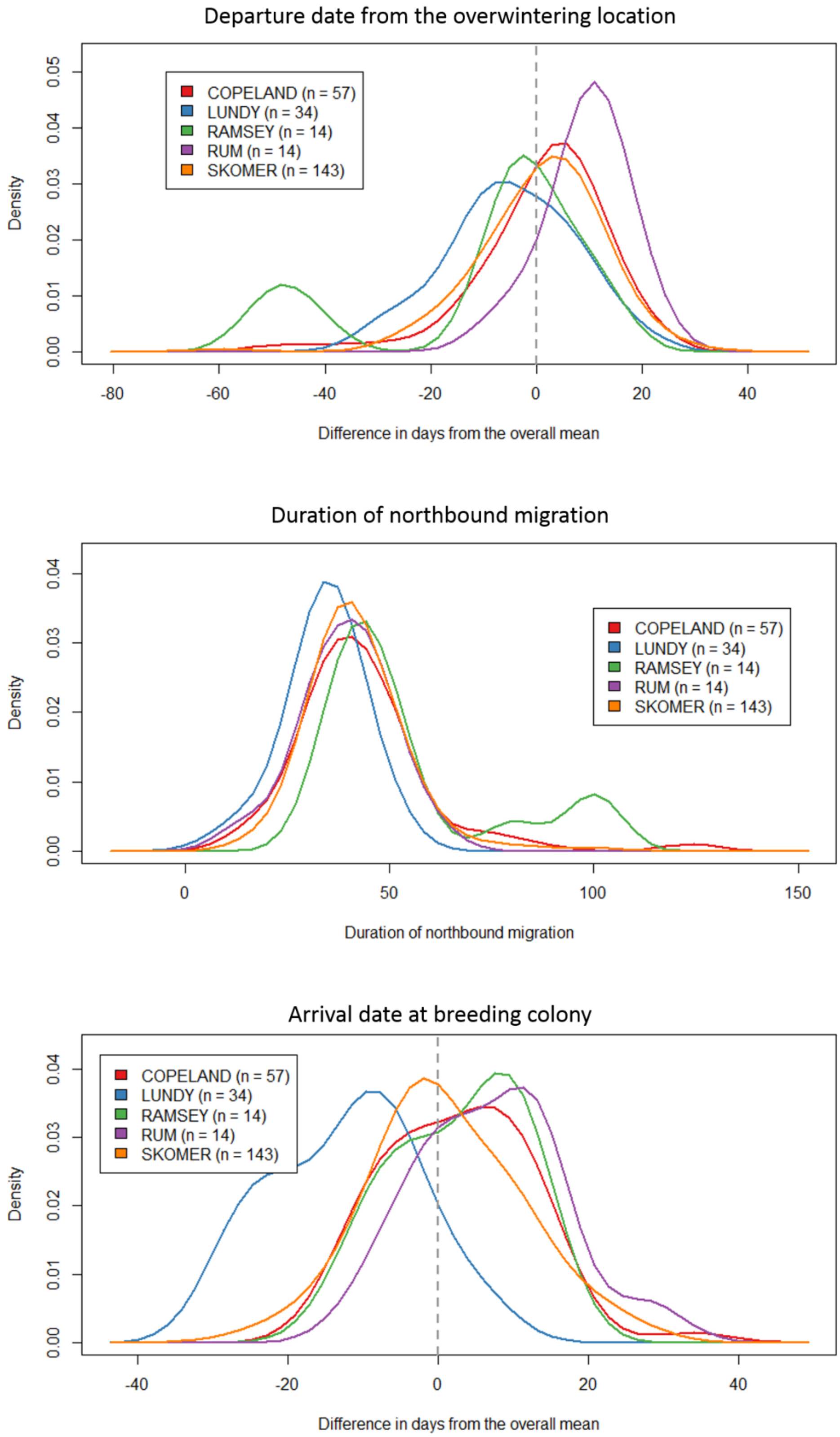

Figure 2.8. Cross-colony comparison of the return migration timing in Manx shearwaters from five different breeding colonies. Dotted line shows mean for the whole dataset and the curves show the distribution of each colony around the overall mean.

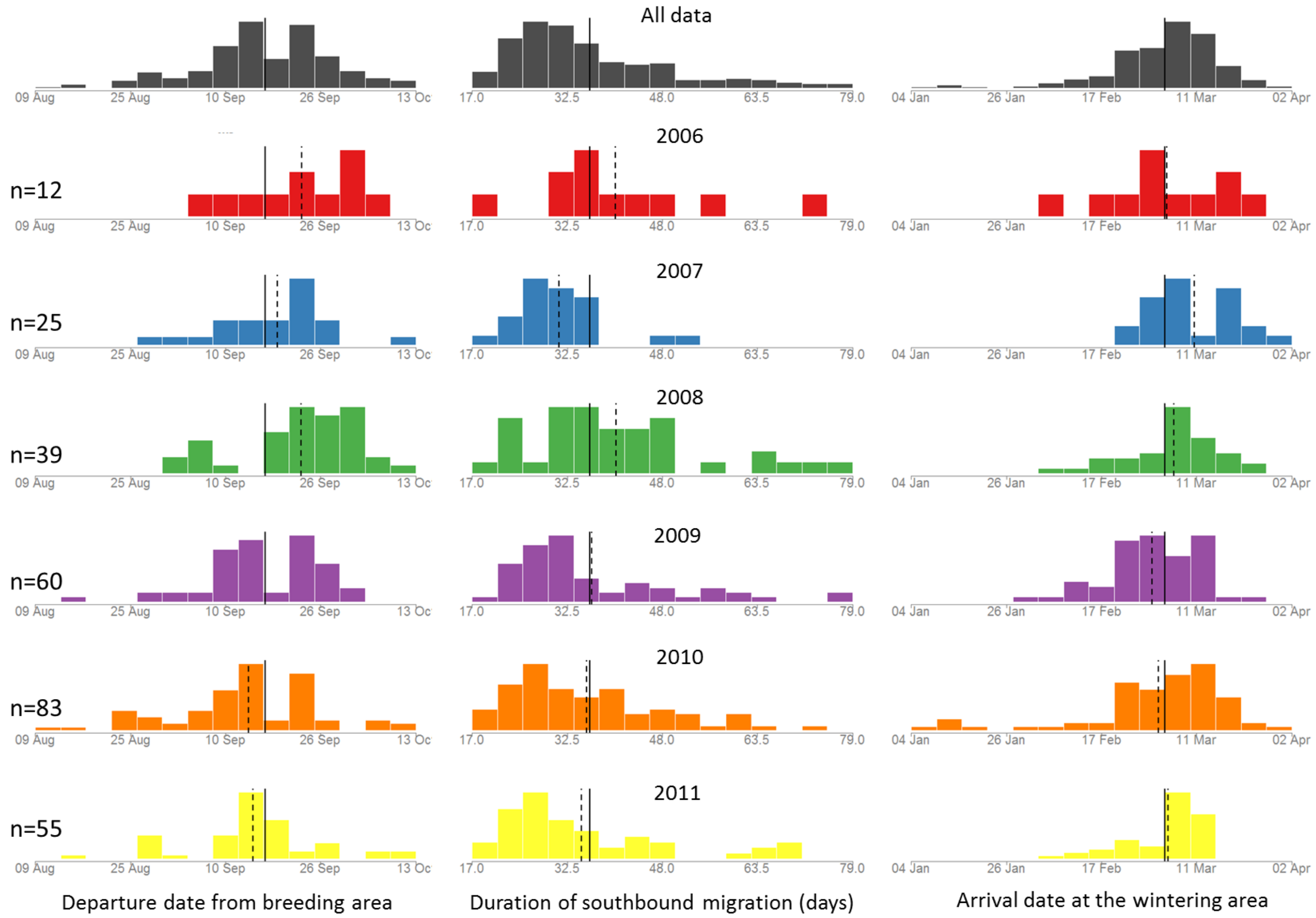

Figure 2.9. Timing of key events in the southbound migration tracked in different years. The top plot in each column shows the data from all years together. The years are plotted in order 2007-2012 (from top to bottom). The solid vertical line shows the median for the whole data set, the dashed line the median for that year.

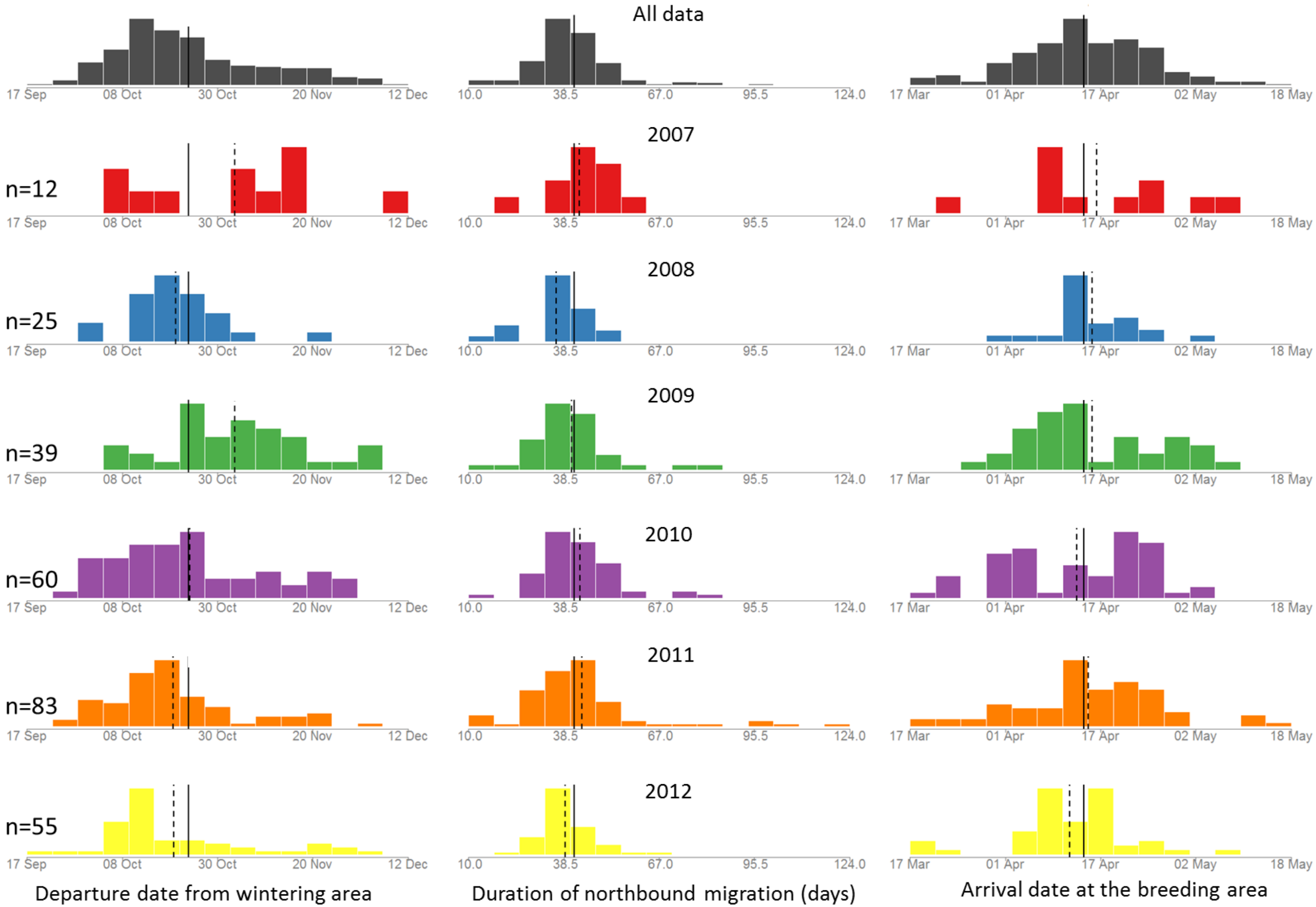

Figure 2.10. Timing of key events in the northbound migration tracked in different years. The top plot in each column shows the data from all colonies together. The years are plotted in order from 2007-2012 (from top to bottom). The solid vertical line shows the median for the whole data set, the dashed line the median for that year.

2.3.4 Sex differences in migration phenology

There were no differences between male and female birds in the timing of post-breeding migration (table 2.7). However, males were on average 3 days earlier than females in the timing of departure and arrival on northbound (pre-breeding) migration (figure 2.11).

Table 2.7 Results of linear mixed effects models showing male and female migration schedules. Statistically significant results (at the p<0.05 level) are highlighted in grey.

	Response Variable	Female (n=119)	Male (n=111)	F	df	P	R2 fixed	R2 random
Southbound migration	Depart breeding area	16-Sep	19-Sep	2.057	1	0.153	0.192	0.230
	Duration (days)	34	32	0.662	1	0.418	0.043	0.270
	Arrive wintering area	19-Oct	20-Oct	0.056	1	0.813	0.145	0.380
	Overwinter duration	135	131	1.793	1	0.184	0.090	0.462
Northbound migration	Depart wintering area	06-Mar	03-Mar	3.994	1	0.049	0.134	0.273
	Duration (days)	40	40	0.005	1	0.943	0.091	0.062
	Arrive breeding area	15-Apr	12-Apr	5.500	1	0.021	0.275	0.304

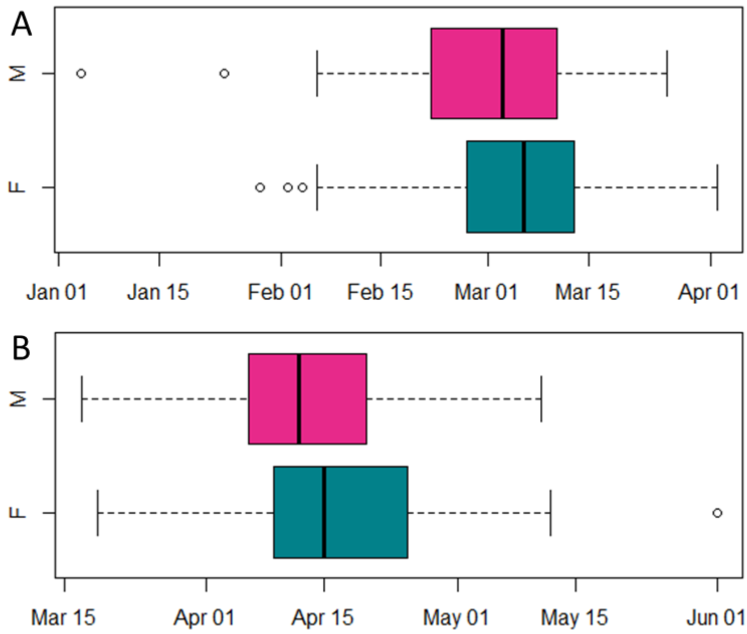

Figure 2.11. Differences between males and females in the timing of pre-breeding migration. Males depart from the wintering area earlier than females (A) and also arrive earlier at the breeding area (B).

2.4 Discussion

2.4.1 Overall timing of migration

Manx shearwaters exhibit a clockwise migration around the Atlantic Ocean. The southbound migratory route passes down the west coasts of Europe and North Africa, crossing the south Atlantic at the narrowest point (approximately between latitudes 8° and -6°) and continuing down the east coast of South America (Guilford et al., 2009; Freeman et al., 2013). On the northbound migration the birds follow the east coast of South America up to the Caribbean and then take a variety of different routes back to the UK across the north Atlantic (Guilford et al., 2009; Freeman et al., 2013). This chapter presents the first multi-colony, long-term study of migratory timing in this species, following individual birds over the course of 6 years of tracking. Previous work on this species estimated timing during one or at most two years.

The timing of migration for birds tracked across all years and colonies in this study broadly matched those put forward by Brooke (1990) (from observation of birds from the Skokholm breeding colony) and Guilford *et al.* (2009) (where birds from Skomer were also tracked with geolocators). Overall, southbound migration begins in mid-September and ends in mid-October. Departure from the overwintering location occurs in mid-March and birds arrive at the breeding colony by mid-April. The only difference is that Brooke (1990) suggests the birds return to the colony (Skokholm, approximately 4km south of Skomer) by mid-March, which is a month earlier than we find from the data collected from all five colonies, and that Guilford et al. (2009) reports from a subset of these data from 2007. A possible explanation for this difference in timing is that the birds sampled by Brooke were at a different stage in their life history (perhaps being older and more experienced, or vice-versa). Alternatively, the sample of birds used in one of these studies may have been unintentionally biased towards either earlier or later breeders. This seems unlikely to be the case however, given the sample sizes involved (146 individuals in this study and at least 40 in Brooke's), and the fact that birds were added to this study over its 6 years, with no bias in the time during the breeding seasons in which birds we recruited. Although unexpectedly large, the difference between timing of arrival from pre-breeding migration recorded here and Brooke's is potentially due to changes in the breeding behaviour and environmental conditions over the four decades since Brooke's study in the 1970s. During this time other seabird species have shown changes in the timing of breeding behaviour with shifts to earlier or later breeding (Votier et al. 2009, Wanless et al. 2009). Common guillemots (*Uria aalge*) also breeding on Skomer Island were studied from 1973 until 2008, and birds in this colony showed a trend for earlier breeding (approximately 6 days earlier) (Votier et al., 2009). The hypothesis for these changes in breeding phenology is that they are a response to changing climate and environmental conditions (Votier et al., 2009). As local and global climates have changed over the last two decades many avian species have been observed shifting their breeding and migration phenology so that they continue to benefit from seasonal peaks in productivity (Frederiksen & Harris 2004; Charmantier et al. 2008; Balbontín et al. 2009; Saino et al. 2010). Manx shearwaters are a long-lived species. Whilst mean life expectancy is difficult to estimate, an individual recovered at the Copeland breeding colony in 2003 was at least 55 years old, making it the oldest known bird in Europe at the time (Coiffait et al., 2008) Consequently, changes in timing of migration are more likely due to behavioural plasticity than climate-driven selection (Charmantier & Gienapp, 2014).

Time taken on southbound migration is generally shorter than the duration of the northbound migration. Given that the migratory route differs more between individual birds on the northbound migration (see chapter 3) it seems likely that the duration of migration may also vary according to the route. Another possible reason for these differences is variation in the amount of time spent at stopover sites – this will be explored further in chapters 4 and 6.

Variation among individuals in journey start date was much greater for the return migration (departing from the wintering area) than the southbound migration. The range of dates for northbound departure was 93 days between the earliest and latest, compared with 63 days for the southbound departure date (across all colonies). This suggests that perhaps there are greater constraints on the timing of post-breeding departure, possibly due to the restriction of the chick needing to achieve an optimal weight before the adults can stop visiting the colony (Brooke, 1990). It may also be the case that there are optimal conditions for passage along the southbound migration route, such as winter weather systems bringing appropriate wind speeds and directions for efficient migration (Felicísimo et al. 2008; Both 2010). Delays in post-breeding departure may increase the chances of encountering poor weather during the journey. It is interesting that the departure date (and subsequent arrival) in the northbound migration is so variable, given that the generally held hypothesis is that for many species beginning breeding earlier in the season increases the likelihood of success (Brooke, 1990; Reed et al., 2009; Hindell et al., 2012; Shoji et al., 2015). However, variation in departure date from the South Atlantic may not always be related to variation in the date of arrival at the breeding colony. For example, birds that leave later may take a more direct route home, allowing them to make up for spending more time in the wintering area. This hypothesis will be explored in chapter 6.

2.4.2 Individual consistency in migratory timing

Individual shearwaters showed substantial consistency in migratory timing between years. Behavioural consistency within individual birds was greatest during the northbound migration, with 24 birds (64%) showing less than five days of variation in departure and arrival across three or more years. This is markedly less than the overall ranges of 93 days for northbound departure and 63 days for southbound departure.

Individual consistency in the scheduling of migration has been observed in a number of bird species, including several seabird species (Balbontín et al., 2009; Vardanis, Klaassen, Strandberg, & Alerstam, 2011; Thorup et al., 2013). Other seabird species have shown a similar level of individual consistency in migratory timing to Manx shearwaters (Reed et al., 2009; Bogdanova et al., 2011; Fifield et al., 2014; McFarlane Tranquilla et al., 2014). Indeed, related Procellariiformes such as Streaked shearwaters (*Calonectris leucomelas*: Takahashi et al., 2014), Cory's shearwaters (*Calonectris borealis:* Dias, et al. 2011) and Black-browed albatrosses (*Thalassarche melanophrys*: Phillips et al., 2005), all display individual repeatability in migratory scheduling, particularly in the post-breeding migration. Often this repeatability in timing of migration is mediated by breeding outcome, with failed breeders leaving earlier (Bogdanova et al., 2011; Yamamoto et al., 2014) Manx shearwaters appear to be unusual in that individual consistency in timing is seen at every point during the non-breeding period, from the date of departure from the breeding area through to the following pre-breeding migration. This suggests that breeding outcome does not influence timing of subsequent migration. However, in this study departure on post-breeding migration was defined as the date at which the bird crossed the -10° longitude line, at which point birds may have actually left the colony sometime before this. Indeed, Manx shearwaters, like some other petrel species (sooty and short-tailed shearwaters *Puffinus griseus* and *Puffinus tenuirostris*), desert the chick up to 23 days before fledging (Brooke, 1990). It would therefore make sense that breeding outcome is not the only influence on timing of post-breeding migration.

As detailed in section 2.4.1, it appears that the population average timing of arrival at the colony may have changed significantly over the past four decades, most likely due to behavioural plasticity in response to changing environmental conditions (particularly timing of resource availability). Given that individual birds will likely have experienced different conditions and timing over their long life spans, it is plausible that these same environmental drivers of plasticity may be the root cause of these individual differences. This is seen in the many avian species which show strong correlation of event timing to coincide with biotic and abiotic factors such as favourable oceanographic conditions (Ramírez et al., 2016), plant biomass (Hinks et al., 2015) and marine plankton peaks (Abraham & Sydeman, 2004).

An alternative hypothesis is that individual repeatability over consecutive years may be the long-term results of carry-over effects, with the outcome of one part of the annual cycle leading to a delay/advance in the next. Such carry over effects have been identified in a range of seabirds, including other Procellariiformes (Crossin et al., 2012;

Catry et al., 2013; Szostek & Becker, 2015). The contribution of carry-over effects to the timing of the annual cycle (including migration) is quantified in Chapter 6. For example, consistency in the timing of northbound (pre-breeding) migration could be explained by looking at the route taken by each bird and the time spent in stopover areas. It is possible that a bird which consistently leaves earlier on northbound migration will have a longer route than a bird which leaves later. The migration route, wintering site and stopover behaviour are explored in chapters 3 and 4.

2.4.3 Colony differences in migratory phenology

Although several studies have investigated the migration and wintering behaviour of seabirds from breeding on different colonies (Gaston et al., 2011; Frederiksen et al., 2012; McFarlane Tranquilla et al., 2013; Fijn et al., 2013; Gilg et al., 2013; Fort et al., 2013; Fifield et al., 2014; Orben et al., 2015; Weimerskirch et al., 2015; Frederiksen et al., 2016) the dataset presented here follows individuals from five different breeding colonies over the course of three or more years. Many of these studies focus primarily on spatial aspects of non-breeding behaviour. This study analysed data from multiple years and multiple colonies to examine inter-colony differences in individual migratory timing over multiple years in detail.

The five colonies used in this study lie at a range of latitudes, with Rum the most northerly at 57.0° and Lundy the furthest south at 51.2°. The timing of some key migration events varied significantly between the five colonies. The median date of departure from the breeding colony varied over 23 days across the latitudinal range, with the median date of return to the breeding colony varying by an even greater margin of 34 days. There was a general trend towards later dates of departure and arrival for birds from colonies at higher latitudes (Rum latest and Lundy earliest). The only exception to this is the onset of southbound migration for birds from Rum which was slightly earlier than at both Skomer and Copeland (which are both further south). This may be partially due to the varied distribution of dates from Rum, the colony for which there was only one full year of data for all but one individuals. The general trend of later arrival from migration further north is in agreement with Brooke (1990) who hypothesized that this trend was related to weather conditions. The shearwater colonies on Rum occur at a much higher altitude (500m and above, at the top of the three main peaks Hallival, Askival and Trollval) and snow may cover the breeding burrow entrances until late spring (Brooke, 1990) delaying the onset of laying (Thompson, 1987). This latitudinal difference may also come about if local peaks in resources are different around the different colonies. If this is the case, birds might be expected to time their arrival and subsequent breeding with those resources, as has been seen with other species, in order to maximise breeding success (Wanless et al., 2009; Regular et al., 2014). However, tracking studies which took place later in the breeding season show Manx shearwaters from all colonies making long distance foraging trips of over 200km (Dean et al., 2012; Dean et al., 2015). This implies that resource availability local to the breeding colony may be of lesser importance. Finally, it is important to consider that the distanced travelled on migration may impact on the timing of both departure and arrival. Lundy and Rum (at opposite ends of the latitudinal range in this study) are approximately 700km away from each other, a difference that may affect the overall migratory distance travelled by birds from these colonies. This will be explored in the next chapter of this thesis.

There were no consistent trends in the migratory timing of birds breeding on Ramsey Island and Lundy Island. Both of these colonies are undergoing rapid expansions in population size after the eradication of rats and current estimates suggest that both are growing faster than the rate of recruitment from local reproduction. This implies that immigration from other colonies is likely to be occurring. If immigration is taking place, it is likely that a substantial proportion of these birds are individuals that could not compete with others on their natal colonies, possibly because they are inexperienced. Due to the nature of the breeding burrows on these colonies it was not possible to estimate age or breeding experience for the individuals in this study.

2.4.4 Effect of year on migration phenology

The data collected here spans 6 consecutive breeding and migration periods from 2007 to 2012, enabling investigation of inter-annual differences. After taking into account the variation due to colony differences, and individual repeatability, the dates of departure and arrival on the southbound migration, the duration of the wintering period and northbound migration showed significant variation between years. There was no clear temporal trend across the years, nor was any one year markedly different from the others. This implies that inter-annual differences in migratory timing over this period (and across all colonies) were driven by stochastic effects, rather than a long-term trend. However, it may also be that this six year period is not enough to detect the changes in phenology relating to long-term climate shifts that have been found in other seabird species (Szostek, Bouwhuis, & Becker, 2015; Szostek & Becker, 2015; Ward et al., 2016).

Whilst many studies have looked at the effects of environmental variation on seabird behaviour, mostly these have focussed on population level mortality and breeding success or related breeding behaviour (such as the provisioning of offspring) (Catry et al., 2013; Jenouvrier, Peron, & Weimerskirch, 2015; Soldatini et al., 2016). A smaller number have examined the impact of extreme weather events (such as winter storms).

Severe weather stochasticity has been shown to have a significant effect on arrival time in passerine species (Robson & Barriocanal, 2011). This is also the case for seabird species such as the European shag (*Phalacrocorax aristotelis*) and common guillemot (*Uria aalge*), which showed delayed breeding after a period of high wind during the winter (Harris & Wanless, 1996). These events, often termed seabird wrecks are well documented in the northern Atlantic Ocean (Sandvik et al., 2005; Votier et al., 2005); but the effects of this sort of extreme environmental variation on longer distance migrants is less well understood. In species such as the Manx shearwater it is possible that migrating individuals encounter weather conditions that interfere with the efficiency of their commute, such as unfavourable wind directions which increase travel costs (Felicísimo et al., 2008).

2.4.5 Differences between the sexes

The timing of departure from the overwintering area differed between the sexes, with females departing three days later than males. This was sustained through the northbound migration, leading to female birds arriving three days later at the breeding area (in agreement with Guilford et al., 2009). Early arrival of males at the breeding area is widely reported in migratory species (Kokko et al., 2006), and seabirds are no exception. Male crested penguins (*Eudyptes* spp.) also show differences in the departure and arrival date at the breeding colony, although to a greater degree (9 days before females, Thiebot et al., 2014). Early arrival of males has also been observed in Scopoli's shearwaters *Calonectris diomedea* (Müller et al., 2014). This reflects theories regarding the role of the sexes in the pre-breeding period, where males are thought to spend more of their time in nest site defence and maintenance, which may require earlier attendance at the colony (Brooke, 1990; Thiebot et al., 2014). Given that the date of arrival in the breeding area recorded here is not a direct indicator of the date that birds first arrive on the breeding colony (for this see chapter 5) it is possible that males and females still get to the breeding colony in synchrony, but male birds spend more time foraging to replace body condition on arrival in UK waters.

Sexual segregation in non-breeding distributions occurs in many procellariiforme species, especially those that show dimorphism between larger males and smaller females (Phillips, Bearhop, McGill, & Dawson, 2009). Despite forming long-term pair bonds (Brooke, 1990), and sharing a similar wintering destination, breeding pairs of Manx shearwaters do not migrate together (Guilford et al., 2009), behaviour that is also seen in Scopoli's shearwaters (*Calonectris diomedea*, Müller et al., 2015).

2.4.6 Conclusions

This chapter identifies key patterns in migratory timing and partitions this among colonies, years, sexes and individuals. We find a significant degree of individual consistency and a possible latitudinal effect of breeding colony on migratory timing, with birds breeding at higher latitudes arriving and departing the breeding colony later than the more southerly colonies. However, looking at the timing of migration may become more informative when simultaneously considering other factors that may affect it. Here we have explored the role of individual variation, year, sex and colony in shaping the timing of migration, but there other factors may also play a role. Subsequent chapters explore variation and behavioural consistency in migration route, stopover behaviour and breeding phenology. The relationships between these other factors and migratory timing are then investigated in chapter six, which views these as part of the entire annual Manx shearwater behavioural cycle.

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Chapter 3

Manx shearwater migration: migratory path, overwintering location and individual variation

3.1 Introduction

Many species living in seasonal ecosystems move, sometimes over great distances, in order to benefit from changes in resource availability, or to return to a specific location to breed (as in the case of marine turtles and anadromous fish). Often the journeys undertaken form prominent parts of a species' annual cycle, and can have long-term consequences for subsequent life-history stages (sometimes termed carryover effects, Harrison et al., 2011; O'Connor et al., 2014). Migration has been described in a large range of avian species, from small birds such as hummingbirds and blackcaps to large, soaring raptors (Meyburg et al., 2004; Németh & Moore, 2012; Newson et al., 2016). The multitude of means by which birds overcome the challenge of migration and how this influences life-history decisions, population dynamics and ecosystem function has formed the basis for a huge area of research and innovation in the fields of zoology and ecology (Newton, 2011).

Birds migrating over sea face a different set of challenges to those encountered by those migrating over land. In addition to being able to navigate over an apparently featureless ocean (Alerstam, 2006), they must also avoid unfavourable weather conditions, as the ocean offers nowhere to shelter or land, apart from the sea surface. Extreme weather at sea regularly leads to mass mortality events in many migratory species (Newton, 2007), including seabirds (Newton, 1998). In addition, wind conditions may strongly limit the timings of such migrations, for example they have been shown to limit the transatlantic crossing of shearwaters (Felicísimo, Muñoz, & González-Solís, 2008). Among these migrants, seabird species are restricted to the sea, and their remarkably long migrations mean that they have to stop and refuel (Shaffer et al., 2006; Guilford et al., 2009; Dias, Granadeiro, & Catry, 2013; Freeman et al., 2013). During these stopovers, seabirds are often faced with patchy and unpredictable resources (Dias, Granadeiro, & Catry, 2012; Mcknight, et al., 2013).

Unlike terrestrial migration, which can be monitored from known observation points along the flight paths of the birds, the journeys of migratory seabirds are difficult to study. Seabird biologists must rely on coastal sea watching and ship-based surveys (often restricted to main shipping pathways) (Camphuysen & Fox, 2004; Skov & Durinck, 2001) and ringing recoveries, all of which can be inaccurate and unrepresentative (Bairlein, 2001). As a result, far less is known about the migration of seabird species than of their terrestrial counterparts. Only since the availability of miniaturised tracking devices, mainly in the last decade, have researchers begun to fully understand the complex migratory behaviour of different seabird species (Nicholls & Robertson, 2007; Phillips et al., 2007; Nevitt, Losekoot, & Weimerskirch, 2008; Kubetzki et al., 2009; Carey, Meathrel, & May, 2009; Egevang & Stenhouse, 2010; Votier et al., 2010; Montevecchi et al., 2011; Guilford et al., 2011; Landers et al., 2011; Péron & Grémillet, 2013; Pollet et al., 2014; Thiebot et al., 2014; Ramos et al., 2015). Because of the unique challenges facing migrant seabirds and their potential value as indicators for the marine ecosystems they use throughout their life history (Einoder, 2009), fully understanding seabird migratory behaviour is of prime importance for marine conservation (Shaffer et al., 2006; Ballance, 2007; Wynn et al., 2007; Bauer & Hoye, 2014).

A major tool in the study of seabird migration has been the archival light-logger, the geolocator (or "global location sensor", GLS). This device provides twice daily positional estimates based on light curves, which, although relatively inaccurate when compared to GPS or satellite based trackers (Phillips, et al., 2004, Shaffer et al., 2005), perform well for recording long distance movements (more than 200km), especially given the device size (<2g) and longevity (> 1 year). As such, geolocators have revealed the migration of smaller (1kg and below) seabird species (Shaffer et al 2006, Gonzales-Solis 2007) Because of this a number of seabird species have now been tracked during the non-breeding period with great success (Militão, Bourgeois, Roscales, & González-Solís, 2013, Kubetzki et al., 2009, Harris et al., 2009, Bogdanova et al., 2011, Dias et al., 2011, Lorentsen & May, 2012, Mcknight et al., 2013, Hedd, Montevecchi, Phillips, & Fifield, 2014, Ratcliffe et al., 2014).

Despite the broad use of geolocators on seabird species, there have been comparatively few long-term studies using these devices, and even fewer investigating migratory behaviour simultaneously across several breeding colonies. Recent studies of other seabird species have shown that migratory behaviour differs between breeding populations of the same species, even when the non-breeding distribution is similar (Fort et al. 2012, Frederiksen et al. 2012, McFarlane Tranquilla et al. 2013, Ratcliffe et al. 2014). These differences can be in terms of changes to migratory timing, destination and potential effects of habitat change (McFarlane Tranquilla et al., 2013; Oro, 2014). Intraspecific variation can be an important factor in understanding behavioural plasticity within a species, and therefore the consequences of future environmental change for that species (Charmantier et al., 2008; Charmantier & Gienapp, 2014). These may be range shifts, switching to different food types and changes in timing. Intraspecific differences in migratory behaviour have been identified in a number of migratory avian species, both terrestrial (Delmore *et al.* 2012, Vardanis *et al.* 2011) and marine (Kubetzki *et al.* 2009, Phillips *et al.* 2005). These differences in behaviour within a species can provide evidence of individual specialisation, which has been identified in several seabird species (Furness et al., 2006; Phillips, Bearhop, McGill, & Dawson, 2009; Jaeger, Connan, Richard, & Cherel, 2010; Ceia & Ramos, 2015). Individual specialisation in migration strategy has implications for population resilience when faced with variability in the marine environment (Ceia & Ramos, 2015; Weimerskirch et al., 2015).

The longitudinal nature of the data presented in this thesis permits examination of behavioural variation within the UK Manx shearwater population. The aim of this chapter is to establish: whether migration behaviour (in terms of migration trajectory and distance) varies from one year to the next; if birds from different breeding colonies differ in their behaviour; if male and female birds differ in their behaviour; whether individual birds exhibit spatial fidelity both in the migratory route chosen and the over-wintering area from one year to the next. Individual fidelity in migration route and overwintering location will be discussed in terms of behavioural plasticity and life-history strategies. This chapter will improve understanding of migration behaviour in this species with regards to the potential ecological processes that underlie variation across this population.

This is the first time that seabird migration has been recorded from individual birds breeding on multiple colonies over an extended period of time. As over 90% of Manx shearwaters breed in the UK (Mitchell et al., 2004) this large sample, covering the main breeding range of the species, is likely to be representative of much of the global population. It is useful to compare the migration strategies and overwintering distribution of birds from different colonies and breeding circumstances in order to gain a complete picture of the migratory behaviour across the population. Many previous studies have focussed on a single-colony and may not be representative of the whole population. Indeed, differences in migratory destination have been found between seabirds from different colonies (for example: Atlantic puffins *(Fratercula arctica*, Harris et al., 2009; Guilford et al., 2011;) and more recently northern gannets (*Morus bassanus*, (Fort et al., 2012; Fifield et al., 2014;). Multi-colony studies are scarce but important, revealing important foraging hotspots for a species (Frederiksen et al. 2011) and identifying key threats (Fort et al., 2013).

Bird-borne loggers were used to describe the complete migration route and overwintering location of Manx shearwaters in 2006/2007, using data gathered from 12 individuals (Guilford et al., 2009). These birds were breeding on Skomer Island (UK) in 2006. Additionally, the study described stop-over behaviour and demonstrated the daily behavioural cycles that occur during migration. Over the six years following this 2006 study, geolocators have been deployed on over 140 individual Manx shearwaters, from five different breeding colonies around the UK (Isle of Rum, Scotland; Copeland Islands, Northern Ireland; Skomer and Ramsey Islands, Wales; and Lundy Island, England) see figure 1.1. Although an impressive tool for tracking long distance movements, geolocation data has significant positional error (Phillips et al., 2004). All location estimates used here to infer migration routes may not be exactly accurate. However the size of this dataset permits a high degree of confidence in the broad-scale movements recorded from this species.

3.2 Methods

The overall methods of bird capture, logger attachment, data collection and pre-processing are covered in detail in the methods section of chapter two, including the number of individuals tracked. Tables 2.1 and 2.2 in chapter two report the number of birds tracked from each breeding colony.

3.2.1 Processing migration trajectories and calculation of migratory distance

Migration tracks were obtained from geolocation light data and pre-processed using the methods described in chapter two. Since latitudinal estimates from GLS data are asymmetrically unreliable around the spring and autumn equinox (Hill & Braun, 2001), locations 7 days on the summer side and 21 days on the winter side of each equinox were labelled and omitted. To remove additional positional error, tracks were smoothed using a cubic spline interpolation method applied separately to longitude against time and latitude against time, each time using cubic spline smoothers with 10 degrees of freedom. All statistical analyses were performed on these smoothed data.

To determine the overwintering location areas for each track, all locations recorded between November 1st and January 1st were extracted (this period allowing for the latest arrival and earliest departure from overwintering area as determined by Guilford et al., 2009). These locations were then used to compute a median overwintering location for each track. Positional estimates falling within an 80% occupancy kernel for these points were considered to be during the bird's overwintering period. Locations with a longitude east of -10°W were excluded from the analyses as these are close to the breeding colony and likely correspond to the bird's breeding season. Overall migratory distances were calculated by summing great-circle distances between consecutive points across each southbound and each northbound migration track. Kernel density estimates, mean tracks and great circle distances were calculated with R version 3.0.2 (R core team, 2013).

3.2.2 Analysis of northbound migration route and overwintering location

Variation in northbound migration routes north of the equator (where significant variation in migratory routes was apparent) was investigated by comparing the degree of longitudinal variation of routes at fixed latitudes, following a similar methodology to Vardanis *et al.* (2011). For each northbound migration track, the longitude of the first position after crossing each of the following latitudes north of the equator: 0°; 10°; 20°; 30°; 40°; and 50° was extracted (using MATLAB: Mathworks, Natick, Mass.). These values were then compared across different individuals and colonies.

Kernel density estimation was used to calculate occupancy kernels from the overwintering locations for each track. All kernel density estimates were calculated using a grid size of 300 by 300 cells (with the dimensions of the grid varying according the range of latitudes and longitudes in the overwintering proportion of each track) and an optimum bandwidth selected by least-squares cross validation on all tracks using the "kernelUD" function in the R package adehabitat (Calenge, 2006).

For visualisation of overall migratory trends, a mean track for each individual, colony and year was calculated (Freeman et al., 2011). The yearly spatial median overwintering locations were calculated for each individual and for each of the five breeding colonies.

3.2.3 Statistical methods

Individual spatial fidelity in migration route was investigated using two statistical approaches. First, a spatial nearest neighbour analysis was performed on the smoothed migration tracks for both northbound and southbound migrations (Freeman et al. 2011, Guilford et al. 2011a). Nearest neighbour distances provide a metric of spatial dissimilarity between two tracks. For each location on a migration track, the distance to the nearest location on the comparison track is calculated. The degree of spatial similarity between a pair of tracks can then be quantified by the averaging of the distances from each point on track one to its nearest point on track two, and vice-versa. Hereafter we use the term nearest neighbour distance to refer to this average pointwise distance between two tracks. Low nearest neighbour distances therefore indicate high similarity between two tracks. Nearest neighbour distances between pairs of tracks were summarised by calculating the mean across all pairs within in the following four groups: within-individual (tracks by the same bird in different years); between-individual (tracks by different individuals in any years); within-colony (tracks by different birds within the same colony); and between-colony (tracks by birds in different colonies). Randomization tests were then used to determine whether mean nearest neighbour distances differed between the within-individual and between individual groups, or between the within-colony and between-colony groups. These two tests therefore assess the strength of evidence for individual and colony consistency in migratory route, and were each carried out for the southbound and northbound migrations separately.

As in Guilford et al., 2011, each randomization test yielded a p-value estimating the probability of seeing an absolute difference in the mean nearest neighbour distance between two groups at least as big as that observed from the data, simply by chance under a null hypothesis that there is no difference between the two groups. This was achieved by comparing the observed difference in mean nearest neighbour distances between the two groups with samples from the distribution of expected distances under this null model. Each sample from the null distribution was drawn by sampling two null groups of track pairs at random from the entire dataset of tracks; with the first null group containing the same number of pairs as the first observed group, and the second null group having the same number of pairs as the second observed group. The mean nearest neighbour distance over all pairs of tracks within each of these null groups was then calculated, and the difference between them taken as a single sample from the null distribution over expected distances. 100,000 samples were drawn from this distribution for each test, and the p-value was calculated as the proportion of these null samples with absolute value at least as big as the observed mean.

Whilst randomization tests of mean nearest neighbour distances between groups enable the identification of individual route fidelity across whole routes, it does not permit investigation into the relative importance of individual, annual or colony-level factors. A second analysis evaluated longitudinal differences in migration route at specific longitudes during the northern part of the return migration. At each of the following six latitudes (0°, 10°, 20°, 30°, 40° and 50°), the variation in longitude explained by colony, year and individual (nested within colony) was tested, using the same model-based comparison approach as in chapter two (see table 2.3 page 40).

Briefly, after determining the best-fitting model for each response variable by AIC, the importance of each of these predictors was evaluated by model comparison tests and the marginal and conditional R-squared values of the best-fitting model were calculated (after Nakagawa & Schielzeth, 2013) in order to partition the variance in longitudinal crossing points between the explanatory variables. Because sex was not known for all birds, its effects on migratory route were investigated by fitting additional models to the subset of the data for which sex data were available (231 northbound migrations out of 275). For each latitude, the best fitting model from the previous analysis was refitted to the smaller subset and compared with a model with sex added as an additional fixed-effect term. In order to test individual consistency in the northern portion of the migration route, a repeatability analysis was conducted on these longitudinal data using methods developed by Nakagawa & Schielzeth, 2010.

Occupancy kernels for the overwintering areas were analysed using randomization tests to investigate differences between years, colonies and individuals. For each test, the mean percentage kernel overlap between kernels in each group (i.e. each year, colony or individuals for those with multiple tracks) was compared against a null distribution of mean overlaps calculated by randomising membership of each track to these groups (Breed et al., 2006). Percentage overlap was measured as the volume of the intersection between the two estimated density functions, avoiding the need to condition the test on a specific occupancy threshold. Randomization tests were carried out in R using kernel density estimation and overlap functions from the adehabitat package.

3.3 Results

The broad movement patterns and overwintering locations of Manx shearwaters was similar across all years, colonies and individuals and was similar to those found by Guilford et al. (2009). Figures 3.1-3.4 display overall mean tracks for each of the five breeding colonies. Birds left the breeding colonies and flew south along the west coast of Europe and northern Africa, before crossing the Atlantic around the Equator and continuing south along the east coast of South America. The wintering area was an extensive region along the coast of Argentina. The northbound migration followed a reverse route along the coast of South America, after which birds varied in the degree of clockwise, westerly movement into the Caribbean before crossing the North Atlantic. Figures 3.2 to 3.5 illustrate the mean migration pathways recorded from each colony, along with the smoothed position estimates from all tracked birds.

3.3.1 Colony differences in migration path

Shearwaters from different breeding colonies differed on their southbound migration routes (figure 3.1). In particular, most birds from Rum showed a northerly movement away from the colony before flying south. Within-colony pairs of tracks showed highly similar routes, with a mean nearest-neighbour distance of 1006.7km (1039.5 km s.d., n = 675). Within-colony pairs of tracks were significantly more similar than between-colony pairs of tracks, which had a mean nearest neighbour distance of 1151.7km (1417.7 km s.d., n = 1071; difference = 145.028 km, p = 0.023).

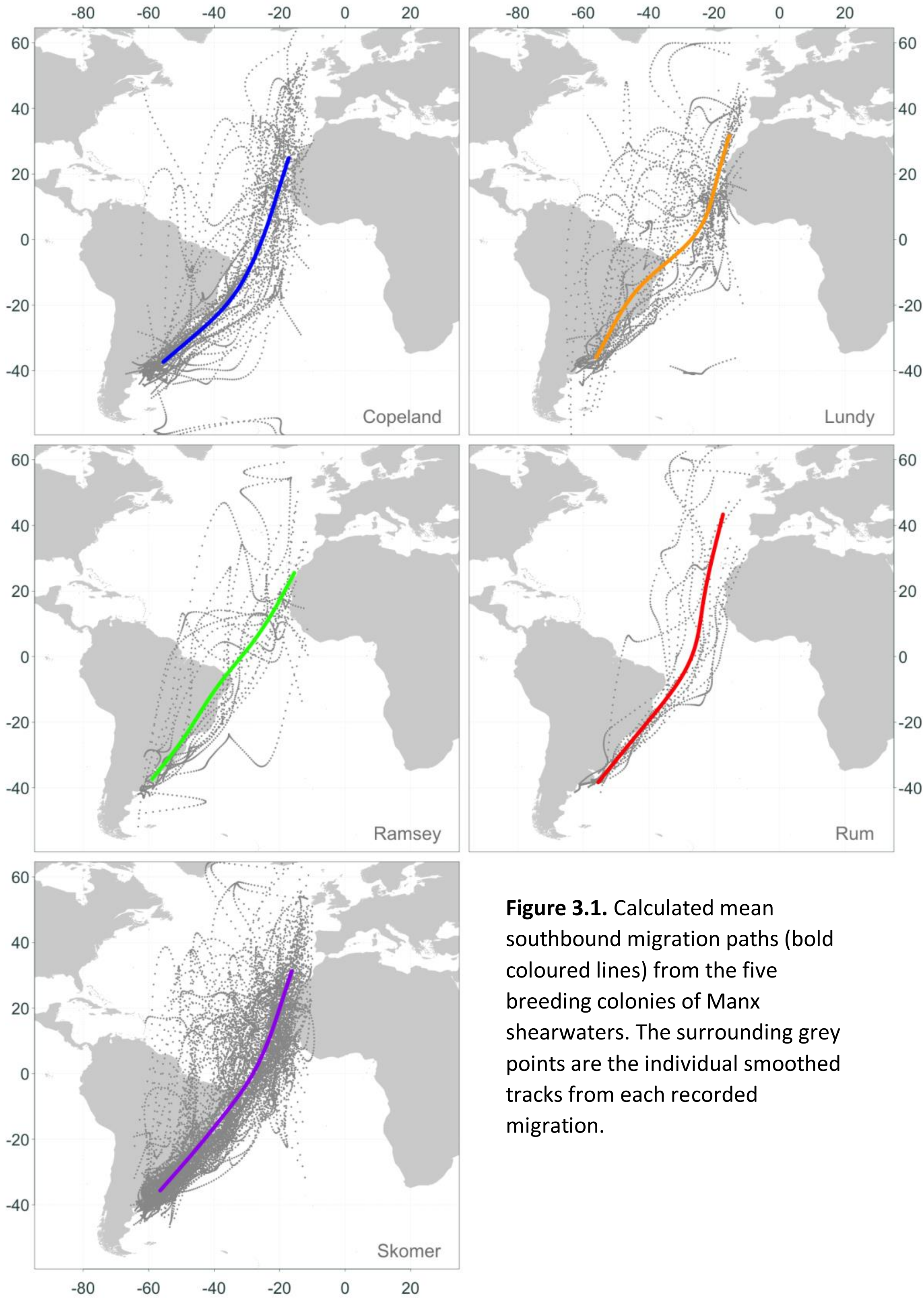

Figure 3.1. Calculated mean southbound migration paths (bold coloured lines) from the five breeding colonies of Manx shearwaters. The surrounding grey points are the individual smoothed tracks from each recorded migration.

Colony differences were less apparent during the northbound (pre-breeding) migration (figure 3.2). Within-colony pairs of tracks showed highly similar routes, with a mean nearest-neighbour distance of 672.9km (305.2 km s.d., n = 3634). Within-colony pairs of tracks were significantly more similar than between-colony pairs of tracks, which had a mean nearest neighbour distance of 713.5km (467 km s.d., n = 4038; difference = 40.547 km, $p < 0.001$).

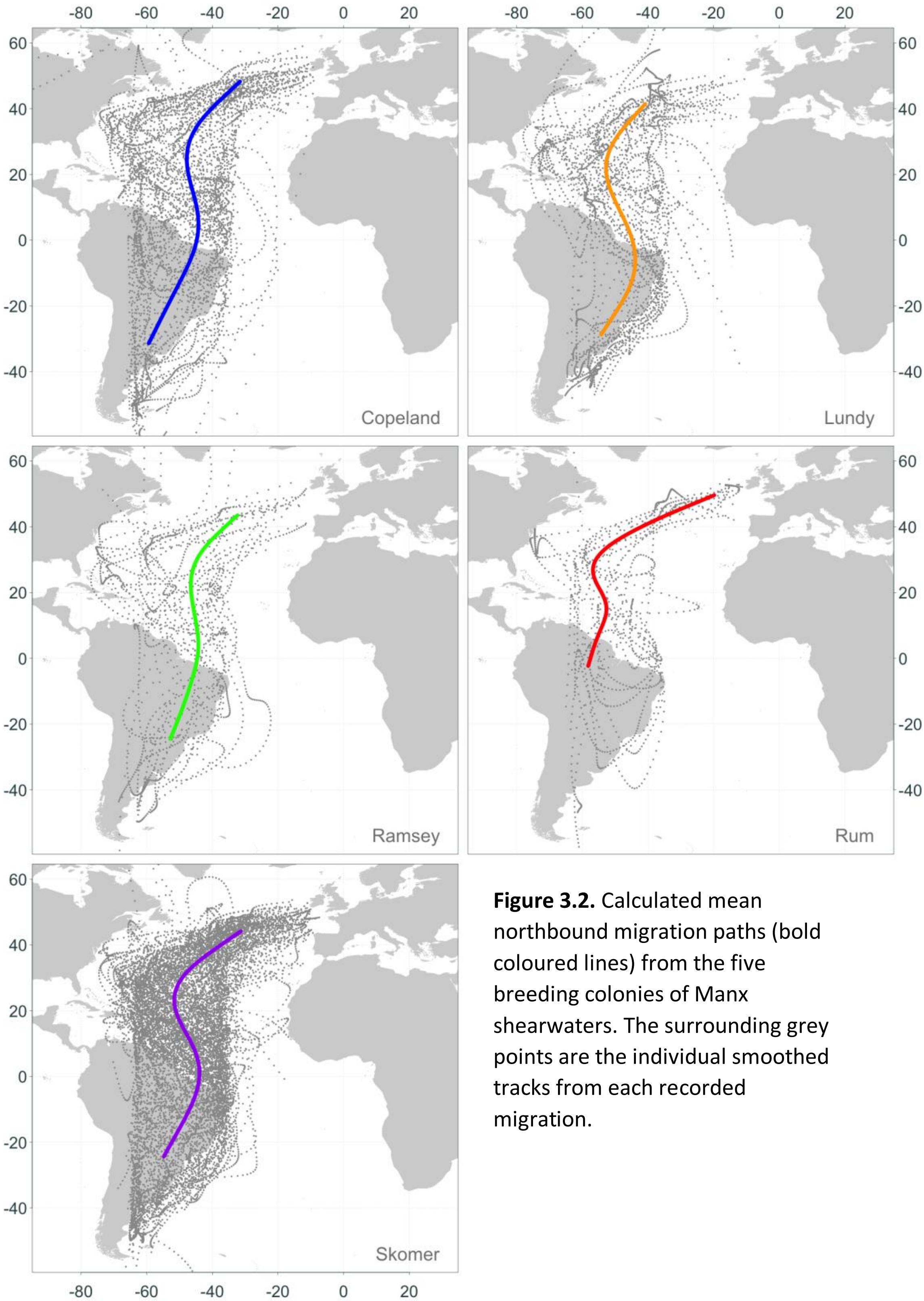

Figure 3.2. Calculated mean northbound migration paths (bold coloured lines) from the five breeding colonies of Manx shearwaters. The surrounding grey points are the individual smoothed tracks from each recorded migration.

Further analyses into the degree of longitudinal movement during the second half of the northbound migration revealed significant differences between colonies in the longitude at which birds crossed latitude 40° and 50° (table 3.1, figures 3.3 to 3.5).

Table 3.1. Summary of linear mixed effects model outputs examining the effects of year, colony and individual on the degree of longitudinal variation in the northbound migration route. Significant (<0.05) p-values are highlighted in grey.

Response Variable	**Colony (fixed effect)**	**p-value**	**Year (fixed effect)**	**p-value**	**R2 model**	**R2 fixed effects**	**R2 random effects**	**Individual repeatability (standard error)**	**p-value**
Longitude at latitude 0	F_4=0.205	0.935	F_5 =2.346	0.044	0.203	0.066	0.137	0.091 (0.098)	0.053
Longitude at latitude 10	F_4=0.88	0.478	F_5 =3.914	0.002	0.26	0.103	0.157	0.07 (0.080)	0.07
Longitude at latitude 20	F_4=0.991	0.415	F_5 =3.241	0.008	0.317	0.747	0.242	0.181 (0.086)	0.013
Longitude at latitude 30	F_4=2.388	0.542	F_5 =3.781	0.003	0.282	0.093	0.189	0.194 (0.090)	0.007
Longitude at latitude 40	F_4=7.653	<0.001	F_5 =0.796	0.553	0.175	0.127	0.048	0.212 (0.084)	0.002
Longitude at latitude 50	F_4=4.131	0.005	F_5 =0.232	0.947	0.204	0.204	0.001	0.158 (0.212)	0.025

3.3.2 Yearly differences in migration pathway

We found significant differences in longitude of migration route during the earlier half of the northbound migration between years at 0°, 10°, 20° and 30° latitudes (table 3.1), but not in the higher latitudes. There were no significant trends across years, however, northbound migration taking place in 2012 followed a route consistently further to the west (between 5-10° longitude lower than the overall mean) than in previous years (figures 3.6-3.8).

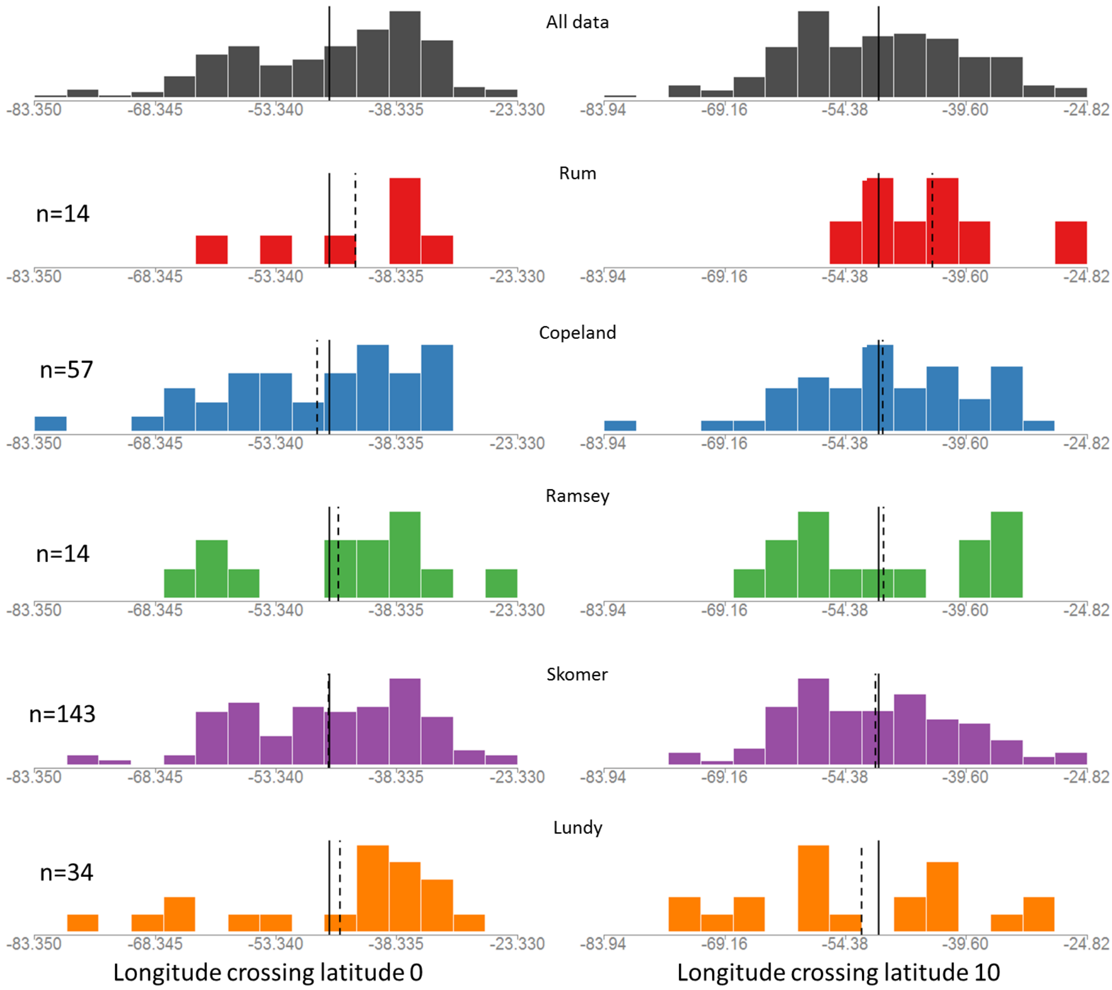

Figure 3.3. Frequency histograms showing colony differences in the longitude at which Manx shearwaters cross latitude 0° and 10° during the northbound migration. The top histogram shows all data, from all colonies. The rest of the plots are in order of decreasing colony latitude; Rum (red), Copeland (blue), Ramsey (green), Skomer (purple) and Lundy (orange). Vertical lines show the colony mean (dashed) and overall mean.

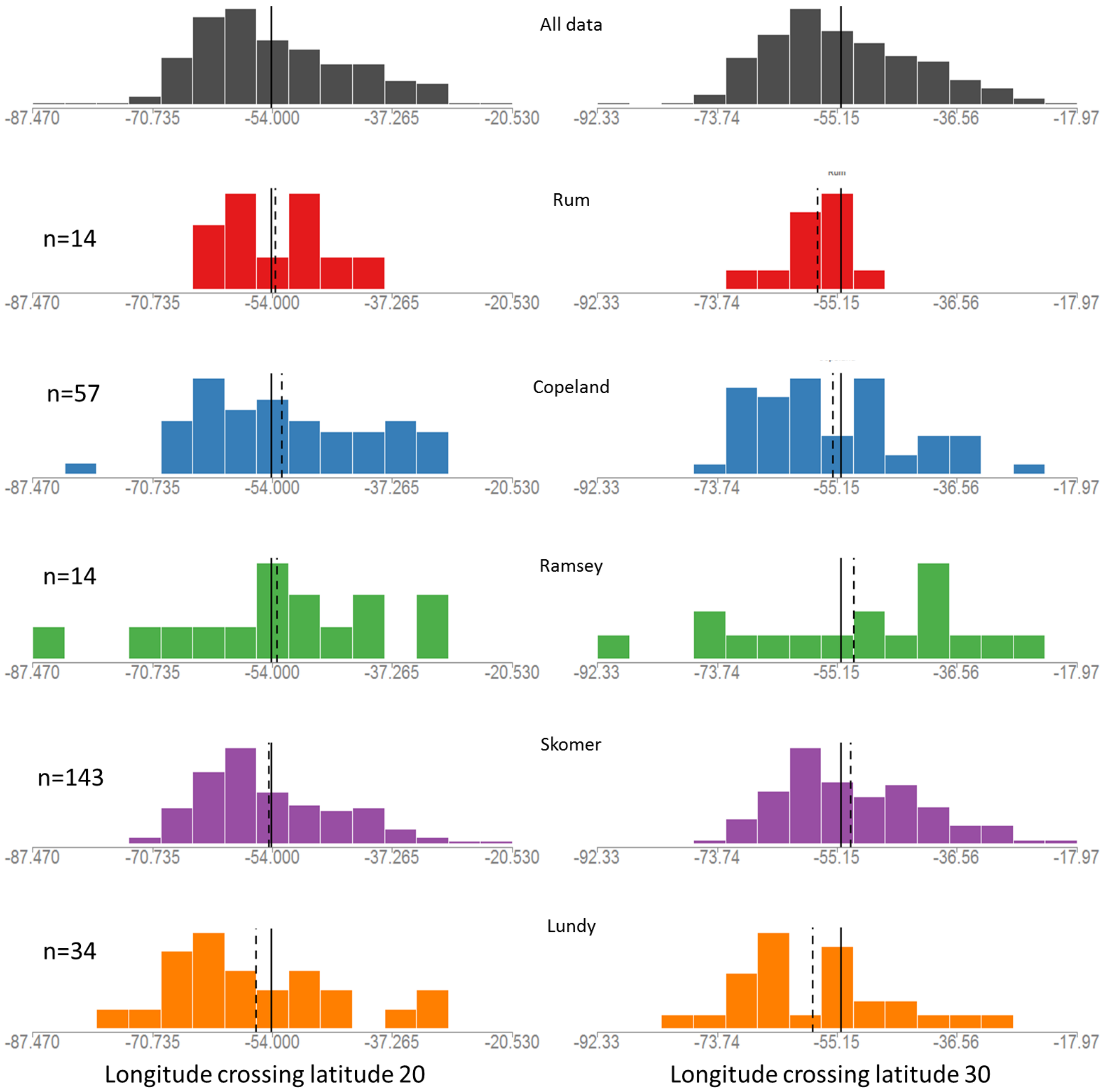

Figure 3.4. Frequency histograms showing colony differences in the longitude at which Manx shearwaters cross latitude 20° and 30° during the northbound migration. The top histogram shows all data, from all colonies. The rest of the plots are in order of decreasing colony latitude; Rum (red), Copeland (blue), Ramsey (green), Skomer (purple) and Lundy (orange). Vertical lines show the colony mean (dashed) and overall mean.

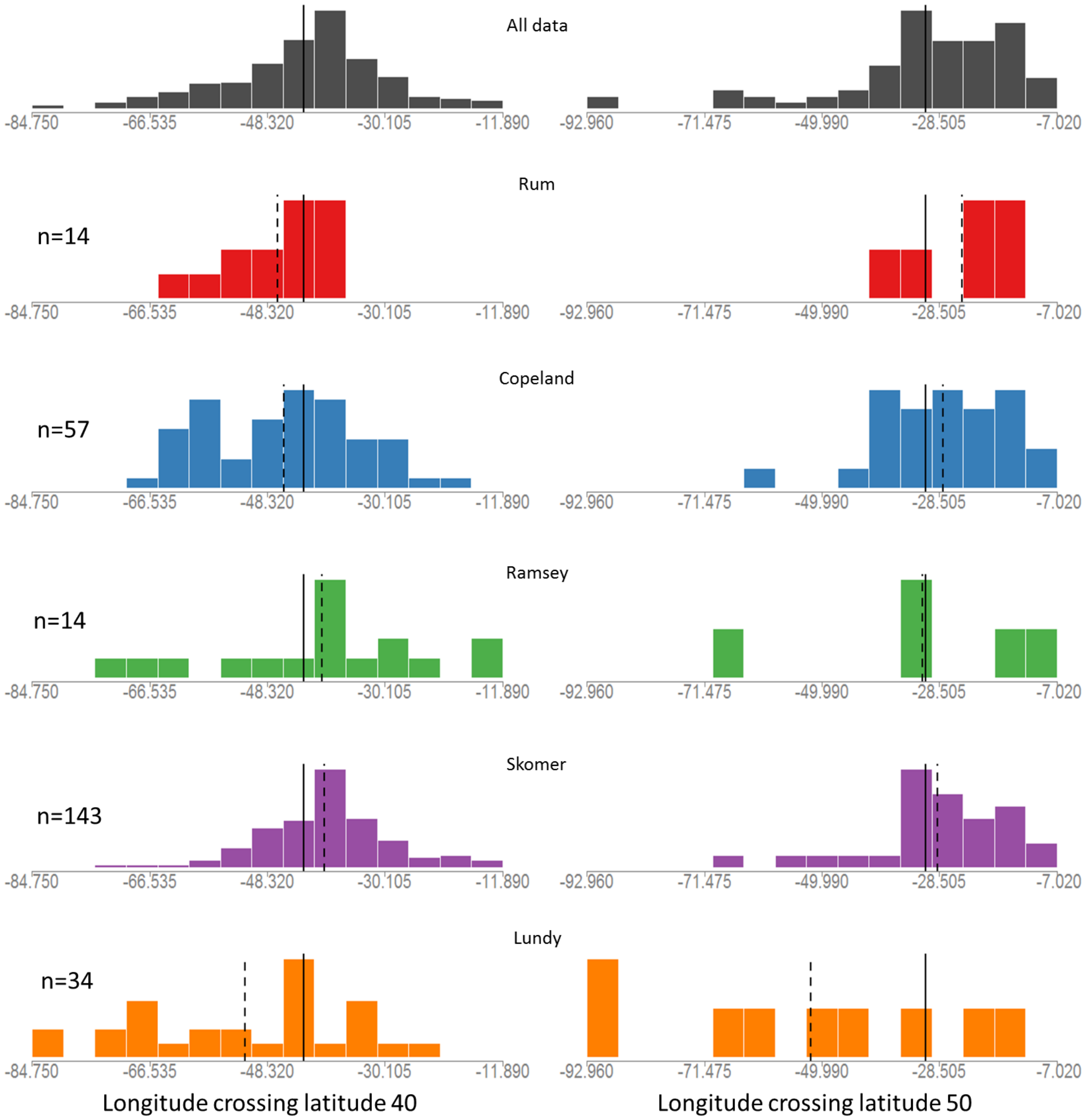

Figure 3.5. Frequency histograms showing colony differences in the longitude at which Manx shearwaters cross latitude 40° and 50° during the northbound migration. The top histogram shows all data, from all colonies. The rest of the plots are in order of decreasing colony latitude; Rum (red), Copeland (blue), Ramsey (green), Skomer (purple) and Lundy (orange). Vertical lines show the colony mean (dashed) and overall mean

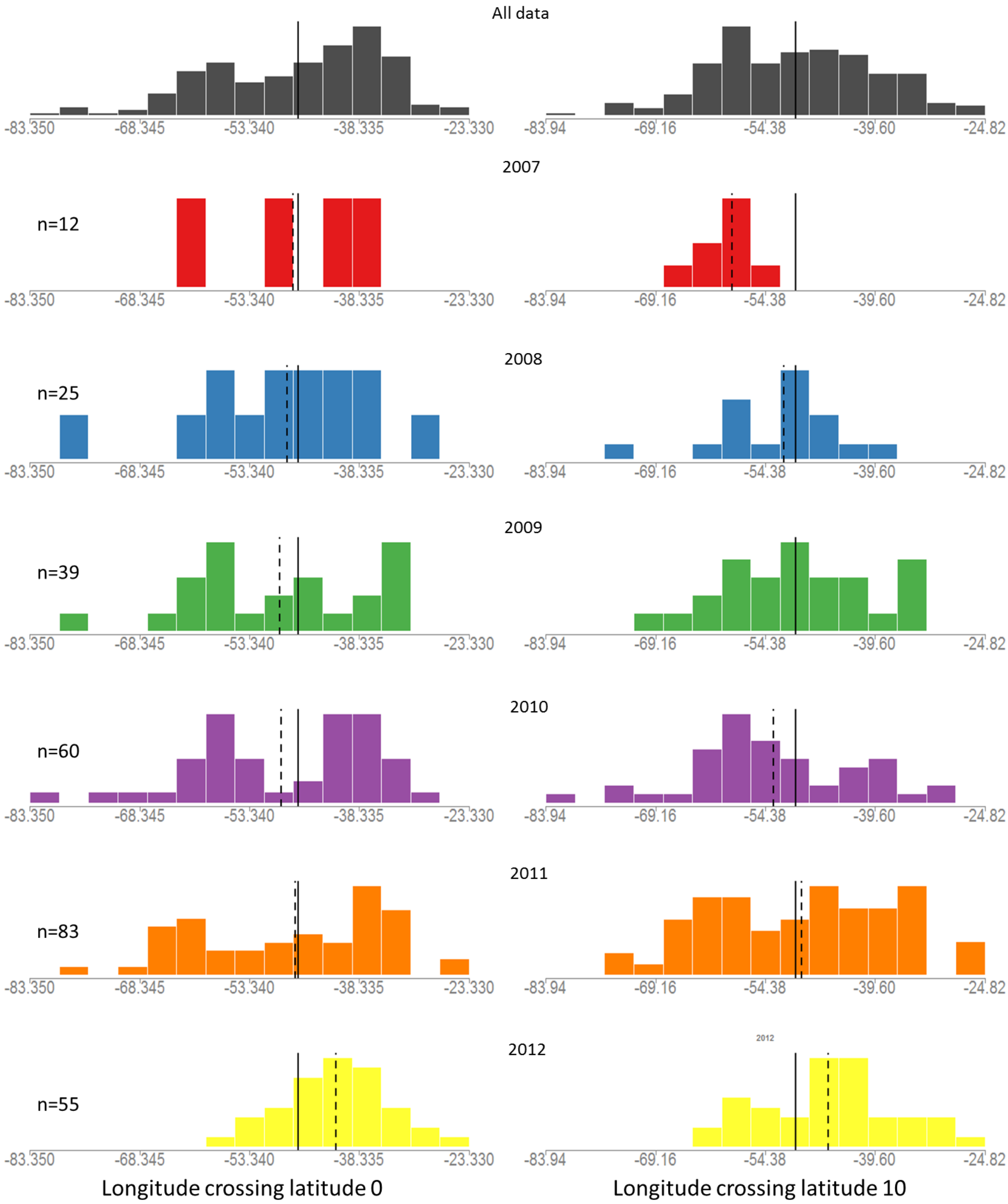

Figure 3.6. Frequency histograms showing yearly differences in the longitude at which Manx shearwaters cross latitude 0° and 10° during the northbound migration. The top histogram shows all data, from all years. The rest of the plots are in order of increasing year; 2007 (red), 2008 (blue), 2009 (green), 2010 (purple) and 2011 (orange), 2012 (yellow). Vertical lines show the yearly mean (dashed) and overall mean.

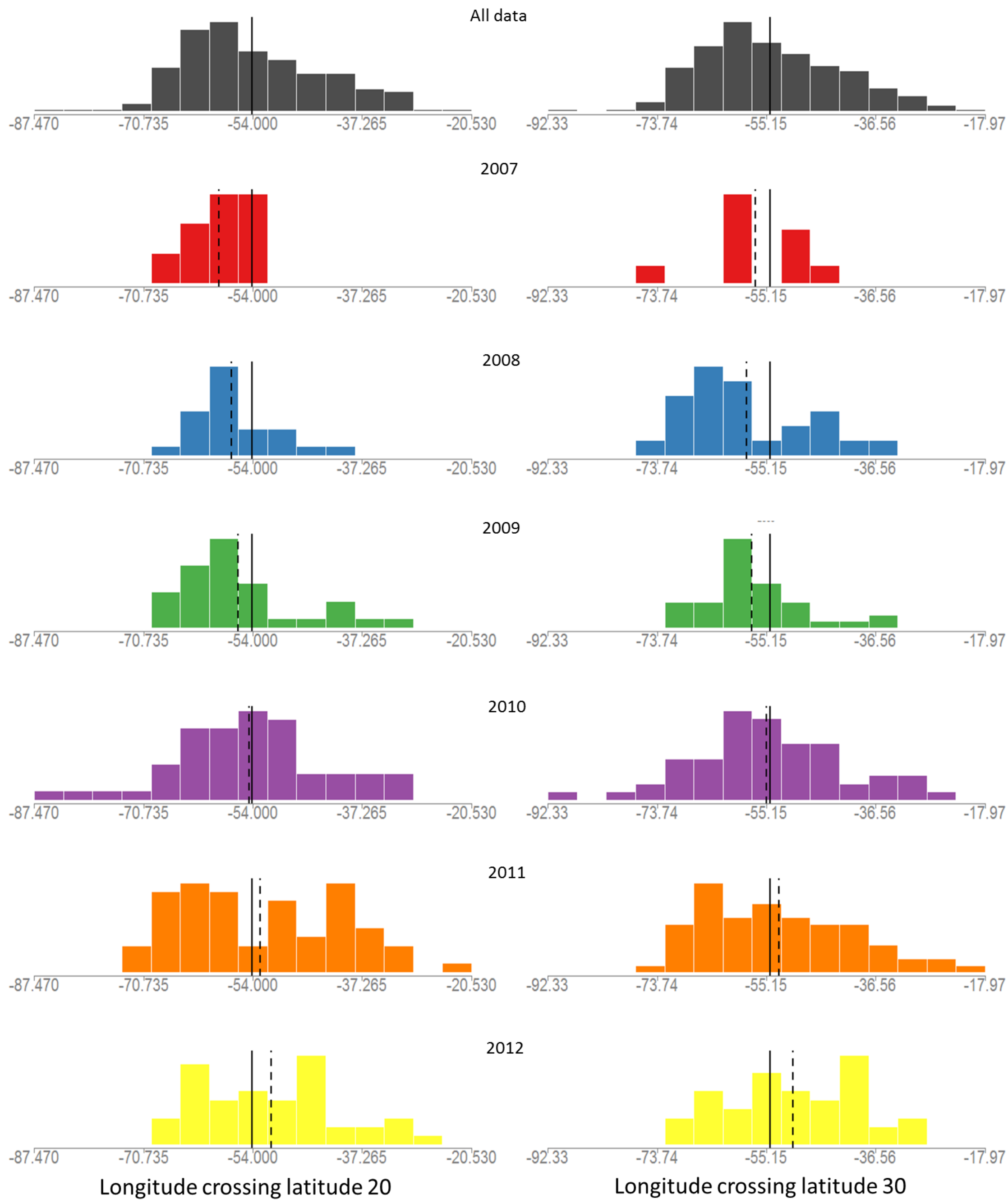

Figure 3.7. Frequency histograms showing yearly differences in the longitude at which Manx shearwaters cross latitude 20° and 30° during the northbound migration. The top histogram shows all data, from all years. The rest of the plots are in order of increasing year; 2007 (red), 2008 (blue), 2009 (green), 2010 (purple) and 2011 (orange), 2012 (yellow). Vertical lines show the yearly mean (dashed) and overall mean.

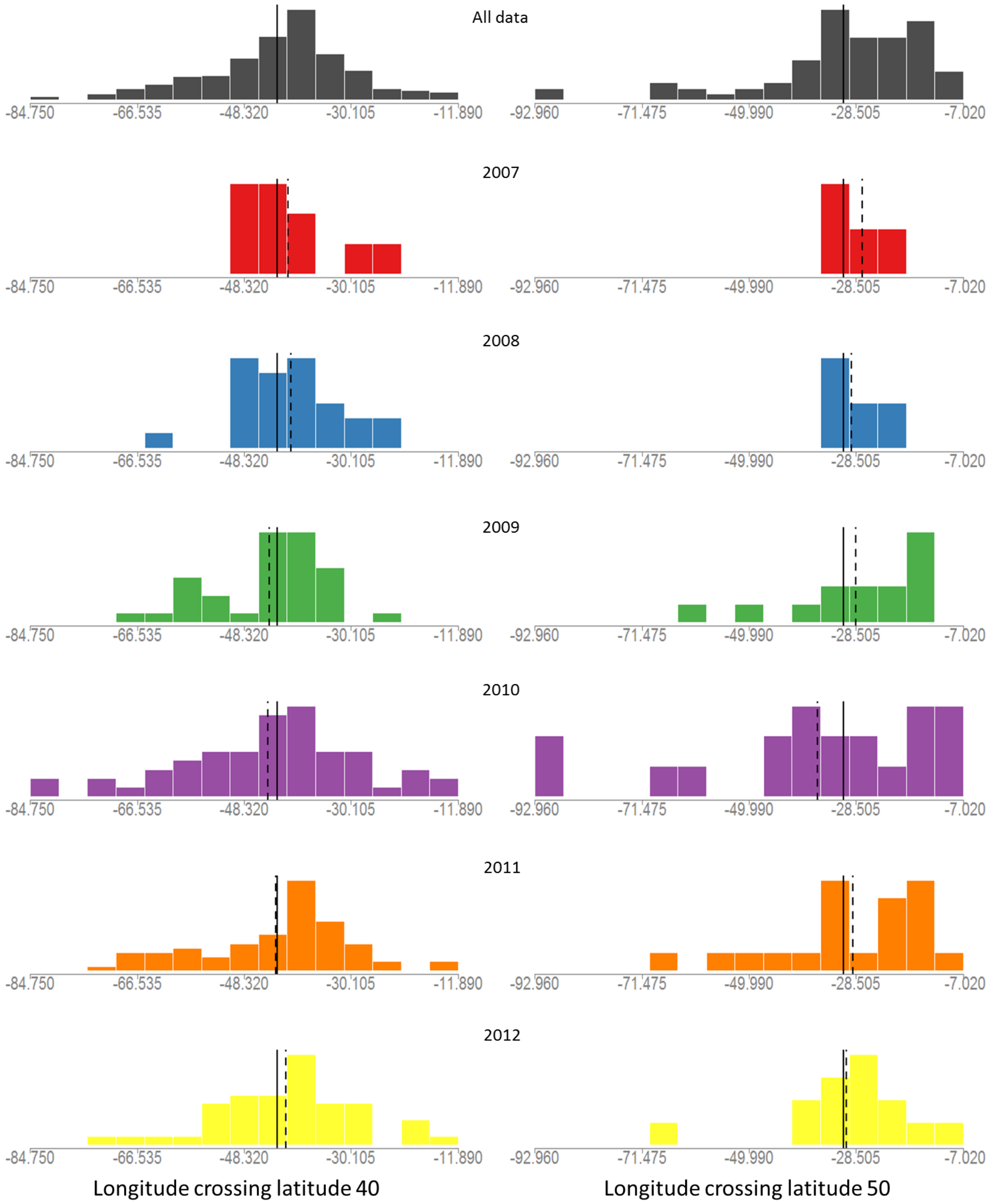

Figure 3.8. Frequency histograms showing yearly differences in the longitude at which Manx shearwaters cross latitude 40° and 50° during the northbound migration. The top histogram shows all data, from all years. The rest of the plots are in order of increasing year; 2007 (red), 2008 (blue), 2009 (green), 2010 (purple) and 2011 (orange), 2012 (yellow). Vertical lines show the yearly mean (dashed) and overall mean.

3.3.3 Individual variation in the migration route.

Considerable inter-individual variation in migration route was found in both southbound (Appendix 3A) and northbound migrations (Appendix 3B). However individual variation did not account for a significant proportion of the overall variation during the southbound migration. Within-individual pairs of tracks showed highly similar southbound routes, with a mean nearest-neighbour distance of 678.9km (1208.9 km s.d., n = 24). Within-individual nearest neighbour distance was lower than between individual nearest neighbour distance, which had a mean nearest neighbour distance of 1095.7km (1286.4 km s.d., n = 1746) but the difference was not statistically significant (difference = 416.772 km, p = 0.108). Nearest neighbour analysis of the northbound migration route showed that within-individual pairs of tracks had highly similar routes, with a mean nearest-neighbour distance of 454.5km (258.1 km s.d., n = 78). Within-individual pairs of tracks were significantly more similar than between-individual pairs of tracks, which had a mean nearest neighbour distance of 694.3km (399.1 km s.d., n = 7672; difference = 239.793 km, p < 0.001). Repeatability analysis indicated the same pattern, with the degree of westerly movement being consistent within individuals (table 3.1). The main source of variation between individuals during the pre-breeding migration occurred after the birds had passed the north-eastern coast of Brazil. Here some individual birds entered the Caribbean, recording a more westerly longitude (less than -60 degrees) whereas others continued north on a more direct route back across the North Atlantic (figure 3.9 & 3.10).

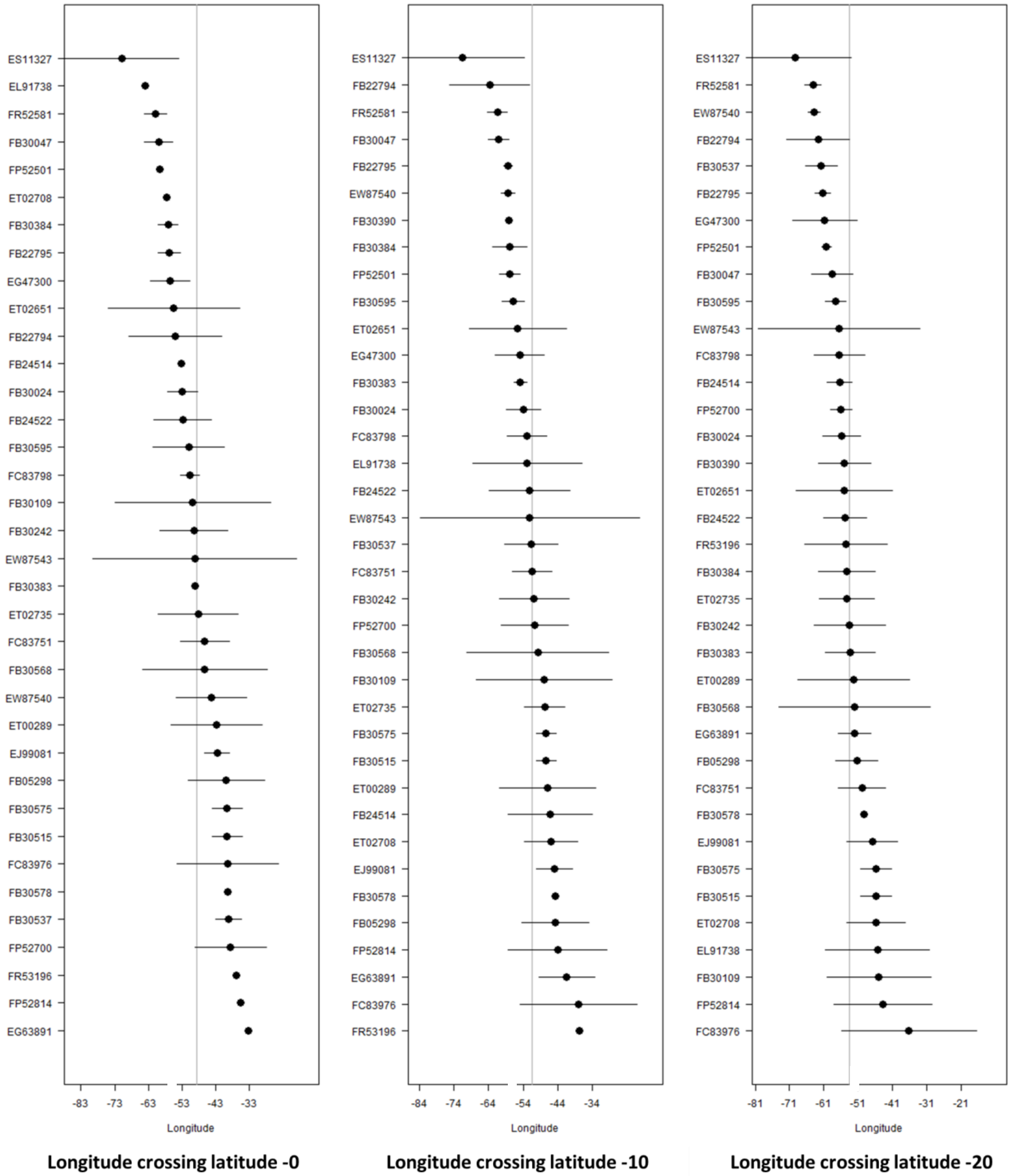

Figure 3.9. Individual variation in longitudes recorded on northbound migration, as the birds crossed latitudes 0°, 10° and 20° north. Each line shows 3 or more years of data from one individual bird, the black dot showing the mean longitude. Individual fidelity in migration route is shown by the spread of the standard deviation bars for each individual (black horizontal lines).

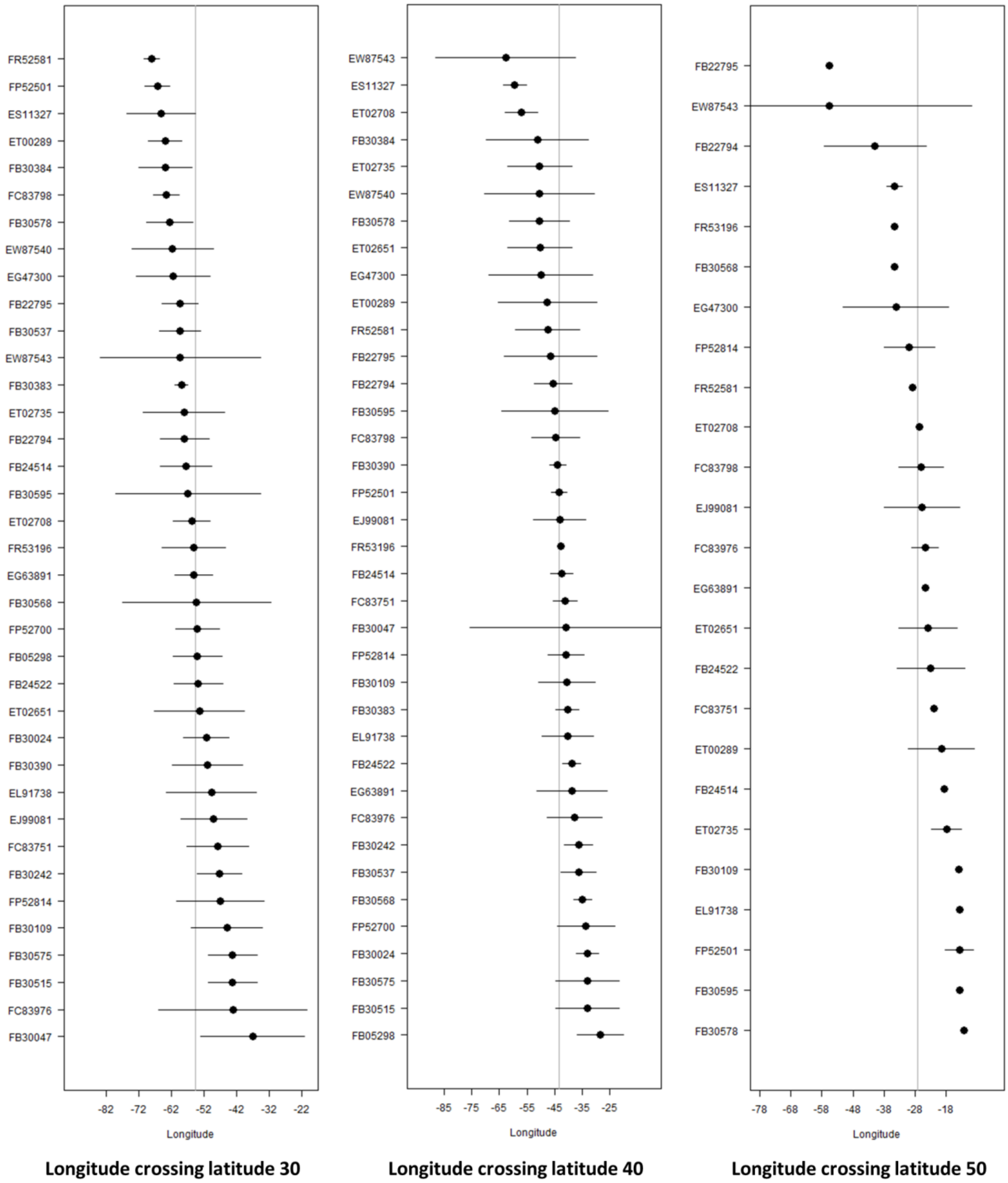

Figure 3.10. Individual variation in longitudes recorded on northbound migration, as the birds crossed latitudes 30°, 40° and 50° north. Each line shows 3 or more years of data from one individual bird, the black dot showing the mean longitude. Individual fidelity in migration route is shown by the spread of the standard deviation bars for each individual (black horizontal lines).

3.3.4 Sex differences in migration route

There were no consistent differences between male and female Manx shearwaters throughout both migration paths. This was true even for the most variable section of the pre-breeding migration route, crossing the northern part of the Atlantic (figures 3.11 to 3.12). Linear mixed effects models showed no differences between the longitude at which males and females crossed the 0° (F_1=1.208, p=0.275), 10° (F_1=1.357, p=0.248), 20° (F_1=0.323, p=0.571), 30° (F_1=1.716, p=0.195), 40° (F_1=0.269, p=0.605), 50° (F_1=0.013, p=0.909) lines of latitude north of the equator.

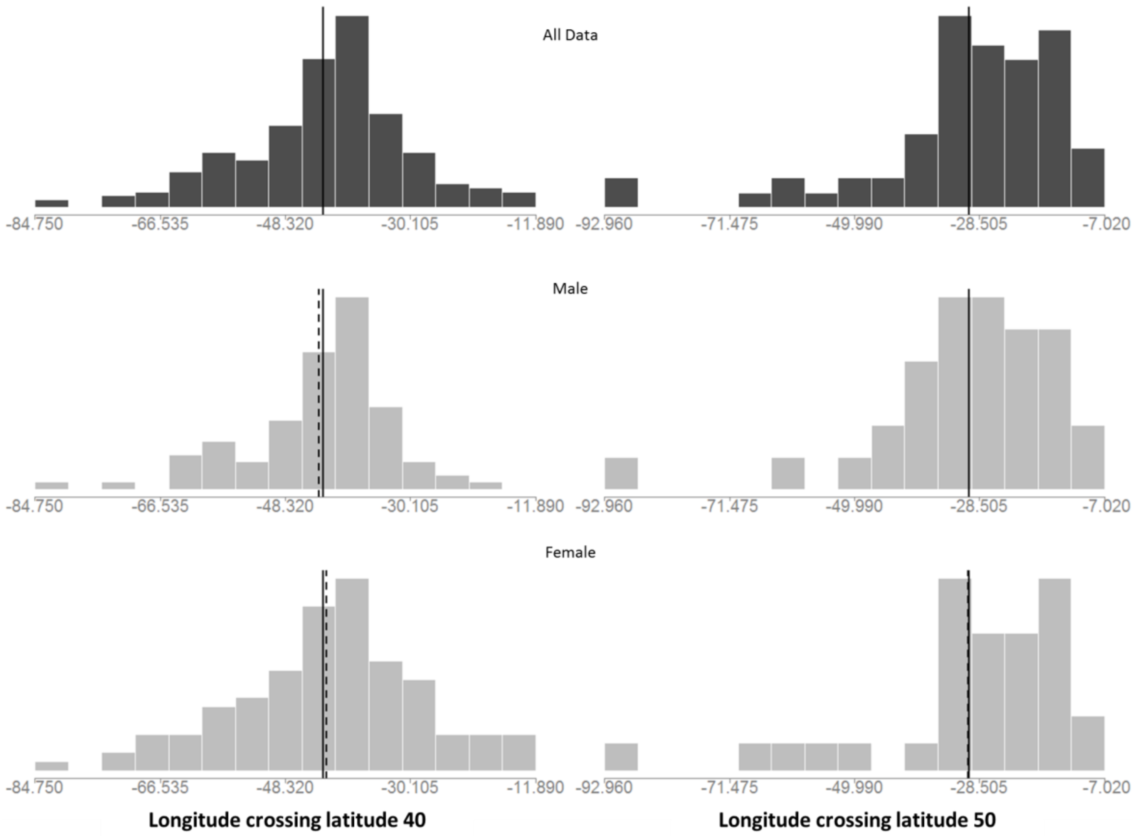

Figure 3.11. Frequency histograms showing sex differences in the longitude at which Manx shearwaters cross latitudes 40° & 50° during the northbound migration. The top histograms show all data, from all years. The middle plot shows data collected from male birds, the bottom female. Vertical lines show the yearly mean (dashed) and overall mean.

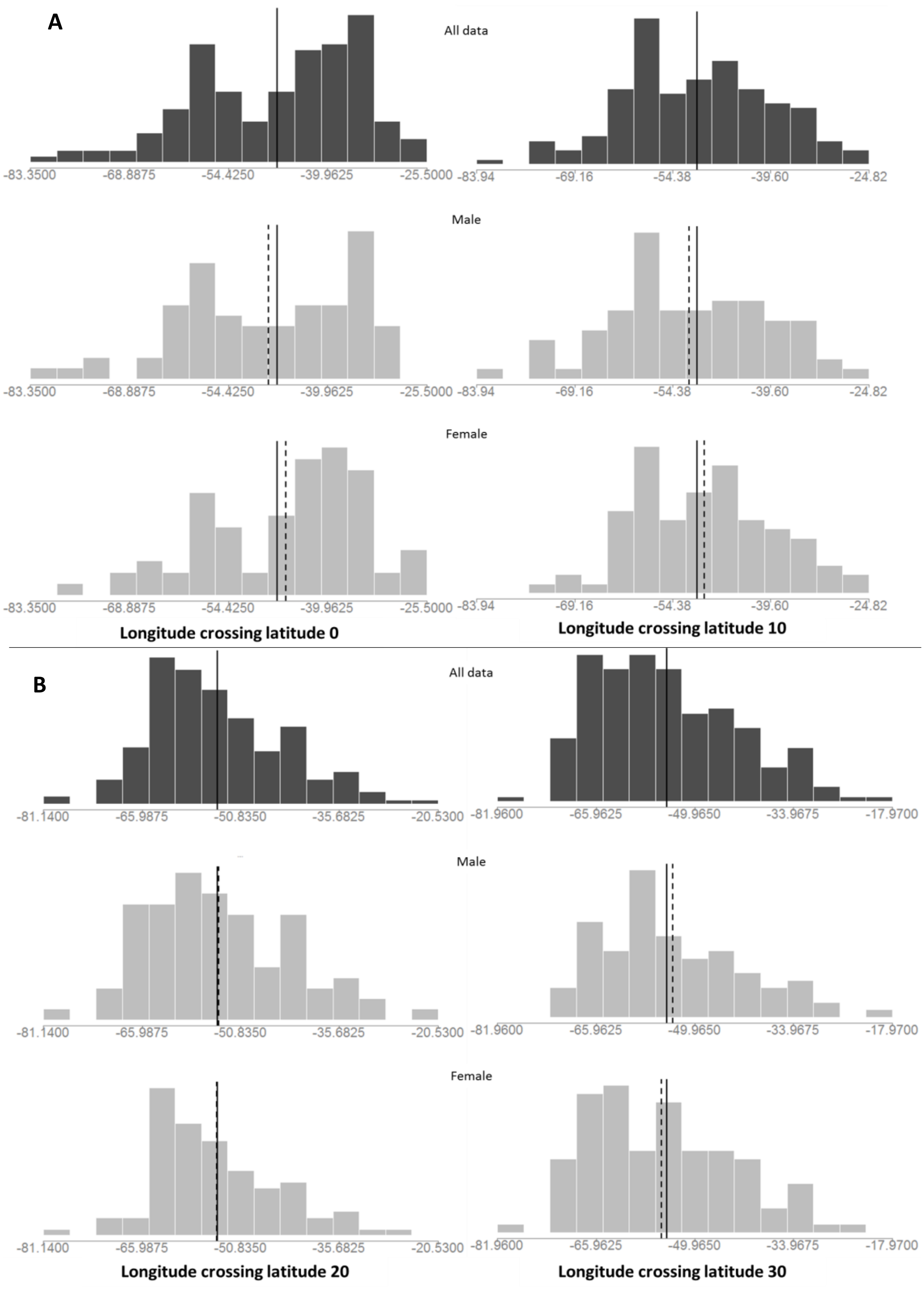

Figure 3.12. Frequency histograms showing sex differences in the longitude at which Manx shearwaters cross latitudes 0°, 10° (A) and 20°, 30° (B) during the northbound migration. The top histograms in each plot show all data, from all years. The middle plot shows data collected from male birds, the bottom female. Vertical lines show the yearly mean (dashed) and overall mean.

3.3.5 Migration distance

Total migratory great-circle distances were calculated for each southbound and each northbound track. There were no significant patterns when comparing birds from different colonies, in different years or between the sexes (table 3.2). Shearwaters breeding on Rum appeared to travel further (around 2100km on the southbound migration, 400km on northbound) than those from other colonies but this difference was non-significant.

Table 3.2. Total distance of migration track recorded for each colony. Breeding colonies are ordered by latitude. The dark vertical line in the middle of each plot shows the median distance.

SOUTHBOUND MIGRATION DISTANCE									
2006	**2007**	**2008**	**2009**	**2010**	**2011**	**F**	**p**	**R2-fixed**	**R2-random**
7750 2794	9125 2807	9003 7321	10286 4927	12375 7606	9825 4352	1.736	0.812	0.088	0.462
Rum	**Copeland**	**Ramsey**	**Skomer**	**Lundy**		**F**	**p**	**R2-fixed**	**R2-random**
13364 5616	8984 4016	11238 5336	9943 6736	11204 5607		0.394	0.137	0.088	0.462
Male	**Female**					**F**	**p**	**R2-fixed**	**R2-random**
9293 3970	11402 7660					0.109	0.743	0.046	0.253
NORTHBOUND MIGRATION DISTANCE									
2007	**2008**	**2009**	**2010**	**2011**	**2012**	**F**	**p**	**R2-fixed**	**R2-random**
20777 5378	17155 8305	16458 7474	18766 11701	16389 4918	14912 4459	1.561	0.173	0.036	0.230
Rum	**Copeland**	**Ramsey**	**Skomer**	**Lundy**		**F**	**p**	**R2-fixed**	**R2-random**
17456 2942	17261 6441	17117 6476	16642 9008	16935 5315		0.376	0.826	0.036	0.230
Male	**Female**					**F**	**p**	**R2-fixed**	**R2-random**
17263 10444	16516 5272					0.109	0.743	0.046	0.253

3.3.6 Overwintering Areas

Manx shearwaters from the five breeding colonies in this study all migrated to a large area off the coast of Argentina and Uruguay (table 3.3, figure 3.13). The only exception to this trend was one individual from the Lundy Island colony (FB32225, see figure 3.14), which overwintered in an area of the Atlantic north of Brazil and east of the Caribbean for two consecutive years (2011, 2012). When the percentage overlap in wintering location was compared across years (accounting for variation between colonies and individuals) there was no significant difference (mean overlap 67.7%, s.d. 3.94%, p=0.251). Similarly, the mean overlap in overwintering area of 68.3% (s.d. 3.7%; figure 3.18 inset) indicated no significant difference between colonies (p=0.054).

Table 3.3. Median overwintering locations and variance for each breeding colony. One bird from Lundy show an overwintering location much further north of the area used by all the other birds, leading to the higher variance in the Lundy latitude records.

Colony	Med Lat	Var (degrees)	Med Long	Var (degrees)
Rum	-39.74	21.17	-60.17	16.03
Copeland	-40.95	24.96	-61.66	10.69
Ramsey	-39.98	25.53	-61.29	15.84
Skomer	-40.01	23.05	-61.26	15.37
Lundy	-38.2	112.81	-60.72	20.04

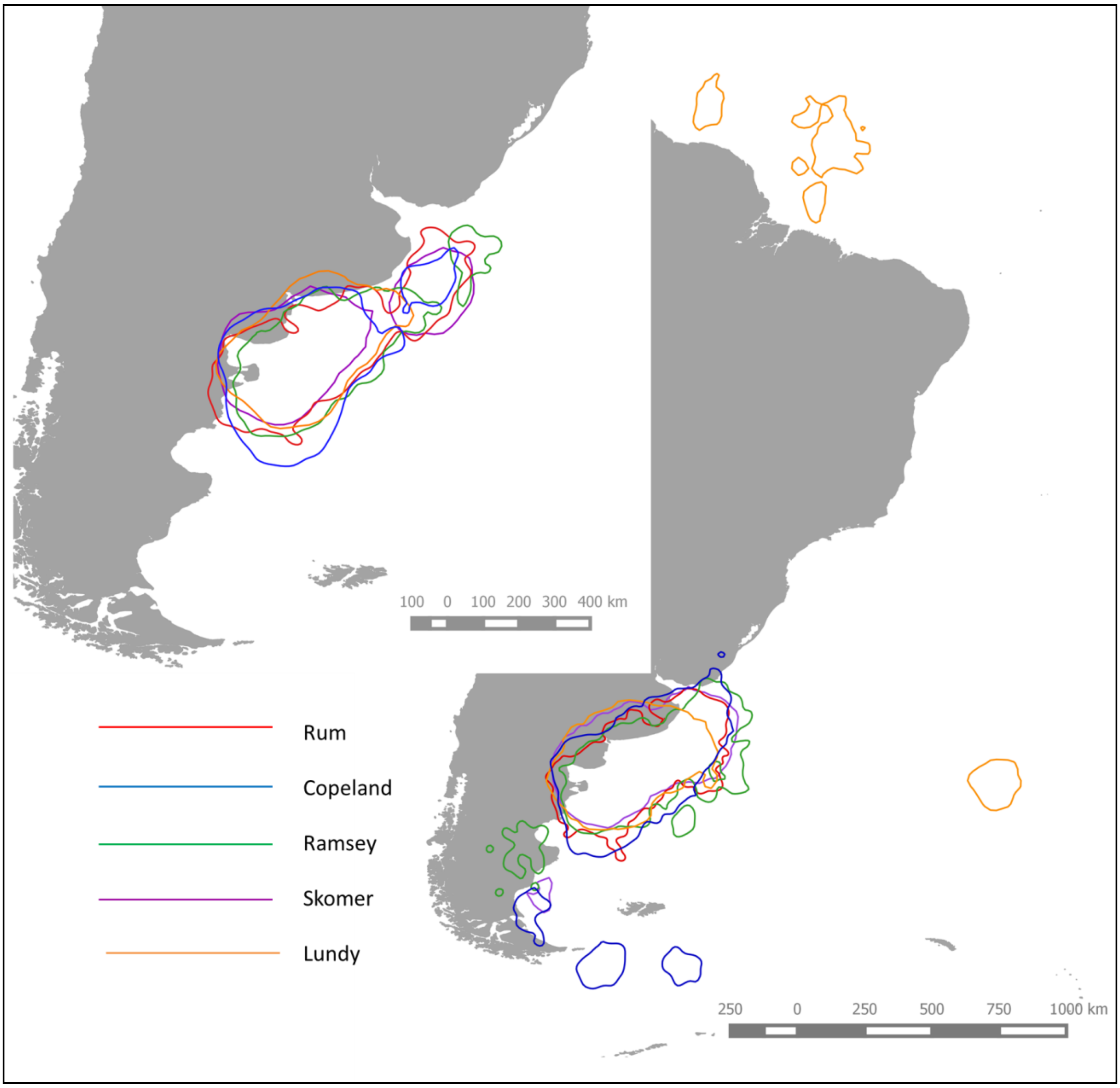

Figure 3.13. Kernel density estimates for the overwintering distribution of Manx shearwaters from different breeding colonies. 95% occupancy and 75% occupancy (inset).

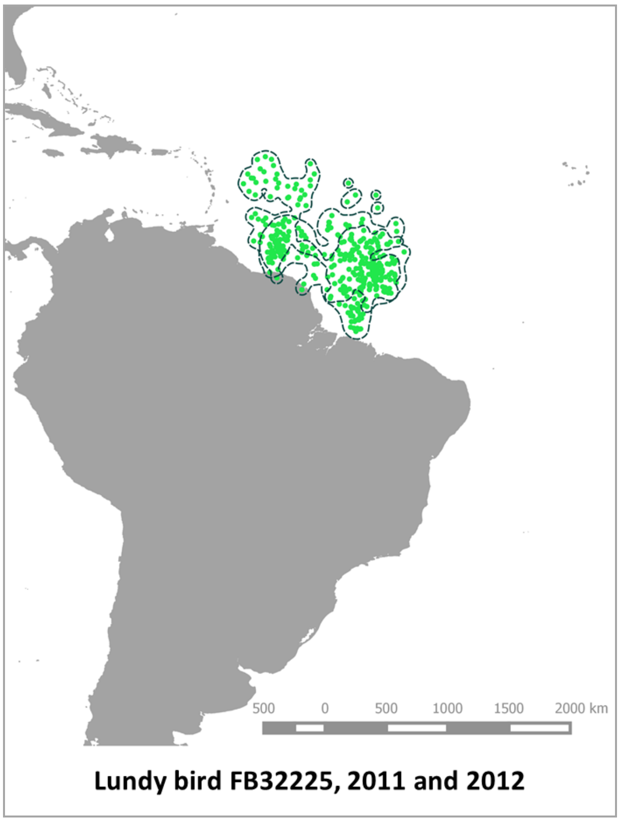

Figure 3.14. Kernel density estimates (95%) and raw location points for the one shearwater that overwintered north of Brazil.

Overwintering area use was highly conserved within individual Manx shearwaters. Birds returned to a similar region in the south Atlantic from one year to the next. Occupancy kernels for each overwintering area were compared between and within individual shearwaters, showing a significantly higher degree of overlap within repeated annual records for individual birds (p<0.001, randomisation test). Appendix 3C illustrates the degree of overwintering site fidelity for Manx shearwaters tracked for two or more years.

3.4 Discussion

The Manx shearwater migration pathway illustrated here is consistent with findings from previous geolocation studies on this species, although these followed birds from Skomer (Guilford et al*.* 2009) and Copeland (Freeman et al*.* 2013) only. Although there were some differences, the general route remains the same over six consecutive years (2006-2012), across a large number of individual birds and across 5 breeding colonies. After leaving the breeding colony in late September birds fly south along the west coast of Europe and Africa, crossing the Atlantic Ocean at the narrowest point and continuing along the east coast of South America. Shearwaters arrive at the main overwintering location off the coast of Argentina in late October and remain there for around four months. On leaving the overwintering area in early March, Manx shearwaters follow the coast of South America as far as Rio Grande do Norte, Brazil (-3.9°, -34.6°). After this some birds take a relatively direct route back across the North Atlantic to the UK, whereas others fly further west into the Caribbean and follow the Eastern seaboard, US before crossing the north Atlantic at a higher latitude. When interpreting the results it is important to remember that the absolute metrics recorded from geolocators (distances, mean routes etc.) are subject to error (Phillips et al., 2004; Shaffer et al., 2005; Lisovski et al., 2012).

3.4.1 Differences among colonies

This is the first time that the Manx shearwater migration has been tracked simultaneously from five different colonies. Previous migration studies of seabird species have found a range of variation between individuals from different colonies, which can differ in overwinter destination; for example wandering albatross, *Diomedea* *exelans* and south polar skua *Catharacta maccormicki* (Weimerskirch et al., 2015a; Weimerskirch et al., 2015b). Conversely, other species show shared wintering destinations between colonies (e.g.: thin-billed prions, *Pachyptila belcheri* (Quillfeldt et al., 2015); black-legged kittiwake, *Rissa tridactyla* (Frederiksen et al., 2011); and guillemots, *Uria* spp. (McFarlane Tranquilla et al., 2013)). This study found that almost all birds from all colonies visited one main overwintering region (off the coast of Argentina), and followed relatively similar routes in order to get there. This is in contrast to several other shearwater species, including Cory's (*Calonectris borealis,* Dias, Granadeiro, & Catry, 2012b; Missagia et al., 2015), sooty (*Ardenna grisea,* Shaffer et al., 2006), Balearic (*Puffinus mauretanicus,* Guilford et al., 2012) and flesh-footed (*Ardenna carneipes,* Reid et al., 2013). Birds from these species, breeding on different colonies and sometimes on the same colony, show greater variation in wintering destination than the Manx shearwater.

The main difference in the southbound migration route taken by birds breeding on different colonies was in the northerly movement recorded in several birds from the Isle of Rum. These birds showed a distinct movement northwards, sometimes as far as the coast of Iceland, before flying south. This was also seen in one bird from Skomer, one from Lundy and one from Copeland, but nearly half of the Rum birds demonstrated this behaviour. Unfortunately, all but one of these birds were only tracked for one season, so it is difficult to know if this behaviour occurs every year, but given that the one individual from Skomer undertook this journey in both 2010 and 2011 it seems possible. An explanation for this behaviour could be that birds are utilising a food resource to improve post-breeding body condition before migration as seen in other seabird species (Schmidt-Wellenburg et al. 2008; Arizmendi-Mejía et al. 2013). Aside from this, southbound migration routes remain fairly similar, perhaps because variability is constrained by the continent of Africa to the east and South America to the west. All birds cross the south Atlantic at the narrowest point, which may be due to either the presence of stopover locations (some were identified here by Guilford et al., 2009) or because this follows favourable wind directions (Felicísimo et al., 2008; González-solís et al., 2009; Kemp et al., 2010).

The main source of variation between the breeding colonies is in the final leg of the northbound migration, when crossing the 40° and 50° latitude lines. Birds from Lundy in particular cross these degrees of latitude at a more westerly longitude (around -50°) in contrast to birds from the other colonies which cross the two latitudes around -40° and 30°west respectively. This may be because Lundy shearwaters breed at a slightly lower latitude, which may require a different route back across the north Atlantic. Birds from Copeland and Rum fly a longer distance on the northbound migration (although not significant), which may also be due to the more northerly positions of these colonies. A more detailed study of the spatial behaviour immediately before return to the breeding colony would be necessary to unravel the drivers behind this colony variation.

Manx shearwaters from all colonies overwinter in an area off the coast of Argentina. The only exception to this was one individual from the Lundy breeding colony, which overwintered in an area north of Brazil (approximately 12°N, -45°W). This is a novel result, and as yet the reasons for the different behaviour in this individual remain unclear. The Atlantic puffin (*Fratercula arctica*) has a dispersive migration, birds from the same colony going in different directions, but some individuals spend more time in a relatively small location compared to individuals which move from north of the UK to the Mediterranean during the northern hemisphere winter (Harris et al. 2009; Fayet et al., 2016). Gannets breeding in North America also show variation in wintering destinations, with a small number of individuals flying east across the Atlantic where the majority fly south (Fifield et al., 2014). Genetic analysis of the relatedness between shearwaters from different colonies may help to explain the colony variation in non-breeding behaviour.

From a conservation perspective, our finding that there is very little differences in the overwintering area used by Manx shearwaters from all five study colonies is important. Around 90% of the global population of this species breeds in the UK (Mitchell et al., 2004) and as the sample taken here is likely representative of the rest of the population,this area off the coast of Argentina is likely to be important for the survival of this species. It seems prudent to study how human activities in this area may be effecting the population. This could be through competition with fisheries (Karpouzi, Watson, & Pauly, 2007) and oil or plastic pollution, both known to be of conservation concern to seabird species (Votier et al., 2005; Lieske, Fifield, & Gjerdrum, 2014; Wilcox, Van Sebille, & Hardesty, 2015).

3.4.2 Spatial fidelity within individuals

Examining repeat migration tracks from each individual Manx shearwater highlighted differences between birds in the migration route. These differences were conserved from one year to the next (see Appendix 3A) indicating a level of behavioural consistency. Some aspects of the migratory route were more variable between individuals (and conserved within individual) than others, for example the northerly course taken from the north-east coast of Brazil back to the breeding colony. This variation can be described by the degree of westerly movement made before bearing across the north Atlantic towards the UK. Some individuals head almost straight back to the UK after crossing the equator, whilst others take much more circuitous route, moving west before heading back east to the colony. Individual variation in migratory species is becoming well documented, with contrasting routes and stopover strategies being found in migratory passerines and raptors (Catry et al. 2011a; Delmore et al. 2012b) and other procellariiformes (Phillips et al. 2005; Dias et al. 2013). The variation in migration route may be driven partly by the stopover behaviour exhibited in this species. Birds may have a regular stopover area, which is visited every year, the location of which somewhat dictates the route followed, as is often the case of terrestrial migrants (Alerstam, Hake, & Kjellén, 2006; Newton, 2011; Åkesson et al., 2012 and many others). Alternatively, birds may stop opportunistically when they encounter food, or weather that forces them to rest. Stopover behaviour is explored in more detail in chapter 4.

This behavioural consistency was mirrored in the wintering area, and was recorded from birds breeding on all colonies with repeat years of data. This raises questions regarding individual strategies during the wintering period. Why do some birds travel even further south, rather than staying in areas that are used by other individuals? The region used by Manx shearwaters is a highly productive expanse of ocean utilised by a number of shearwater and petrel species (Petry et al., 2008). The Patagonian continental shelf edge runs throughout the areas used study during overwintering by the birds in this. This probably causes upwelling and nutrient mixing, both oceanographic features used by this species for foraging during the breeding season (Dean et al., 2012). It may be that shearwaters remember areas of productivity from one season to the next and therefore they head to a location they have experienced before. Individual spatial fidelity in foraging behaviour is documented in other seabirds (Piatt et al., 2006; Weimerskirch et al., 2013; Patrick et al., 2014; Wakefield et al., 2015) although at varying spatial scales, so perhaps spatial memory has a similar function here. Alternatively, perhaps genetics plays a role in the degree of southerly movement a bird makes during post-breeding migration, and it is this that drives the variation between individuals. Very few studies have looked at the genetic control of migration behaviour (Berthold et al., 1992; Ueta & Ryabtsev, 2001), none so far in seabird species.

The individual repeatability of migration route and the overwintering area leads to interesting possibilities in the study of navigation in this species. How seabirds orientate and locate patches of ocean in a seemingly uniform environment is a fascinating subject. A variety of mechanisms have been suggested to explain how birds navigate at sea, including magnetic sense, olfaction and celestial compasses (Nevitt, Reid, & Trathan, 2004, Guilford et al., 2011, Gagliardo et al., 2013).

Individual behavioural repeatability or consistency has been identified in a wide range of seabird species (Phillips et al., 2005; McFarlane Tranquilla et al., 2014; Patrick et al., 2014; Yamamoto et al., 2014; Ramírez et al., 2015; Wakefield et al., 2015; Dehnhard et al., 2016; Fayet et al., 2016), but individual behavioural flexibility, or plasticity, is also recorded (Harding et al., 2007; Quillfeldt, Voigt, & Masello, 2010; Dias et al., 2011; Shoji et al., 2016). Indeed, some seabirds show both repeatability in certain behaviours and flexibility in others (Votier et al., 2010; Dias et al., 2013). There are advantages to both strategies: plasticity allows a long-lived individual to adapt to environmental stochasticity, such as varying foraging behaviour to match resource heterogeneity (Carneiro et al., 2015; Kowalczyk et al., 2015); consistency may reduce competition for resources between individuals of the same species (Linnebjerg et al., 2013; Ceia & Ramos, 2015). The role of behavioural consistency in the Manx shearwater is unclear without exploring the fitness consequences of this variation.

3.4.3 Other sources of variation

In this study of space-use during migration and overwintering there were no differences found between the sexes. Manx shearwaters show no sexual dimorphism, so perhaps it is not surprising that their flight paths are very similar between the sexes. Where other seabird species show sexual segregation in wintering areas, this is often accompanied by a size difference (Phillips et al., 2009; Müller et al., 2014). Given that female and male Manx shearwaters have slightly different roles in the at-colony behaviour before egg-laying (males spend more time in burrow defence and spend more time at the nest, Brooke, 1990) it might be expected that they would differ in their pre-breeding migration, perhaps to minimise energy expenditure. However, that was not the case here, or perhaps the variation was too subtle to be detected in this analysis.

The southbound migration and overwintering area did not vary across the years covered in this study (2006-2012). However, northbound migration tracks recovered from 2012 showed some differences in the first part of the route crossing the equator and north of South America. During this year, birds generally flew routes further to the east (away from the coasts of North and South America) than in earlier years. With this pattern only being seen in one year, it is likely a response to different weather conditions, especially wind, experienced during that migration period. Other seabird species are susceptible to changes in wind directions and speeds during migration (Felicísimo et al., 2008), especially since favourable winds could reduce flight costs (Weimerskirch et al., 2005).

3.4.4 Conclusions

Both colony and individual differences in both south and northbound migration routes are presented, in addition to individual consistency in the overall wintering area. Although the reasons for the individual differences recorded here are unclear, the behavioural variation provides potential evidence for differing migration strategies. Some birds repeatedly take a longer, more westerly migration route during the pre-breeding migration, compared to others which fly in a more direct trajectory across the north Atlantic. In order to better understand variation in migration route it is necessary to take into account the timing of migration and if, or how often, individuals stop-over during their journey. The relationship between these variables is further explored in chapter six.

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Chapter 4

Stopover behaviour during migration in the Manx shearwater

4.1 Introduction

Long distance migration, whether by air, sea or land, is a physically demanding activity (Alerstam 1991; Alerstam et al. 2003; Bowlin et al., 2010; Hedenström, 2010; Dias et al., 2012). Animals often reach the limits of their physical abilities, which can impact on their future fitness and in extreme situations result in death (Horton & Morris, 2012). As the breeding season is also energetically demanding and often precedes or follows a long distance migratory journey, a trade-off occurs between the energy required to migrate to a distant non-breeding area, and that needed for future breeding (Arizmendi-Mejía et al., 2013). Migratory birds have evolved a range of behaviours to reduce the risks, of mortality and reduced breeding season fitness, of these long journeys, one of which is to undertake stopovers en route to their destination (Hutto, 1998; Alerstam et al., 2003; Newton, 2006; Åkesson & Hedenström, 2007; Hedenström 2008; Bowlin et al., 2010; Newton, 2011; Dias et al., 2012). A stopover, also called staging behaviour, refers to a pause a migratory animal takes during its journey (Warnock, 2010). This allows the individual to regain some body condition, take on food (and water in terrestrial migrants) or wait out adverse weather conditions.

Stopover behaviour has been identified in a wide range of bird families, across a spectrum of migratory and flight strategies; including swans and geese (Nolet & Gyimesi, 2013; Chudzińska et al., 2015), various passerines (Schaub, Jenni, & Bairlein, 2008; Kellermann & van Riper, 2015; Mccabe & Olsen, 2015), shorebirds (Farmer & Parent, 1997; Verkuil et al., 2012; Thorne & Read, 2013) and raptors (Alerstam, Hake, & Kjellén, 2006; Kochert et al., 2011; Vansteelant et al., 2014). For terrestrial migrants, locations used repeatedly and consistently for stopover by a species are useful to ornithologists since they enable detailed study of migratory populations en route (Thomas Alerstam et al., 2003). These stopover locations are often defined by some environmental feature, for example a reliable source of food or water, or a safe location for roosting and resting (Kochert et al., 2011; Gómez, et al., 2012; Thorne & Read, 2013).

In contrast to terrestrial migrant birds, only recently has the behaviour of pelagic seabird species during their migrations started to be recorded in any detail. For the most part this is because the at-sea behaviour of seabirds is difficult to observe, particularly in oceanic waters where many migratory seabirds spend the non-breeding season. Since the invention of miniaturised tracking technology, stopover behaviour and locations have been identified in several seabird species, including terns (Fijn et al., 2013; Mcknight et al.,2013; Winden et al., 2014), auks (Mosbech et al., 2011), gulls (Klaassen, et al., 2011; Stenhouse, Egevang, & Phillips, 2011), and shearwaters (Shaffer et al., 2006; Guilford et al., 2009; Dias et al., 2012), suggesting that this may be a common behaviour in many seabird species.

Understanding individual behaviour in free ranging seabirds is useful for both species management and determining the drivers and mechanisms behind the evolution of such behaviours (Senner, Conklin, & Piersma, 2015). Many terrestrial migrant species have very consistent stopover sites (Thomas Alerstam et al., 2003). This may be due in part to geographical movement restrictions (mountain ranges or stretches of ocean) or long term reliability in the location of stopover habitat (lakes, rivers, woodlands). However, studies of individual fidelity in space use in terrestrial and marine migrants have revealed a mixed picture. Some species show a degree of fidelity to their route

(Gschweng et al., 2008; McFarlane Tranquilla et al., 2014; Yamamoto et al., 2014; Fifield et al., 2014), but others showing high between-year variability (Berthold, Kaatz, & Querner, 2004; Alerstam, 2006; Dias et al., 2011; Stanley et al., 2012). However, most of these studies focussed on the migration trajectory and not on the locations of stopovers. The extent of individual consistency in stopover behaviour is therefore relatively poorly known. Stopovers in seabirds could be expected to occur in high productivity areas, which may be more predictable if linked with bathymetry or tidal fronts (Fort et al., 2012; Deppe et al., 2014). Alternatively, stopover behaviour may occur opportunistically, or be forced should the individual encounter adverse flight conditions (this might be storms or unfavourable wind directions or speeds (Newton, 2007; González-Solís et al., 2009; Mateos & Arroyo, 2010)). Quantifying how stopover locations vary between years, colonies, and the degree of individual consistency in stopover location may shed light on this by indicating the relative importance of deliberate targeting of areas, shifting resources and behavioural specialization of sub-populations.

The presence of stopover behaviour in the Manx shearwater was initially identified in the non-breeding behaviour of 12 Manx shearwaters tracked from Skomer Island in 2006, using archival light and saltwater immersion loggers (Guilford et al., 2009). These stopover locations were determined as areas where the change in longitude between successive days was less than 0.8° (east or west). In addition, three types of behaviour during migration were distinguished using saltwater immersion data; resting, foraging and flight, with the foraging and resting behaviour being closely associated with stopover areas. More recently, machine-learning methods identified areas of the

Atlantic used by Manx shearwaters from Copeland Island for mid-migration foraging behaviour in 2007, 2008 and 2009 (Freeman et al. 2013).

This chapter analyses light and saltwater immersion data during the migration of Manx shearwaters from multiple colonies and years. These data were classified using a machine-learning algorithm to construct behavioural time series over the migratory period and identify stopovers in order to investigate whether Manx shearwaters show individual repeatability and inter-year and inter-colony variation in stopover locations. The presence of individual repeatability would indicate deliberate targeting of specific areas by individuals; yearly differences would suggest that environmental variability influences the location of stopover behaviour; and inter-colony variability in stopover locations might indicate behavioural specialization of these subpopulations, as well as having implications for the susceptibility of the global population to extreme weather events and anthropogenic impacts.

4.2 Methods

Archival light and saltwater immersion loggers (British Antarctic Survey, also referred to as saltwater immersion loggers) were deployed on birds from five colonies of Manx shearwaters between 2006 and 2012. The data were collected using the methods outlined in chapter 2. A total of 194 separate migration trips (both the southbound post-breeding and northbound pre-breeding migrations) from 112 individual birds were recorded. Each of these tracks comprised a paired set of locations and of saltwater immersion data. Table 4.1 summarises the numbers of birds tracked from each colony.

Table 4.1 Numbers of Manx shearwaters with saltwater immersion and geolocation data collected in each year on each breeding colony. The date refers to the year the data were retrieved.

Colony	2007	2008	2009	2010	2011	2012	Number of individual birds	**TOTAL** tracks
Skomer	6	14	23	20	18	10	46	**70**
Copeland		7	13	12	11	9	28	**52**
Ramsey				4	2	0	6	**6**
Lundy				14	13	5	19	**32**
Rum					13	0	13	**13**

4.2.1 Data processing

Raw geolocation data were processed using the BASTRACK programmes (as described in chapter 1) to estimate the location of the bird once per day, at noon. The resulting locations were filtered to include only positions associated with uninterrupted light curves as reported by the software. Locations north of 80°N and south of 80°S latitude were also removed, as Manx shearwaters from the UK are highly unlikely to be found at these latitudes (see chapter 2, Guilford *et al*., 2009 and Freeman *et al*., 2013) and these records are therefore assumed to be erroneous. All locations records within 7 days on the summer side and 21 days on the winter side of the spring and autumn equinoxes (in March and October respectively) were removed due to increased error in estimates of latitude obtained during these time periods. The main outbound (southbound, post-breeding) and inbound (northbound, pre-breeding) migratory movements were separated from positions recorded during breeding and overwintering, by splitting the tracks as they entered or left the breeding and overwintering areas, using the same method as in chapter 2. After this filtering, 21 complete southbound and 136 complete northbound migration tracks remained.

In addition to the light-based spatial locations, the raw saltwater immersion data from each migration period were processed to calculate a range of immersion metrics for each day. GLS immersion data loggers record the proportion of time spent wet (indicating that the bird is on or in water) during 10-minute periods. The loggers detect the presence or absence electrical conductivity every 3 seconds, and sum these detections across the 10 minute period to record the proportion of time immersed as a value between 0 (conductivity never detected, indicating no time on the water) and 200 (conductivity detected on all occasions, indicating the entire period on the water); intermediate values indicate some proportion of time on the water. Each 10-minute period may be further classified as a 'wet' event if this value exceeds 100, corresponding to more time spent on the water than off it during that period (Yamamoto et al., 2008; Dias, Granadeiro, & Catry, 2012b; Péron & Grémillet, 2013). These 10-minute immersion data were summarised across the hours of daylight (as indicated by the light logger) for each day to compute a series of immersion metrics, detailed in Table 4.2. These metrics are intended to quantify different aspects of immersion patterns over each time period, including the variability and consistency of these patterns, as well as the overall amount of immersion.

Table 4.2. Immersion metrics calculated across the daylight hours for each day, from 10-minute immersion records.

Metric	*Description*
Minimum	Minimum saltwater immersion value
Maximum	Maximum saltwater immersion value
Variance	Variance of saltwater immersion values
Differential	Differential of saltwater immersion value during the day (a sequential measure of variation)
Proportion wet	Proportion of time spent in 'wet' events
Logit Proportion wet	Logit-transformed proportion wet (rescaling to a continuous variable)
Total wet events	Total number of 'wet' events
Mean wet bout length	Mean duration of 'wet' bouts (mean number of contiguous 'wet' events)
Total wet bouts	Total number of 'wet' bouts (number of runs of successive 'wet' events)

4.2.2 Gaussian mixture modelling

Whilst the calculated immersion metrics are intended to represent different aspects of the daily patterns of immersion, many of them are likely to be highly correlated. Calculation of the empirical Pearson correlation matrix across the set of 9 candidate metrics confirmed that this was the case, with over half of pairwise correlations exceeding 0.7. This set of candidate immersion metrics was therefore reduced to a smaller set of less correlated variables for use in the behavioural classifier that still represent the data reasonably well, but are more biologically interpretable.

Principal components analysis of these metrics identified the two first principal components as explaining more than 96% of variance in the dataset. These two components appeared to represent the magnitude and variance of immersion data: the first component had large positive loadings for: minimum and maximum immersion value, proportion and logit-transformed proportion wet, total wet events, and mean wet bout length; and the second had large positive loadings for the total number of wet bouts, and the variance and differential of the immersion data. These two principal components could have been used directly in the classifier, however they are slightly less interpretable than the raw metrics, and potentially difficult to reconstruct in future studies. Therefore instead of using the principal components, the two metrics with the largest loading coefficients for each component was used instead. The two retained metrics were: proportion of time spent 'wet' and variance of the saltwater immersion data. The correlation between these two metrics was 0.15, whilst the absolute pairwise correlation coefficients among the excluded metrics were all greater than 0.4.

These two metrics were therefore retained and used to classify the dominant behaviour for each day on migration as either a day spent in flight, or a day spent resting or foraging. A three-cluster GMM was applied to the dataset of these two immersion metrics across all individuals, colonies and years to classify daily behaviour into one of three mutually exclusive behavioural classes. A three-cluster model was used after Guilford *et al.* (2009) where a GMM and Bayesian inference process identified three different behaviours from migration tracks.

GMM uses Gaussian-shaped functional forms to partition the environmental space into a fixed number of clusters. Each cluster is represented by a separate multivariate

Gaussian, providing a model for the range of values each cluster is likely to take. Provided new observations of these variables, the model can therefore assign a the most likely class membership. Note that the likelihood function used to fit the model is multinomial (indicating the probability of class membership) rather than Gaussian and the model makes no assumption of normality about the data used to train it. For a fixed number of clusters, a GMM can be specified in a number of ways, by varying whether the Gaussians should be isotropic (having the same spread in all directions), or nonisotropic, and whether all of the Gaussians should have the same or different: volumes, shapes (if non-isotropic) and orientations (if non-isotropic). Ten candidate three-cluster GMMs representing all possible combinations of these options were fitted to the data using the R package `mclust` version 4.2. The best-fitting GMM type was selected as the one with the smallest Bayesian Information Criterion, which trades off model complexity against goodness of fit. The optimal model used non-isotropic Gaussians with varying orientations, but the same shape and volume. This model was then used to predict the most likely behaviour during each day for each migration track. Figure 4.1 shows the distribution of the proportion of time spent wet and variance versus each of the classes inferred by the GMM.

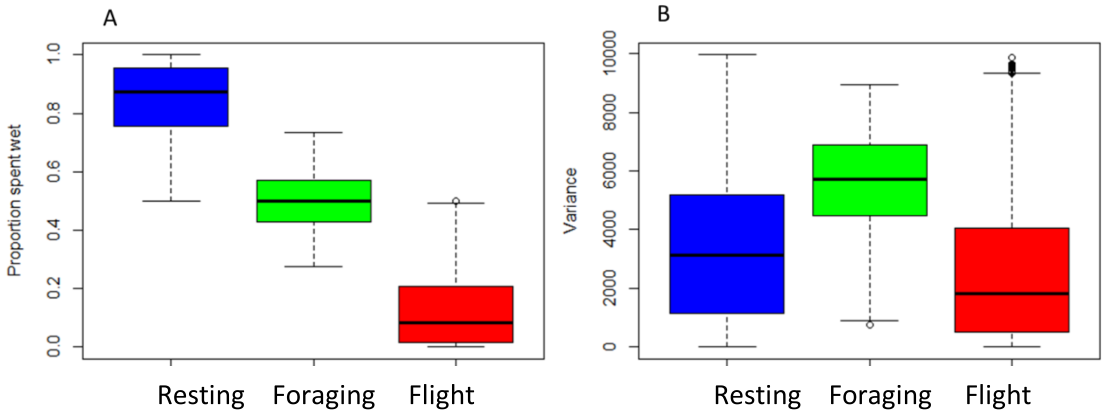


Figure 4.1 Distribution within each of the three behavioural classes of the two selected immersion metrics during each day during migration: A) proportion of time spent in 'wet' events and B) variance in saltwater immersion value. Classes can be interpreted as follows: Class 1 = resting (on water; consistently high immersion values), class 2 = foraging (bouts of time spent on and off water; intermediate and highly variable immersion values), class 3 = flight (in the air; consistently low immersion values).

4.2.3 Identification of stopover locations

The classified locations were visualised using R 3.0.2 and ArcGIS 10.0 (ESRI) with the GME extension (Redlands) (example in figure 4.2). Stopover locations during the southbound and northbound migrations were then identified by choosing only those locations that had been classified as class 1 or 2 ("resting" or "foraging" behaviour) and were part of a run of positions (more than three) that were classified as such. Only stopover behaviour taking place in the north Atlantic was analysed in this study, as it is difficult to delineate exactly where the switch between wintering behaviour and migration takes place in the southern Atlantic.

Kernel density estimation (KDE) was used to calculate occupancy kernels from the stopover locations for each bird, year and colony. These estimates were calculated on a computational grid of 300 by 300 cells, with the dimensions of the grid varying according to the range of latitudes and longitudes of the stopover behaviour for each track. The optimum bandwidth selected by least-squares cross validation across all tracks using the "kernelUD" function in the R package adehabitat (Calenge, 2006). Overlaps between each pair of kernels for each bird, year and colony, were calculated as the approximate volume of the intersection between the two density estimates. Since each density estimate has a volume of 1, this results in an overlap statistic between 0 (no overlap) and 1 (complete overlap). This approach obviates selection of an arbitrary occupancy threshold at which to binarise the kernel when calculating the intersection. Kernels were then thresholded at the 50%, 75%, and 95% density levels to visualise the major stopover areas. These density thresholds were then plotted using R and ArcGIS.

4.2.4 Statistical analysis of stopover locations

Similarity in stopover locations (for those tracks exhibiting stopovers) was quantified by calculating nearest neighbour distances between stopover locations between pairs of tracks, following the same method as in Chapter 3, but considering only those locations classified by the GMM as stopover behaviour. After calculating stopover nearest neighbour distances for all pairs of tracks, the mean nearest neighbour distances were calculated for each of the following groups: within-bird (pairs of tracks from the same bird in different years); between-bird (pairs of tracks from different birds); within-colony (pairs of tracks from different birds within the same colony); between-colony (pairs of tracks from birds in different colonies); within-year (pairs of tracks from the same year); between-year (pairs of tracks from different birds in different years); within-sex (pairs of tracks from different birds of the same sex); and between-sex (pairs of tracks from birds of different sexes). As in Chapter 3, randomization tests were performed to test whether differences in the mean nearest neighbour distances between the within and between groups for individual, colony, year and sex were significant. Specifically, these tests assessed the probability of observing a difference at least large as the observed difference under a null hypothesis that the true mean nearest neighbour distance within the groups was the same. This p-value was estimated by drawing 100,000 random samples from the distribution of distances expected under the null model (accounting for the number of track pairs in each group), and determining the proportion of those samples at least as great as the observed value.

4.2.5 Statistical analysis of stopover frequency

The effects of individual, year and colony on the proportion of time spent in each behavioural class and on the proportion of time spent in stopover behaviour were analysed using binomial generalised linear mixed models (GLMM). This analysis followed the procedure used in chapters 2 and 3: models with year, colony, and year and colony as fixed effects and individual nested within colony as a random effect were fitted, along with an intercept-only null model; the best-fitting model was determined by Akaike Information Criterion (AIC); and model comparisons were used to evaluate the importance of each of the fixed effects terms. Marginal and conditional R-squared values were calculated (after Nakagawa & Schielzeth, 2013) in order to partition the variance in stopover behaviour due to the fixed and random effects. The best fitting model was then refitted to a subset of the data for which the sex was known, and the explanatory power of sex (as a fixed effect) was evaluated by model comparisons.

4.3 Results

4.3.1 Overview

Figure 4.2 illustrates the combined behavioural and location information constructed for each track, showing the behavioural state at each location along the migration route. Runs of consecutive resting or foraging states from these tracks were interpreted to be stopover behaviour. Stopover behaviour occurred in all individuals that were tracked, from every breeding colony and in every year. On southbound migration (from the breeding colony to the overwintering location) the main areas where stopover behaviour occurred were in three main clusters: north of the UK, to the south of Iceland; just north of the Equator, off West Africa (south of the Cape Verde islands and off the coast of The Gambia, Guinea-Bissau, Guinea and Sierra Leone) and the north coast of Brazil (off the mouth of Rio Mearim). Figures 4.4, 4.7 and 4.10 illustrate these main areas, summarised across colonies, years and sexes. During the northbound migration (return to the breeding colony), stopover behaviour can be seen in a widespread area across the north Atlantic. Again, several regions stand out, particularly within the Caribbean (north of Cuba and the Dominican Republic) and an area in the mid-north Atlantic (directly south of Greenland and on a similar latitude to Newfoundland).

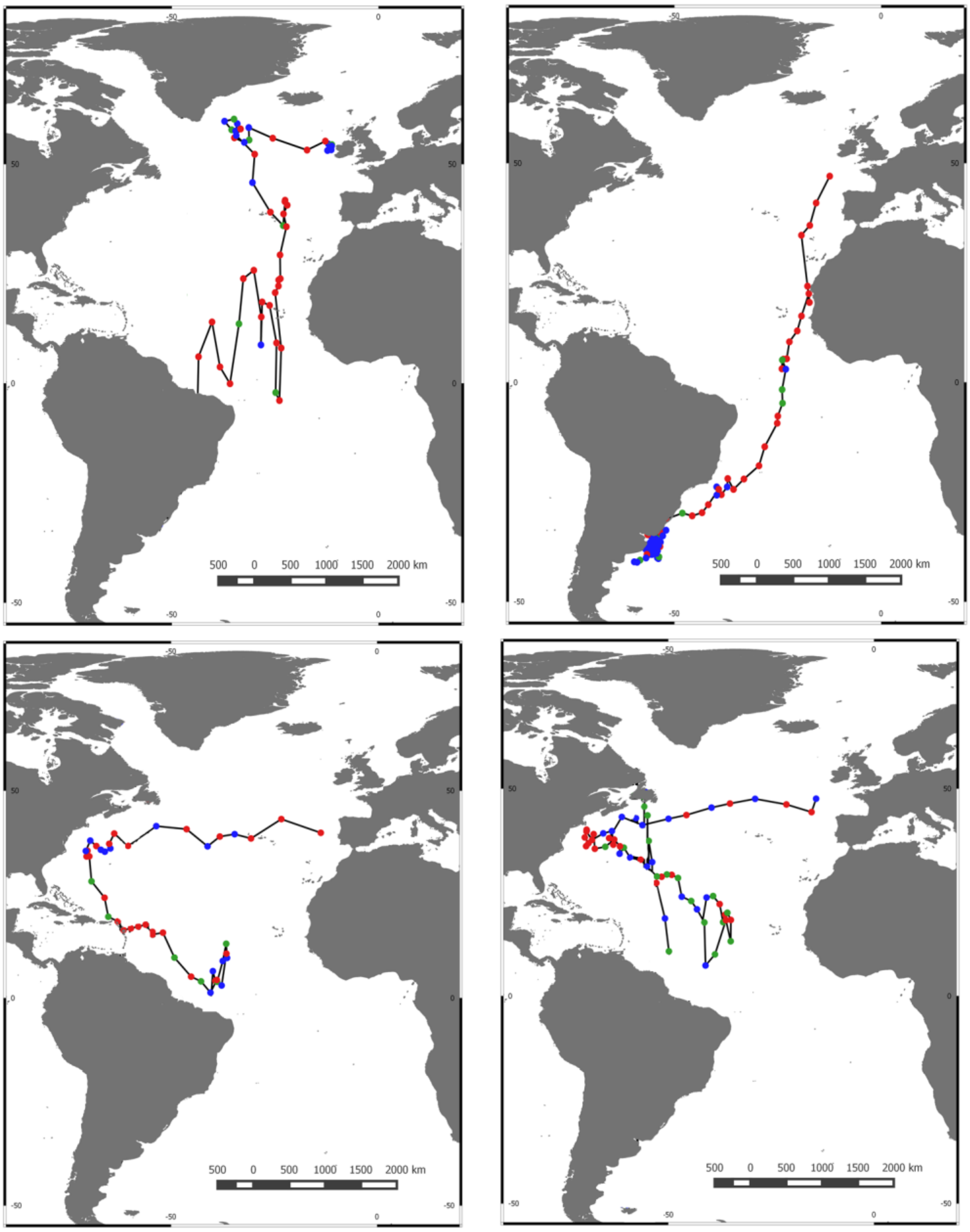


Figure 4.2 Examples of the location estimates during individual migration routes classified by the GMM. The top two panels show the post-breeding (southbound) migration and the bottom two panels the pre-breeding migration (northbound). Class 1, blue = resting, class 2, green = foraging, class 3, red = flight

4.3.2 Individual stopover behaviour

Stopover behaviour was identified in all migration tracks during both post and pre-breeding migrations. Appendix 4A illustrates the range of location classified as stopover sites from data collected on individual birds with repeat migrations. There was a significantly smaller (difference = 1144.2km, p = 0.011) mean nearest neighbour (NN) distance between track pairs on the southbound migration by the same bird (616.6km ±488km s.d., n = 6) than between birds (1760.8km ±1135km s.d., n = 372; figure 4.3). During northbound migration, mean stopover NN distances were significantly lower (difference = 379.3km, $p < 0.001$) among different tracks by the same bird (742.0km ±479km s.d., n = 99) than between different birds (1121.2km, ±717km s.d., n = 12,147; figure 4.3).

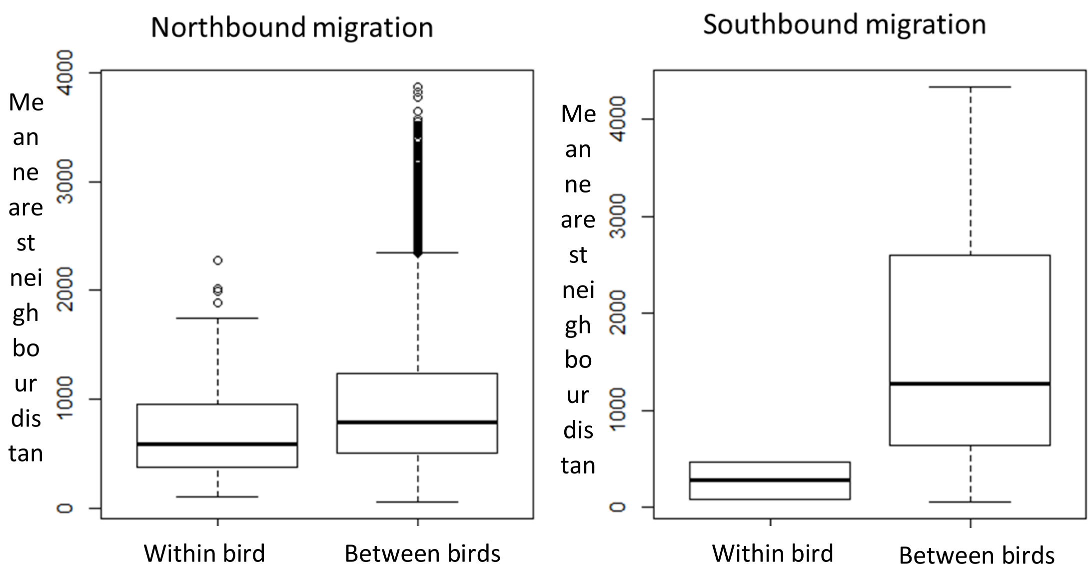


Figure 4.3 Mean nearest neighbour distances in stopover locations between different tracks by the same individual and between tracks by different individuals during pre-breeding (northbound) and post breeding (southbound) migrations.

4.3.3 Colony differences

Manx shearwaters from all five breeding colonies (Rum, Copeland, Ramsey, Skomer and Lundy) exhibited stopover behaviours during both the northbound and southbound migrations. Birds from all colonies were recorded stopping in areas to the west of Africa and north of Brazil during their southbound migration (figure 4.4).

Percentage overlap between colony kernel density estimates ranged from 49.8% and 66.3% (figure 4.5). There was no significant difference (difference = 160.2km, p = 0.201) in the mean nearest neighbour distance within colonies (1651.9km ±1081km s.d., n = 119) and between colonies (1812.1km ±1158km s.d., n = 253; figure 4.4).

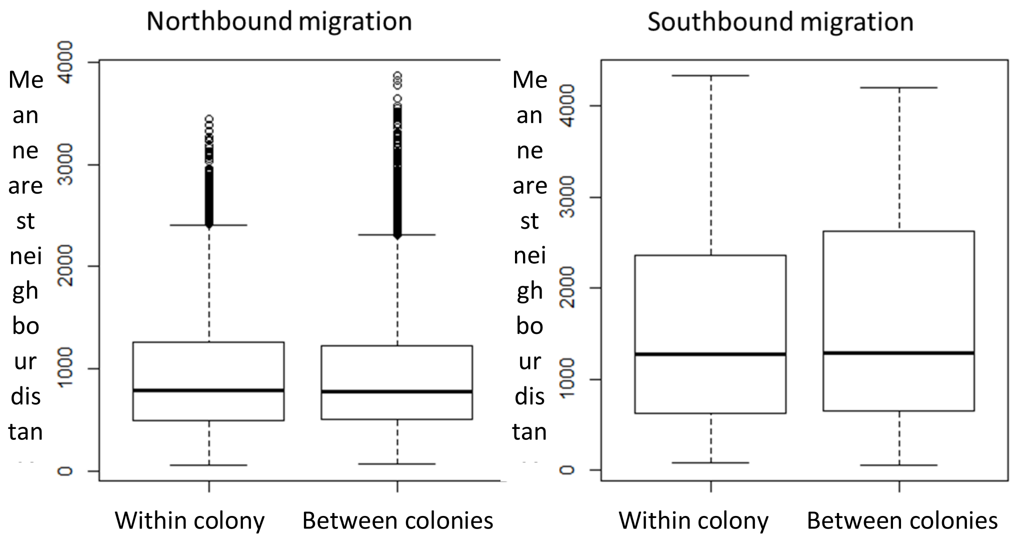


Figure 4.4 Mean nearest neighbour distances in stopover locations between tracks by different individuals in the same colony and between tracks by different individuals in different colonies during pre-breeding (northbound) and post breeding (southbound) migrations.

General areas where stopover behaviour took place on the return (northbound migration) were apparently very similar across all colonies on the return migration, though percentage kernel density overlap ranged between 29.9% and 52.4% (figure 4.6). Mean nearest neighbour distance among tracks by different birds within the same colony (1091.9km ±726km s.d., n = 4071) was significantly lower (difference = 4km, p = 0.001) than among tracks by birds from different colonies (1136.1km ±712.6km s.d., n = 8076; figure 4.4).

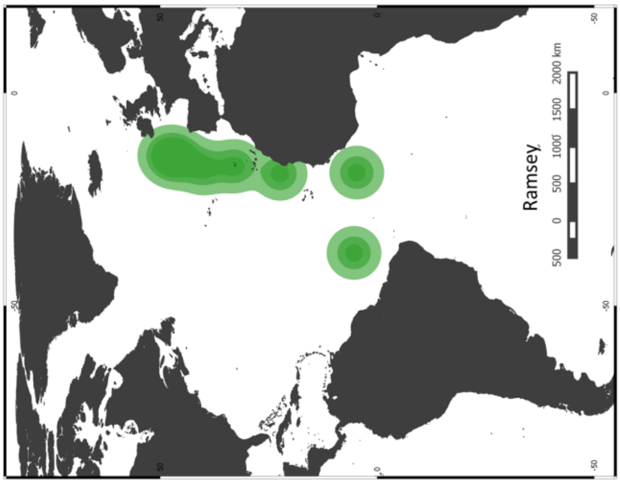
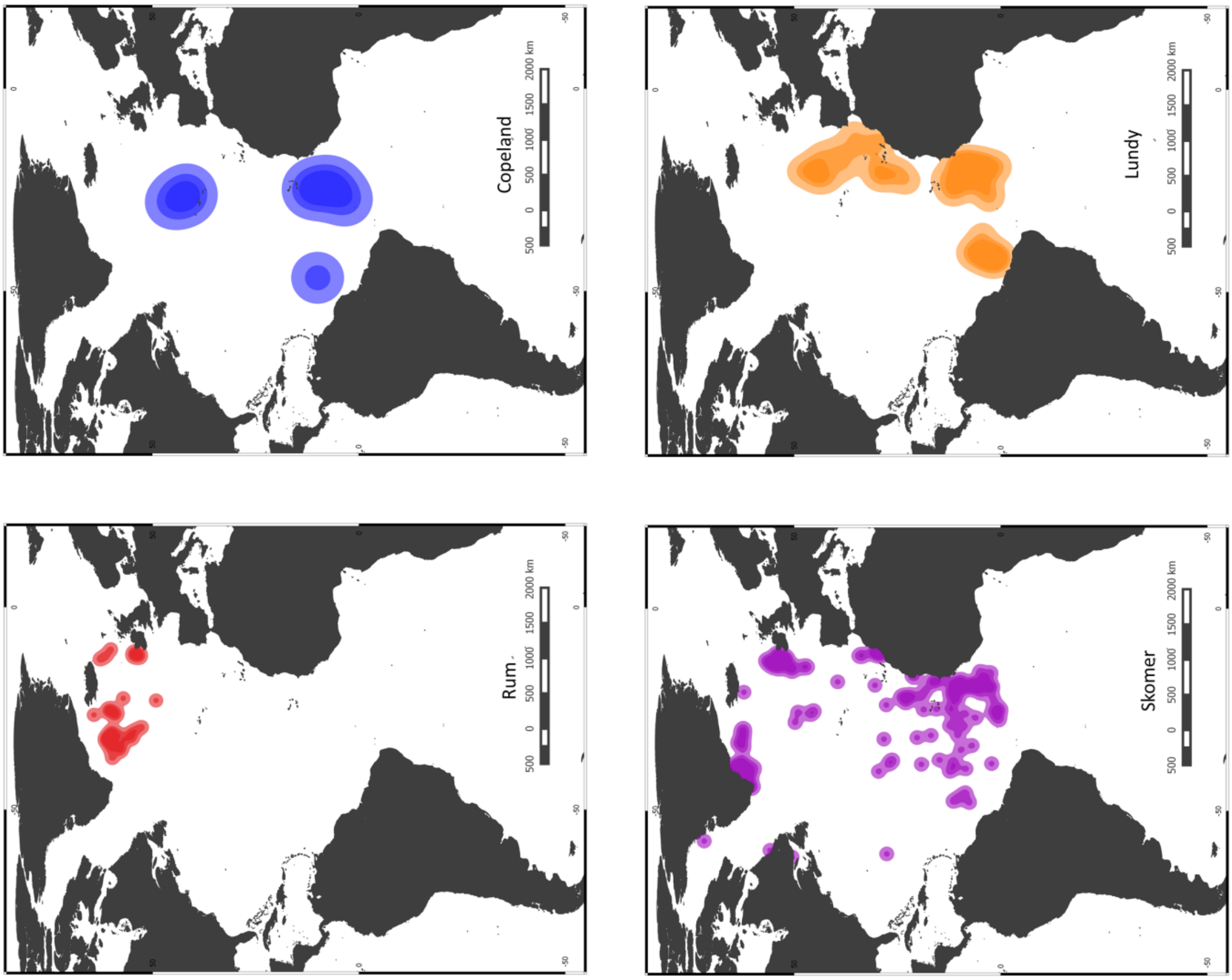


Figure 4.5 Kernel density estimates (50%, 75% and 95%) from stopover locations used during southbound (post-breeding) migration for Manx shearwaters from 5 different breeding colonies



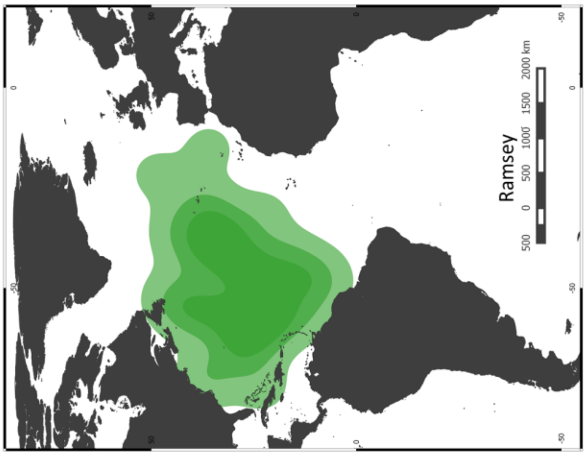
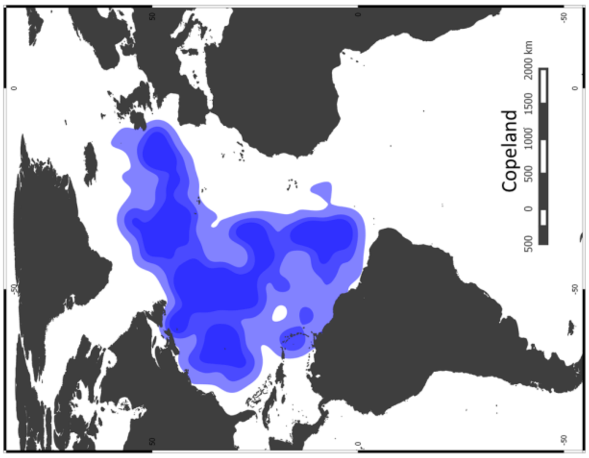
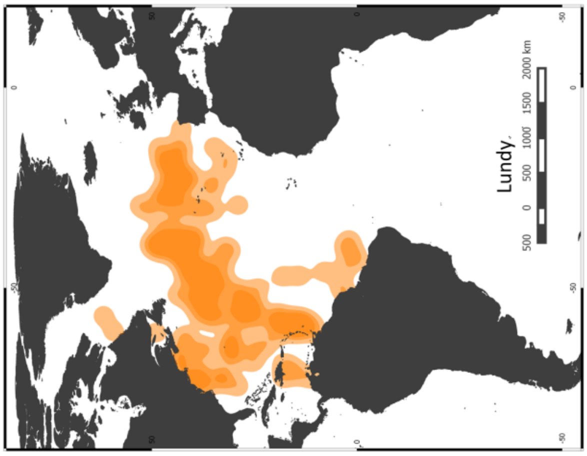
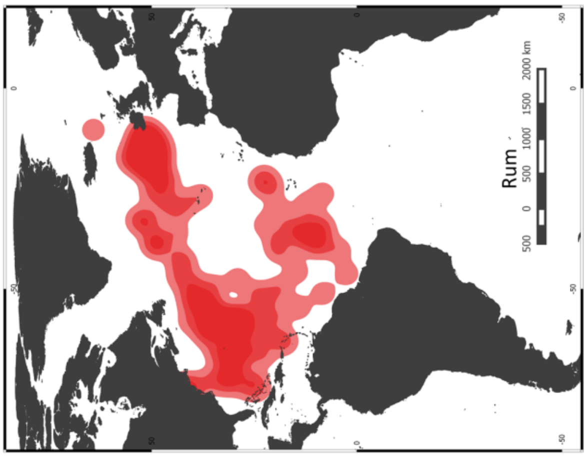
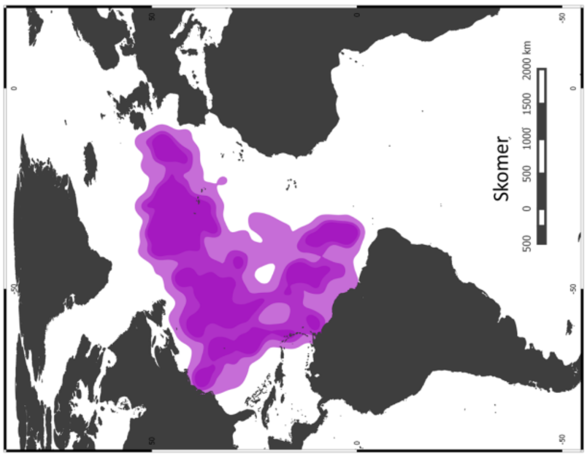


Figure 4.6 Kernel density estimates (50%, 75% and 95%) from stopover locations used during northbound (pre-breeding) migration for Manx shearwaters from 5 different breeding colonies









4.3.4 Annual patterns in stopover behaviour

On southbound migration, the mean nearest neighbour distance between stopover locations in different pairs of tracks were not significantly different (difference = 183.8, p = 0.196) between tracks by different birds within the same year (1617.9km, ±1173km s.d., n = 83) than between tracks by different birds across years (1801.1km ±1134km s.d., n = 289; figure 4.9). Percentage overlap of kernel density estimates ranged between 27.9% and 56.4% on southbound migration (figure 4.7) and between 35.6% and 62.2% on northbound migration (figure 4.8). On northbound migration, mean nearest neighbour distance between stopover locations was significantly smaller (difference = 41.0km, p = 0.011) among tracks within the same year (1088.9km ±715km s.d., n = 2537) than among tracks by different birds in different years (1129.8km ±718km s.d., n = 9610; figure 4.9).

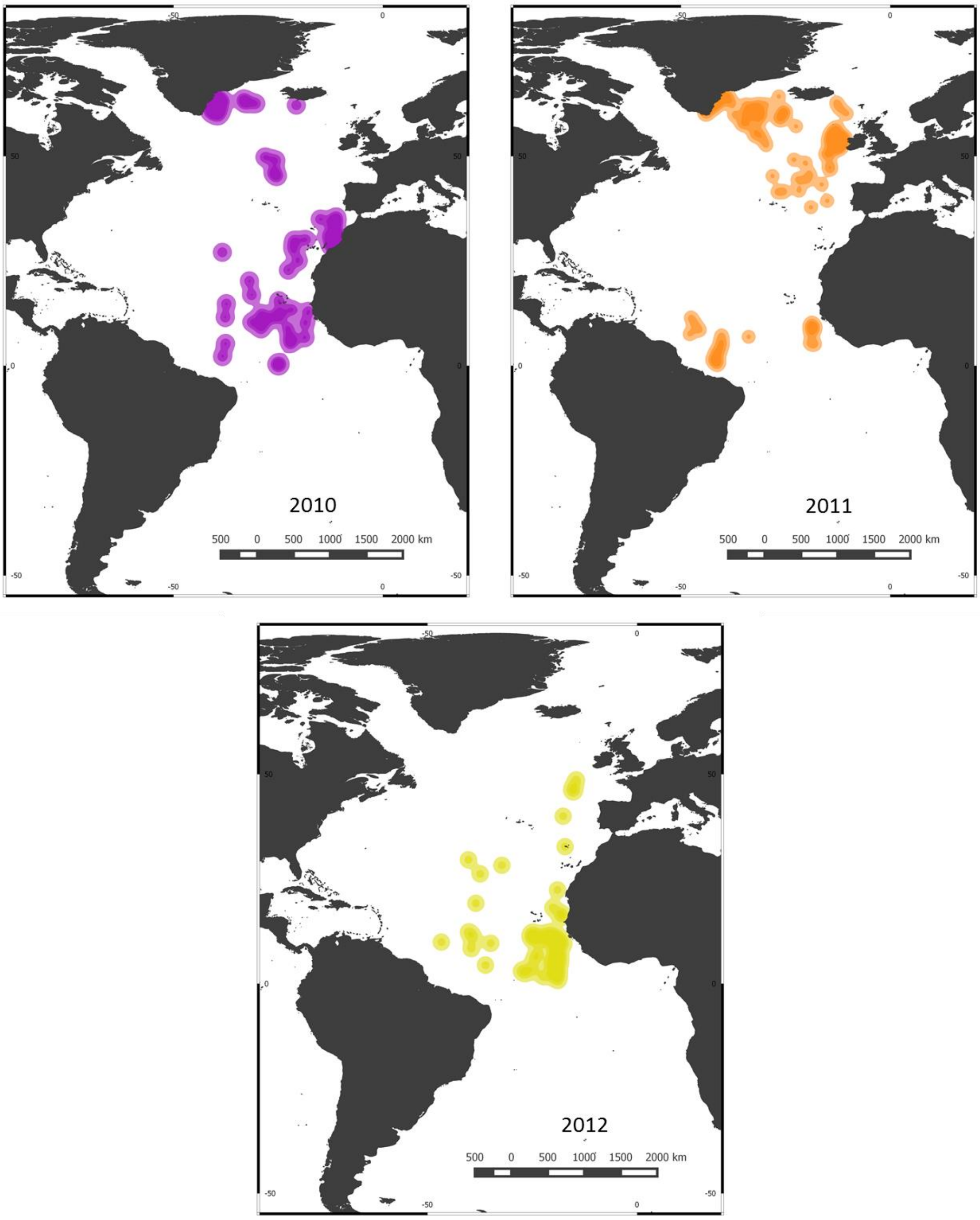


Figure 4.7 Kernel density estimates (50%, 75% and 95%) from stopover locations used during southbound (post-breeding) migrations in 2010, 2011 and 2012 (birds from all colonies included).

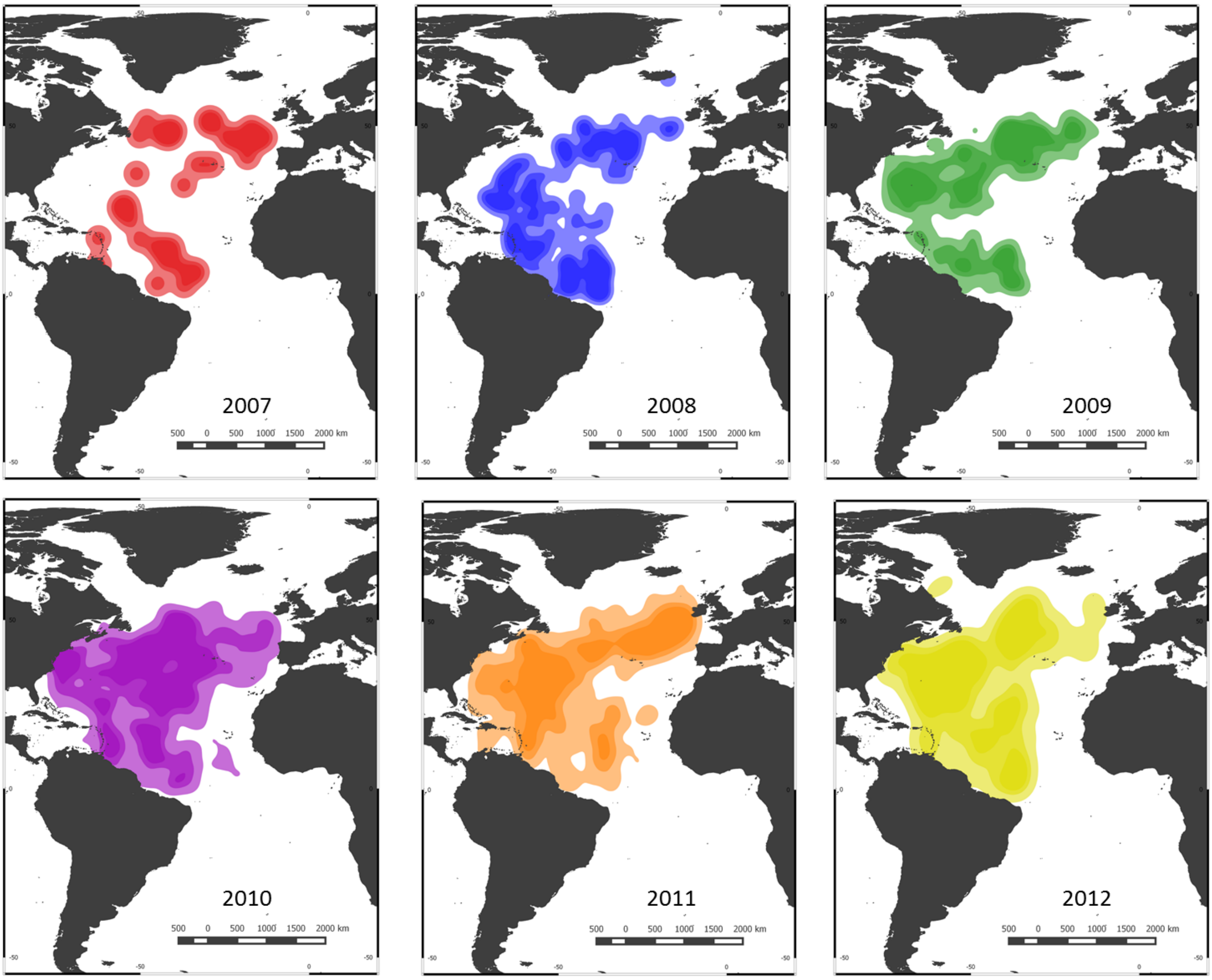


Figure 4.8 Kernel density estimates (50%, 75% and 95%) from stopover locations used during northbound (pre-breeding) migrations over 6 different years (birds from all colonies included).

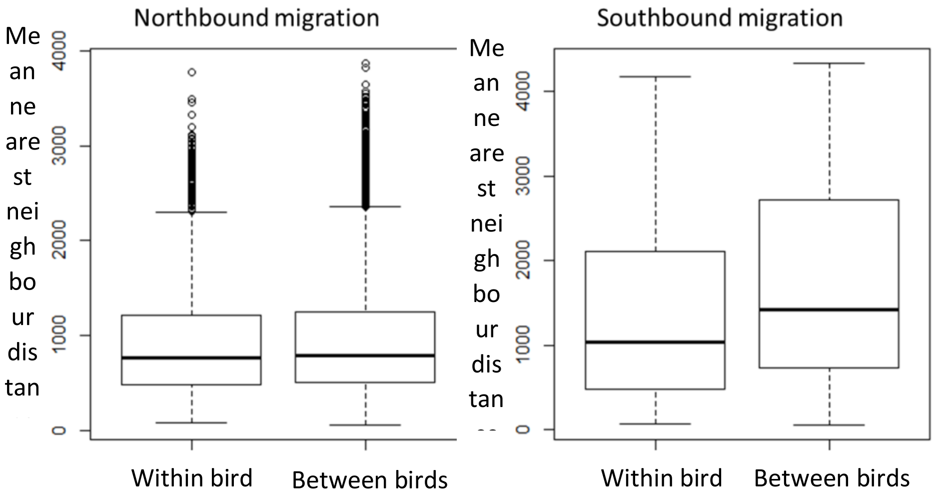


Figure 4.9 Mean nearest neighbour distances in stopover locations between tracks by different individuals in the same year and between tracks by different individuals in different years during pre-breeding (northbound) and post breeding (southbound) migrations.

4.3.5 Sex differences in migration behaviour

Nearest neighbour analysis showed no difference in the mean nearest neighbour distance between stopover locations between tracks by different birds within the same sex (1744.1km ±1127km s.d., n = 94) and between the sexes (1611.8km ±1070km s.d., n = 110) on the southbound migration (difference = 130.3km, p = 0.408; figures 4.10 and 4.12). There was also no difference on the northbound migration (difference = 20.23km, p = 0.178) in mean nearest neighbour distance between the stopover locations in tracks of different birds of the same sex (942.7km ±611km s.d., n = 4592) and tracks by birds of different sexes (962.9km ±625km s.d., n = 4588; figures 4.11 and 4.12).

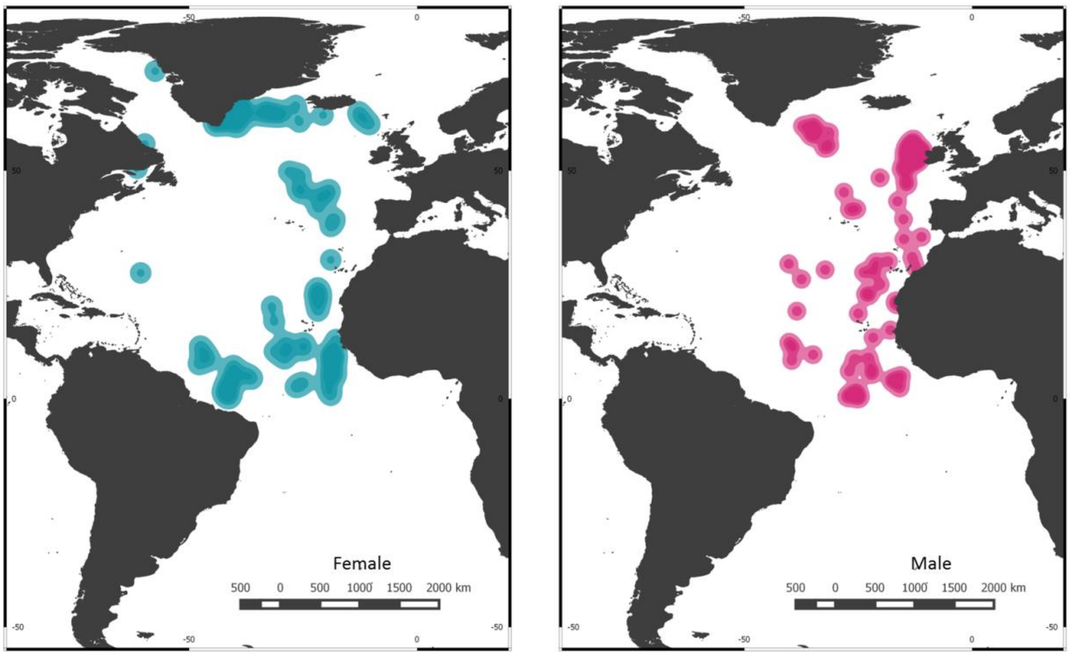


Figure 4.10 Kernel density estimates (50%, 75% and 95%) from stopover locations used during southbound (post-breeding) migrations from female and male birds from all colonies, across all years.

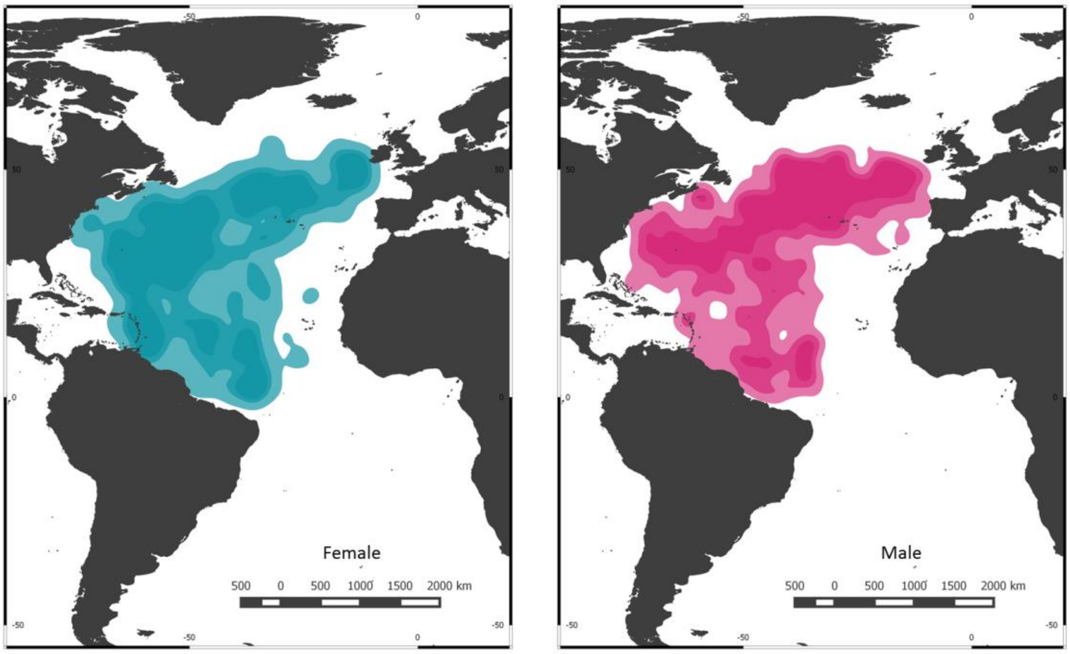


Figure 4.11 Kernel density estimates (50%, 75% and 95%) from stopover locations used during northbound (pre-breeding) migrations from male and female birds from all colonies, across all years.

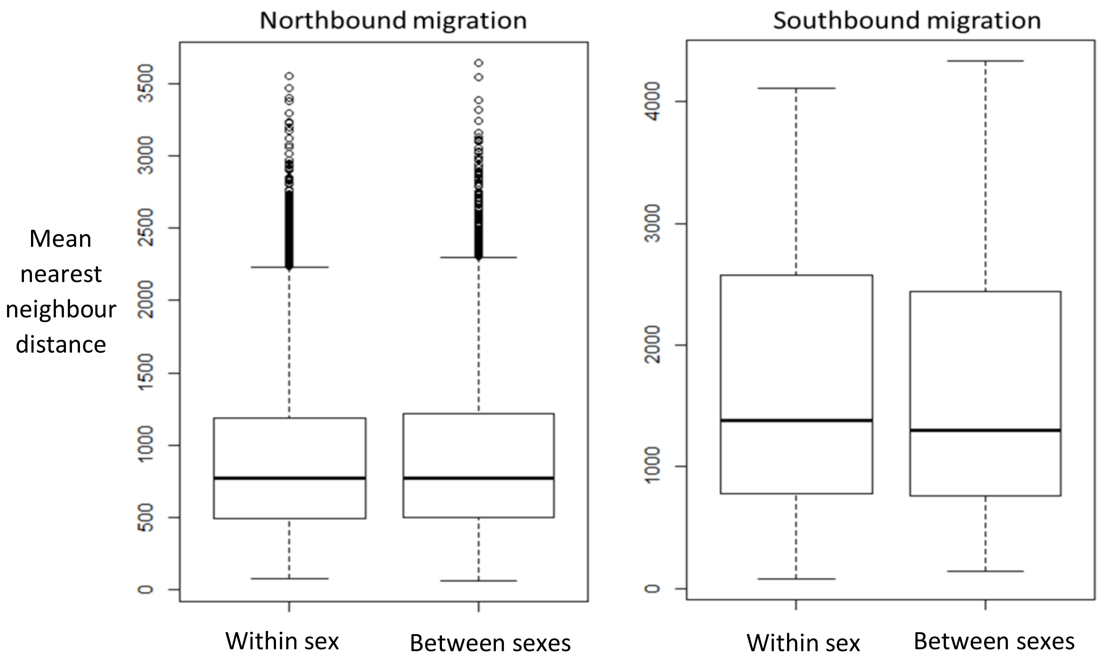


Figure 4.12 Mean nearest neighbour distances in stopover locations between tracks by different individuals of the same sex and between tracks by individuals of different sexes during pre-breeding (northbound) and post breeding (southbound) migrations.

4.3.6 Proportion of migration time spent in stopover behaviour

On average, birds spent a 32.7% (±16.3% s.d.) of their northbound migrations in stopover behaviour, and 35.9% (±20.7% s.d.) of the southbound migration spent in stopover. The proportion of the migration spent in stopover behaviour differed significantly by year in both northbound ($X^2[5] = 109.23$, $p < 0.001$) and southbound ($X^2[5] = 70.697$, $p < 0.001$) migrations. Mean proportions spent in stopover on northbound migration ranged from 23.4% in 2008 to 38.1% in 2010; and in southbound migration the proportion ranged from 24.5% in 2008 to 44% in 2009. On both migrations, there was no effect of colony (northbound: $X^2[5] = 7.6416$, $p = 0.106$; southbound: $X^2[5] = 4.2168$, $p = 0.378$) or sex (northbound: $X^2[1] = 0.009$, $p = 0.925$; southbound: $X^2[1] = 1.267$, $p = 0.260$).

The random effect for bird (nested within colony) explained only a very small amount of variation in the proportion of migration spent in stopover behaviour in both directions (northbound migration: marginal $R^2 = 0.014$, conditional $R^2 = 0.025$; southbound migration: marginal $R^2 = 0.014$, conditional $R^2 = 0.075$).

4.4 Discussion

This chapter identified stopover behaviour from saltwater immersion logger data throughout the two migratory journeys made by Manx shearwaters between their breeding colony and overwintering area. All of the tracks exhibited stopover behaviour, in both migratory directions. It appears that stopover behaviour must therefore be a key strategy used by Manx shearwaters during migration, either for survival or to maintain body condition, as in other marine and terrestrial migrants (Hutto, 1998; Alerstam et al., 2003; Shaffer et al., 2006; Warnock, 2010; Dias et al., 2012). The spatial locations, of these stopovers were compared across the five breeding colonies and six years comprising this dataset, and within and between individual birds.

4.4.1 Individual stopover behaviour

Individual Manx shearwaters have strongly repeatable strategies regarding where to stop during both the southbound and northbound migrations. Locations used for stopover by the same bird in different years were much more similar than the locations used by different birds, on both the southbound and northbound migrations. In fact the within-individual mean nearest neighbour distance between stopover locations on the southbound migration was almost one-third the between-individual difference (617km vs. 1760km). The difference was slightly less stark on the northbound migration (the within-individual mean distance of 742km being around two-thirds the between-individual mean distance of 1121km). By contrast, there was very little evidence of individual consistency in the proportion of each migration spent in stopover behaviour.

The mechanisms dictating when and how often individuals stop could be expected to be different for the two separate migrations. For example, during post-breeding migration body condition may be very different (having just completed an energy intensive breeding season), making frequent stopovers essential. There are known carryover effects from breeding in this species, acting on the post-breeding migration and wintering behaviour (Shoji et al., 2015). Birds may leave for their northbound migration already in good condition and therefore have the freedom to choose if and where they pause. However the proportion of time spent in stopover behaviour was not vastly different between the two migrations in this study, being a little over 30% in both directions.

Individual repeatability in stopover behaviour has been uncovered in many bird species, including thrushes (Delmore, Fox, & Irwin, 2012), raptors (Alerstam, Hake, & Kjellén, 2006; Vardanis et al., 2011) and seabirds (Fifield et al., 2014). The drivers behind stopover strategies in seabirds are still being investigated, especially since it raises interesting navigational questions regarding how birds find suitable locations. The marine environment is highly variable, with resource patches occurring at a variety of spatial scales (Weimerskirch, 2007). At-sea search or navigation mechanisms might include use of olfactory or visual cues (such other animals foraging or areas of water turbulence indicating the presence of fish). Both of these systems for orientation and location of foraging areas have been identified in other seabird species (Silverman, Veit, & Nevitt, 2004; Nevitt, Reid, & Trathan, 2004; Norden & Pierre, 2007; Gagliardo et al., 2013) .

Archival light and saltwater immersion loggers have many advantages for studying long distance movements over several seasons, including their small size, relatively cheap costs (compared to other devices), and longevity. Additionally, similar loggers have been used on a wide range of species, making comparisons with other studies possible. Geolocation data have some drawbacks for identifying spatial variation in individual behaviour, mostly due to limitations in the accuracy of the location estimates (Phillips et al., 2004). Large portions of spatial data also need to be removed around the spring and autumn equinoxes due to the global equality of day lengths at these times of year. This can lead to large gaps in the dataset, particularly where individuals consistently migrate at these times of year, meaning their migrations cannot be accurately measured. Currently, size is limiting what devices can be deployed on smaller species for the long non-breeding period. However, as GPS logging technology improves and becomes further miniaturized, this may enable more accurate studies of individual fidelity.

4.4.2 Colony differences in stopover behaviour

No colony–level differences in stopover behaviour (either location or amount) were identified during southbound migration. Birds from all colonies exhibited stopover behaviour off the east coast of South America and in areas at the narrowest point between Africa and South America. This location is similar to the overwintering location identified for Cory's shearwaters, *Calonectris borealis* (Catry, et al., 2011). However the lack of differentiation between colonies on this migration does not necessarily signify the absence of differences; the much lower number of complete tracks on that route (n=21) means that there is less data and less statistical power to detect a difference. Many migrations had to be excluded from this analysis after removal of equinox points resulted in incomplete migrations.

By contrast, stopover locations differed between colonies during the northbound migration, with the main variation apparently due to the number of stopovers occurring in the north-east Atlantic. Birds from Lundy in particular appeared to stopover less often once they were nearer to the breeding area (figure 4.6). This could be explained by the differences in migration route found in chapter 3, which showed Lundy birds taking a slightly more westerly route during the latter half of the northbound migration (figure 3.2).

Birds from all colonies predominantly stopped in an area in the middle of the north Atlantic during the northbound migration (northern end of the Mid-Atlantic Ridge). The occupancy kernel estimates show an area covering from roughly 36° to 54°N, north of the Azores. Several marine bird species (Atlantic puffin *Fratercula arctica*, black-legged kittiwake *Rissa tridactyla*, little auk *Alle alle,* and sooty shearwater *Puffinus griseus*) also appear to aggregate in this region, both during the boreal winter months and in the summer (Guilford et al. 2011; Frederiksen et al., 2011; Hedd et al., 2012; Fort et al., 2013). This suggests the existence of mid-north Atlantic hotspots (Fort et al., 2012; Bennison & Jessopp, 2015). Manx shearwaters tracked (using GPS devices) during the breeding season from several colonies have been recorded using this mid-Atlantic location amongst others (Rockall Bank, Porcupine bank and edge of continental shelf, Dean, 2012). In addition, birds frequently stopover in a region off the east coast of the USA, near Bermuda, as well as an area to the east of the Caribbean Islands and north of Brazil and French Guiana.

4.4.3 Differences between the sexes

There were very few differences between male and female Manx shearwaters in the stopover behaviour recorded here. Both sexes used similar regions in the north Atlantic and spent a similar amount of time in stopover behaviour. This suggests that migratory stopovers fulfil the same role for both species, most likely resting and refuelling to survive migration, rather than being closely linked to differences in resource requirements during the breeding season that would necessitate sex differences. The lack of behavioural differences between the sexes is not unexpected given that Manx shearwaters are sexually monomorphic. Where sexual segregation of behaviour occurs in seabirds, it is usually in dimorphic species (Phillips, Silk, & Croxall, 2005; Phillip et al., 2009) but not always (Hedd et al., 2014) .

4.4.4 Annual patterns in stopover behaviour

Interestingly, there were significant inter-year differences in stopover locations on the northbound migration; tracks in the same year were more similar than tracks by different birds in different years. There was also significant inter-annual variation in the amount of stopover behaviour between years; with the proportion of migration in stopover varying from around 24% to around 40% on both migrations. These differences suggest that Manx shearwaters across all colonies may adapt their stopover behaviour in response to temporal and spatial variation in resource availability.

Stopover behaviour of Manx shearwaters breeding at Copeland was influenced by environmental factors (Freeman et al., 2013). Stopover behaviour was particularly linked with variation in sea surface temperature, chlorophyll-α and net primary productivity. Whilst many factors can influence spatial and temporal variability in metrics of marine productivity such as these, the effects of the El Niño-Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) are known to be particularly strong. The effects of ENSO and NAO on seabirds in the Atlantic Ocean have recently been documented (Velarde, Ezcurra, Cisneros-Mata, & Lavín, 2004) (Wood et al., 2015 *in prep*) (Sandvik et al., 2005; Szostek, Bouwhuis, & Becker, 2015; Szostek & Becker, 2015) .

4.4.5 Stopover identification and methodology

This chapter employed a novel methodology to identifying stopover behaviour: deriving aggregate metrics from immersion data; using an unsupervised classification procedure to classify tracks into time series of three behavioural states; and identifying sustained periods of non-migratory behaviour to label stopover events. This procedure was automated, relatively objective and computationally efficient. This method could therefore be used to study stopover behaviour in other pelagic bird species for which saltwater immersion data have been collected. Activity loggers such as these devices (and also time-depth recorders, GPS and accelerometers) have been deployed on a wide range of seabird species and different techniques are being developed to objectively identify different behaviours (Dean et al., 2012, Freeman et al., 2013, Linnebjerg et al., 2013, Evans, et al., 2013, Collins et al., 2015, Fayet et al., 2015, Scales et al., 2015). Classification of data by clustering analyses (such as the unsupervised classifier used here) is relatively simple to implement in data analysis environments such as R and Python, by comparison with more complex neural network or hidden Markov modelling used for sequential classification.

The three behavioural identified by the GMM were considered to represent flight, resting and foraging, based on the values of the saltwater immersion metrics corresponding to each class. These behavioural classes, and their relationships with the metrics chosen by the variable selection procedure, have been previously identified in this species using the same type of data (saltwater immersion from archival loggers, Guilford et al., 2009; Fayet et al., 2015). Indeed, two of the previous studies validated these behavioural classes using data from additional loggers (GPS and time-depth recorders, Dean et al., 2012; Freeman et al. 2013).

Each day of the migration track was considered to be a stopover day if the GMM identified the day as being spent in either the foraging or resting behavioural states (i.e. not flight), and which were part of a run of at least consecutive 3 days of such events.

Whilst this analysis combined days spent either in rafting or foraging behaviour as a single type of stopover, it is possible that there may in fact be two distinct types of stopover: resting stopovers (consistently spent resting) and refuelling stopovers (consistently spent foraging). This distinction between stopover types in the Manx shearwater was hypothesised by Guilford *et al*. (2009). Similarly, Warnock (2010) proposed to distinguish between migratory stopping (for a short period of time, in the middle of migration) and staging (where large groups of individuals may gather before a long distance movement.) behaviour in although this suits group migrant species more (such as shorebirds and waterfowl). It may be that resting stopovers occur when a bird has no choice but to stop, either because of physiological limits or adverse weather conditions during the day, and that foraging stopovers may be more targeted at high productivity areas. It might therefore be expected that foraging/refuelling stopovers more often occur at a location that is already familiar to the bird (from previous migrations) and may be a reliably productive location for feeding. If this is the case, higher fidelity to foraging stopover regions than to resting stopovers might be expected.

4.4.6 Conclusions

Stopover behaviour is common to many avian migrants, including both terrestrial and marine species. Stopovers are a strategy to minimise the impact of a potentially costly period of long distance movement, and individual repeatability in stopover location has been identified in a number of species. This chapter reports significant individual consistency in stopover behaviour in the Manx shearwater, and quantifies the areas used for stopover bay a large, representative a sample of the UK breeding population of this species. Several areas in the north Atlantic are used by birds from all breeding colonies, with these locations changing between years suggesting that there are shifting foraging “hotspots” used by birds, especially on the pre-breeding migration. This could have implications for the conservation of not only this species, but other seabirds which use a similar area (Guilford et al., 2011; Frederiksen et al., 2011; Bennison & Jessopp, 2015). There are many potential drivers for the variation in stopover locations shown here, both intrinsic and extrinsic, and some may be explained by other behaviour during migration (for example timing and the migration route). The relationships between different behaviours and timing of key events during migration are explored in chapter 6 of this thesis.

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Chapter 5

Breeding phenology in the Manx shearwater: a multi-colony study

5.1 Introduction

Despite many observational studies at breeding colonies (Brooke, 1990; Gray, 2001; Bried, 2003; Quillfeldt, Masello, & Hamer, 2004; Bourgeois et al., 2008; Guilford et al., 2012) much remains to be understood about the breeding biology of shearwaters. In large part, this is due to difficulties in observing these nocturnal (when on the breeding colony), burrow-dwelling birds. Particularly poorly understood are inter-annual variation and inter-colony differences in the timing of breeding events and whether individuals behave consistently over several years.

Quantifying temporal variation and individual repeatability in timing of key breeding season events is key to understanding how birds may respond to environmental stochasticity. Timing of events such as arrival at the colony and start of incubation are highly correlated with annual temperature trends and peaks in productivity in a number of bird species (Both & Visser, 2001; Frederiksen & Harris, 2004; Charmantier et al., 2008; Lany et al., 2016). If birds are unable to adapt to changing conditions, this may lead to a mismatch between breeding and resource availability, with consequences for reproductive output (Hipfner, 2008; Burthe et al., 2012; Regular et al., 2014). Marine habitats at higher latitudes are changing rapidly, reflecting the combined effects of climate change and anthropogenic activities (Halpern et al., 2008); (Sydeman & Bograd, 2009); (Bicknell et al., 2013); (Fort et al., 2013). In this context, there is a pressing need to improve our understanding of individual and population responses to environmental variability, in order to predict consequences of habitat change for survival and population dynamics.

Studying behaviour in any wild species can require a combination of relatively invasive techniques coupled with intense periods of observation, both of which may have adverse effects on the study species and data quality. The so called 'observer effect' can alter an animal's behaviour even if the individual does not appear outwardly stressed (McDougall, 2011; Walker, Boersma, & Wingfield, 2006). However, single or occasional observations of animals are rarely sufficient to studies of animal behaviour, which usually requires large amounts of data.

A possible solution to this problem was brought by recent advances in automated data logging technology, which now allow researchers to collect high quality and high-resolution data whilst causing minimal disturbance to the study species. This technology also enables observation of the behaviour of organisms living in less accessible habitats, where high intensity observational data collection would otherwise be impossible. Bird-borne loggers (e.g. GPS, geolocators, accelerometers and time-depth loggers (Hunt & Wilson, 2012)) and nest or burrow based recording systems (e.g. RFID (radio frequency identification), temperature and humidity loggers, infra-red cameras (Zangmeister et al., 2009; Ohashi, D'Souza, & Thomson, 2010, Bridge & Bonter, 2011; Taylor & Cockburn, 2012)) have been used to study a range of avian behaviours, including breeding season movements, migration, foraging efforts, social and breeding pair interactions (Taylor & Cockburn, 2012, Hou, Verdirame, & Welch, 2015, Firth et al., 2015). Although there are limitations to these automated systems, which may require calibration with behavioural observations, regular upkeep and reliable power supplies (Bonter & Bridge, 2011, Hunt & Wilson, 2012), there can be no doubt that these methods can be useful tools for ornithologists.

In particular, these methods may be useful studying seabird species, many of which nest in dense colonies that are difficult to access (for the purposes of predator avoidance); either on high cliffs or remote islands. Colonial nesting seabirds can be easily disturbed by the presence of humans, which can lead to nest abandonment and disruption of normal behaviour (Carney & Sydeman, 1999; Gaston, 2004). While bird-borne data loggers have been used on seabirds for nearly 50 years (Kooyman et al., 1971; Croxall et al., 1991), most recently, miniature GPS and geolocators have been used to reveal, often in complex detail, the at-sea movement and behaviour of these birds during both the breeding season and migration (González-Solís, Croxall, & Wood, 2000; Phillips et al. 2006; Votier et al. 2010; Guilford et al. 2012; Carneiro, Manica, & Phillips, 2014; Deppe et al., 2014; Evans et al., 2015; Hennicke, James, & Weimerskirch, 2015). Despite the potential to elucidate breeding season behaviour for large numbers of birds at broad spatial and temporal scales, no studies have so far used bird-borne loggers to quantify the behaviour of seabirds on the colony during the breeding season.

This study used light and saltwater immersion data collected over six years from Manx shearwaters on five colonies to study breeding-season phenology and behaviour. An unsupervised machine learning method was used to identify key behavioural states throughout the breeding season, and the resulting behavioural time series were used to estimate the timing of key breeding season events across all tracks, without the need for direct observation. The timing of key events was then compared across colonies, years, sexes and individuals to partition variation in timing of each event amongst these different explanatory variables.

5.2 Methods

5.2.1 Data pre-processing

This study used both light and saltwater immersion data from loggers deployed on birds from five colonies of Manx shearwaters between 2006 and 2012; collected using methods detailed in Chapter 2. The study site on the Skomer colony is relatively large and has been regularly visited since 2007. Smaller study sites were subsequently been established on Ramsey, Lundy, Copeland and Rum. Whilst ancillary data and direct observation are possible during the breeding season on Skomer, the other colonies could only be visited once every season. Ancillary data and observations are therefore unavailable from these other colonies. Birds that failed to breed on Skomer were excluded from this analysis.

Whereas Chapter 4 used immersion data during the migratory period, this chapter employs these data, in conjunction with data on light levels, during the breeding season. Since loggers on each bird were changed during the breeding period, each breeding period track was obtained by combining the relevant sections from each of the two logger files for each bird/breeding season. The breeding period for each tracked individual in each year was defined as starting on the first date after the bird first crossed a line of -10 degrees longitude on pre-breeding migration, and ending on the first date after the bird crossed this same line on post-breeding migration, as calculated in Chapter 2. Logger data were available for the entire breeding period for 89 tracks from 59 individual birds.

Raw saltwater immersion loggers took conductivity readings every 3 seconds, and logged these over ten-minute periods as an integer between 0 (no conductivity) and

200 (conductivity on all readings). Loggers also recorded light levels over ten-minute periods as a value between 0 (no light) and 64 (full light).

As in Chapter 4 and previous studies (Yamamoto et al., 2008; Guilford et al., 2009; Dias, Granadeiro, & Catry, 2012b; Péron & Grémillet, 2013), a binary immersion variable was also calculated for each ten-minute period, classified as ‘wet’ if the corresponding saltwater immersion value was 100 or greater (indicating at least half of the time spent immersed), conversely ‘dry’ if the value was lower than 100.

These ten-minute period salt and light values, and the binary wet/dry variable were then aggregated over two-hour periods to derive metrics of both the magnitude and the variability of each measure over a comparatively small time window. Since it is unclear which aggregation metrics are likely to be the most representative, 13 different metrics of each of these variables (9 immersion and 4 light metrics) were calculated within each two-hour time window for each breeding period track. These are listed in Table 5.1.

Table 5.1. Immersion metrics calculated across the daylight hours for each day, from 10-minute immersion records.

Metric	*Description*
Mean light	Mean light value
Min. light	Minimum light value
Max. light	Maximum light value
Variance light	Variance of light values
Min. immersion	Minimum saltwater immersion value
Max. immersion	Maximum saltwater immersion value
Variance immersion	Variance of saltwater immersion values
Diff. immersion	Differential of saltwater immersion value during the day (a sequential measure of variation)
Proportion wet	Proportion of time spent in 'wet' events
Logit Prop. wet	Logit-transformed proportion wet (rescaling to a continuous variable)
Total wet events	Total number of 'wet' events
Mean wet bout length	Mean duration of 'wet' bouts (mean number of contiguous 'wet' events)
Total wet bouts	Total number of 'wet' bouts (number of runs of successive 'wet' events)

5.2.2 Selection of metrics

Calculation of the absolute Pearson correlation matrix among all 13 metrics across all tracks indicated that there were significant correlations between many of these metrics. In order to identify a subset of minimally correlated metrics for use in classifying behaviours, a principal components analysis was carried out on these data. The first four principal components explained over 97% of variance in the dataset. The first two components appeared to represent the magnitude and variance of immersion data: the first component had large positive loadings for, minimum, and maximum immersion value, proportion and logit-transformed proportion wet, total wet events, and mean wet bout length; and the second had large positive loadings for the total number of wet bouts, and the variance and differential of the immersion data. The biological interpretation of the next two components was much less clear. Whilst these orthogonal principal components could have been extracted and used in the classifier, the lack of interpretability of these components would have hindered inference about the behavioural states corresponding to the outputs of the classifier. Instead, the metrics with the largest loading coefficients for each of these components was used instead. These metrics were: logit-transformed proportion of time spent 'wet'; differential of the saltwater immersion data; mean light value; and variance of the saltwater immersion data. Absolute pairwise correlation coefficients among the four selected metrics were all lower than 0.7, whereas correlations among the excluded variables all exceeded 0.8.

5.2.3 Classification using a GMM

A suite of GMMs were fitted to the dataset for all birds using version 4.2 of the `mclust` R package. These 90 models represented all combinations of 10 potential model specifications with varying flexibility (variously allowing for scaling, isotropy, and rotation of the mixture components), each with between 1 and 9 mixture components. The optimal model specification and number of mixture component distributions used to fit the global model was selected by minimising the Bayesian Information Criterion (BIC). The optimal model was then used to predict two-hourly behaviour classes during the breeding period for each bird. The optimal model used the 'VEV' specification (enabling ellipsoidal, but equally-shaped and equal volume mixture distributions) and identified 4 different behaviour classes based on the saltwater immersion and light data.

Further investigation showed that proportion-wet data in class 1 was very strongly bimodally distributed around 0 and 1 (no time spent wet, or all time spent wet). Whilst the model did not consider these two peaks to be distinct clusters, they are indicative of distinct behaviours, flying and rafting respectively. This class was therefore split into 2 separate classes, where proportion of time spent wet was either greater or less than 0.5. This resulted in a total of five classes. The final model was then used to assign each two-hour window from each track in the dataset to the most likely of the 5 classes, based on the metrics for that class.

5.2.4 Inferred behavioural classes

The 5 classes identified by the GMM procedure were interpreted as behavioural classes by inspecting the distribution of each of the 4 selected variables within each class (Figure 5.1).

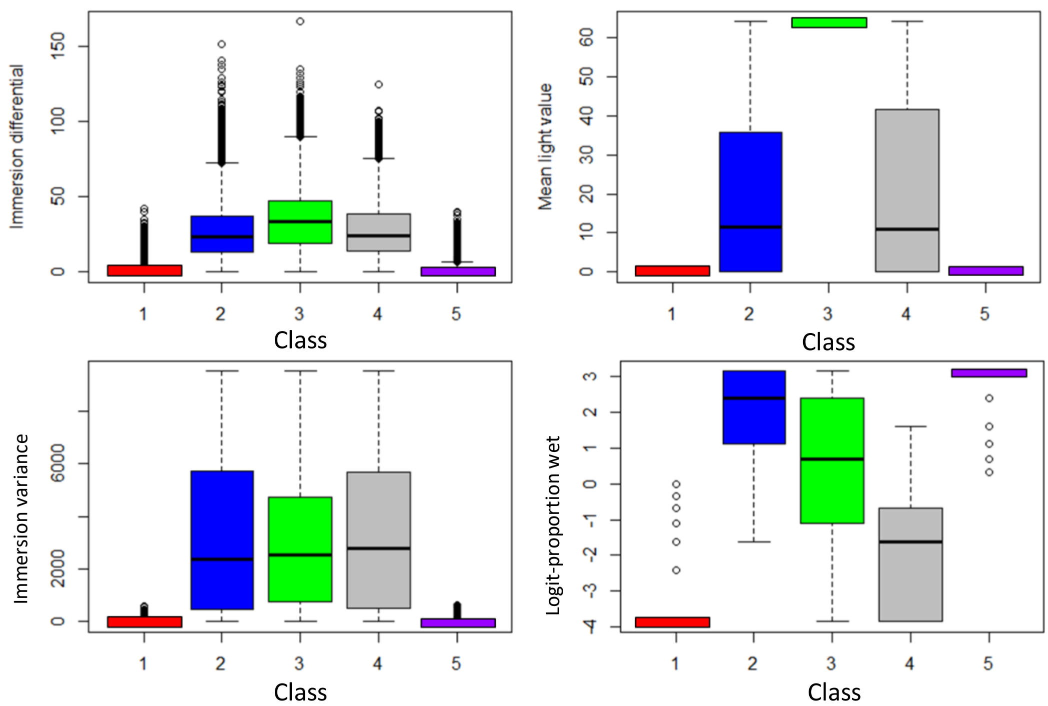

Figure 5.1 Boxplots of the four variables used in the Gaussian mixture model; immersion differential, mean light value, variance of immersion, logit-transformed proportion of time spent wet. The variables are coloured according the class assigned by the GMM.

For example, class 1 (red in figure 5.1) corresponds consistently (low variance and low differential) with dry (low proportion of time spent wet), dark (low mean light value) periods which can only be explained either by time in the breeding burrow, or by nighttime flight. The inferred behavioural states corresponding to each of the classes are given in Table 5.2. The proportion of time spent in each behaviour class was calculated for each track, along with the overall proportion of time spent 'wet' during the breeding period.

Table 5.2. Behavioural interpretation of the five classes identified by the optimal GMM.

Class	*Colour in figures*	*Behavioural state*	*Description*
1	Red	dark & dry	Days spent in the breeding burrow, or nighttime flight. Seen during the incubation stints and also during the migratory period.
2	Blue	wetter movement	An intermediate flight or foraging behaviour, possibly taking place more often at dusk. Seen throughout the annual cycle.
3	Green	daytime flight	Seen during the overwintering period, migration and during the breeding season.
4	Grey	drier movement	Periods of flight, but occurring more often at night than during the day. Occurred during the migration period and also at night during the breeding season.
5	Purple	rafting	Always at night and consistently wet. Seen throughout the annual cycle.

5.2.5 Inferring the timing of key events

For each breeding season track, the time series of dominant behavioural classes in each two-hour window were used to extract the most likely dates of key breeding season events. The first night spent at the colony was assumed to be the first long period spent dry after migration, either inside or outside a burrow. The date of the first night on the colony was therefore estimated as the date of the start of a continuous period of 6 or more hours (3 or more consecutive two-hour time windows) spent in class 1 (dark and dry) and/or class 4 (drier movement). The first day spent in the burrow will be represented by prolonged period being both dry and dark. The date for this event was therefore as estimated as the date at the beginning of the first continuous 12 or more hours (6 or more consecutive two-hour windows) of class 1 (dark and dry) records. Incubation stints will also be dark and dry but of longer duration; the average incubation stint of a Manx shearwater is usually > 5 days (Brooke, 1990). Incubation stints were therefore defined as bouts of consecutive class 1 (dark and dry) records covering at least 48 hours. The dates of the start of the first incubation stint and end of the last incubation stint, and the number and mean duration of incubation stints were then calculated from these estimated incubation stints. Similarly to the first night spent on the colony, the date of the last night spent on the colony was taken to be the date at the end of the last consecutive period of four or more hours of class 1 (dark and dry) and/or 4 (drier movement).

This procedure for identifying dates from inferred behavioural classes was validated for a subset of birds breeding at the Skomer colony by comparing the GMM-inferred dates with estimated dates recorded by direct observation of 14 birds breeding in accessible burrows on Skomer.

5.2.6 Statistical analysis of breeding phenology

Inter-colony, inter-year and inter-sex variation and individual consistency in these dates and the number and mean length of bouts was then assessed using linear mixed models (LMMs). Following the methods outlined in Chapter 2, for each variable tested the optimal model was selected by AIC, and the explanatory power of each of the fixed effects (colony and year) was assessed by model comparison F tests. Marginal (fixed and random effects) and conditional (fixed effects) R^2 statistics were obtained using the methods outlined by Nakagawa & Schielzeth, (2013). Where the random effect (individual, nested within colony) for each final model explained a greater proportion of variation than the fixed effects, repeatability analysis (using the R package `rptR`) was used to ascertain if individual shearwaters behaved consistently from one breeding season to the next. As in previous chapters, sex was only know for a subset of birds, so the effect of sex on each response variable was assessed by refitting the optimal model on this data subset, and comparing this with a model with sex added as an additional fixed effect.

The mean incubation stint length and number of stints were both log transformed prior modelling with LMMs. Whilst both of these variables are ordinal, they are not counts (they can never take value zero, nor can they be considered independent, or clustered events) and generalised mixed effects models for count data would therefore not be appropriate. Visual checks confirmed that the log-transformed variables followed a Gaussian distribution.

The overall relationship between number of incubation stints and the mean length of incubation stints was assessed using a linear mixed model to regress the log number of incubation stints against the log mean incubation stint length, with individual nested within colony as a random effect. Since the regression coefficient of a univariate fixed-effects linear regression coincides with the Pearson correlation coefficient between the two variables, the coefficient in this mixed-effects extension is analogous to the correlation coefficient, but this approach accounted for the potential violation of independence introduced by individual consistency.

5.3 Results

5.3.1 Visualisation of behavioural time series

Behavioural time series constructed from logger data provided an unprecedented continuous view of the behaviour of individual Manx shearwaters throughout their breeding period. As an example of the qualitative perspective these time series provide, figures 5.2 – 5.4 illustrate the succession of behaviours throughout an entire breeding season for a pair of birds breeding in the Copeland Island study plot. The alternating incubation patterns between the two birds show how the pair synchronise their behaviour (figure 5.2). There is a period of one day spent in the burrow together in early April. This is immediately followed by the female spending several days in classes 2 and 3 (figure 5.1, flight and foraging behaviour, green and blue) with no night time returns to the colony, corresponding well with the pre-laying exodus identified in this species (Brooke, 1990; Guilford et al. 2009; Dean 2012). The time series in Figure 5.4 cover the chick rearing period and show the last time the bird spent time at the breeding colony (classes 1 and 4 shown in red and grey).

5.3.2 Validation of estimated dates

Data collected manually by burrow inspection on Skomer were used to validate the breeding dates estimated from the logger data. Burrow inspection allows accurate identification of laying dates, hatching date and an estimation of fledging date for a breeding pair, but was only available for 14 of the birds represented in the logging database (Appendix 5A). There was an average of 2 days difference between the observed laying date and estimated date of first incubation behaviour, and an average of 1 day difference between observed hatching date and the estimated date of last incubation. The last time an individual spent on the colony was on average 11 days before the chick left the burrow and never after.

5.3.3 Timing of breeding behaviour

The main dates and behaviours extracted using the GMM for each of the five breeding colonies are summarised in table 5.3. Annual variation in phenology of the entire breeding season for Copeland, Skomer and Lundy (colonies with the most data) is illustrated in figure 5.5. Both the date of the first night spent on the breeding colony and the first day in the breeding burrow differed between colonies (first night on colony: $F_4 = 7.565$, $p < 0.001$; first day in burrow: $F_4 = 3.245$, $p = 0.0159$, figure 5.6) but not between years (first night on colony: $F_5 = 0.075$, $p = 0.9959$; first day in burrow: $F_5 = 0.975$, $p = 0.4368$). Date of first night on the colony appeared to follow a latitudinal gradient with earlier arrivals in the southern most colonies (median date 2nd April on Ramsey and Lundy) than in the most northerly colony (median date 19th April on Rum)

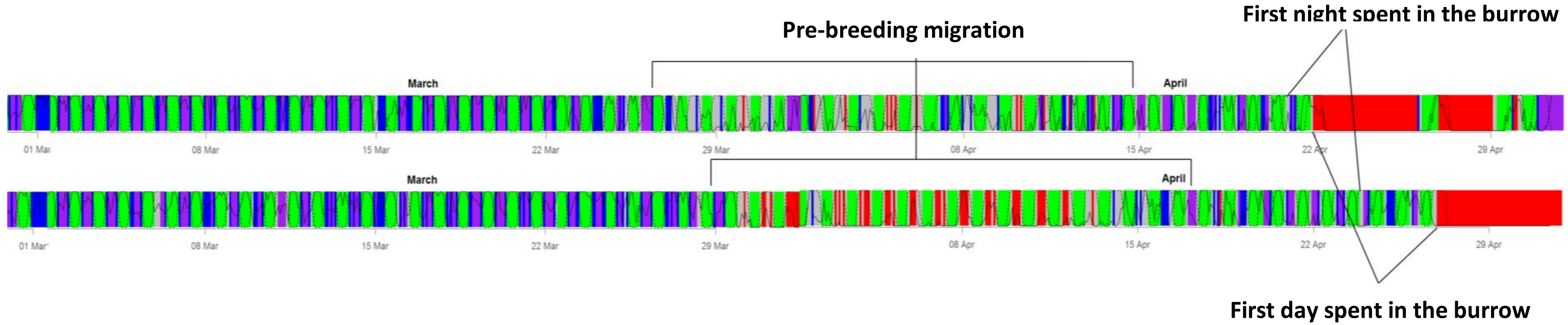

Figure 5.2. Example behavioural time series for a breeding pair of Manx shearwaters (female top, male bottom) from March to April. Colours indicate behavioural states as follows: red = dark & dry (class 1); blue = wetter movement (class 2); green = daytime flight (class 3); grey = drier movement (class 4); purple = rafting (class 5). Lines give the mean values over each two-hour period of the raw immersion (dashed) and light (solid) data.

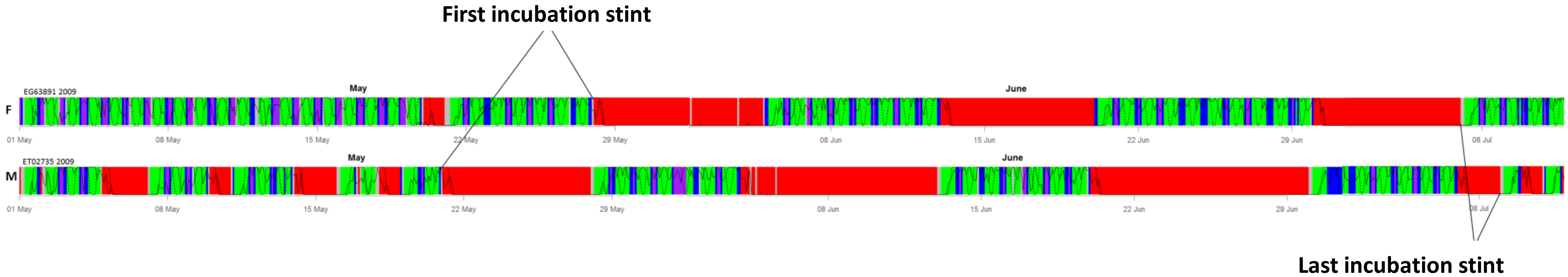

Figure 5.3. Example behavioural time series for a breeding pair of Manx shearwaters (female top, male bottom) from May to June. Colours indicate behavioural states as follows: red = dark & dry (class 1); blue = wetter movement (class 2); green = daytime flight (class 3); grey = drier movement (class 4); purple = rafting (class 5). Lines give the mean values over each two-hour period of the raw immersion (dashed) and light (solid) data.

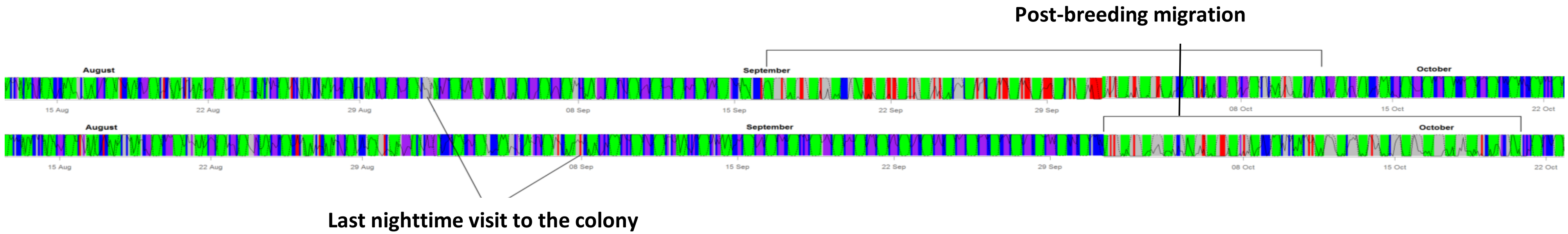

Figure 5.4. Example behavioural time series for a breeding pair of Manx shearwaters (female top, male bottom) from September to October. Colours indicate behavioural states as follows: red = dark & dry (class 1); blue = wetter movement (class 2); green = daytime flight (class 3); grey = drier movement (class 4); purple = rafting (class 5). Lines give the mean values over each two-hour period of the raw immersion (dashed) and light (solid) data.

Table 5.3. Summary of the main breeding dates for each breeding colony collected from the classified data. Values are summarised by their median for dates, or their mean for other values. Standard deviations are given in beneath and are given in days for dates.

	First night on the colony	First day in the burrow	First incubation stint	Last incubation stint	Number of incubation stints	Mean stint length (days)	Maximum stint length (days)	Last night on the colony
Overall	12-Apr	14-Apr	18-May	11-Jul	7.33	3.71	7.86	31-Aug
n=183	11.43	11.56	13.95	11.85	2.83	1.19	2.54	11.51
Rum	19-Apr	21-Apr	20-May	10-Jul	4.62	4.77	9.23	-
n=14	11.86	10.70	13.44	5.36	1.89	1.59	1.74	
Copeland	15-Apr	17-Apr	18-May	12-Jul	7.93	2.97	6.81	04-Sep
n=56	9.35	8.92	11.5	8.3	2.79	1.05	2.57	7.52
Ramsey	02-Apr	11-Apr	14-May	12-Jul	8.67	4.33	9.33	-
n=6	14.43	8.79	16.58	11.19	3.82	1.60	1.70	
Skomer	13-Apr	18-Apr	21-May	13-Jul	7.17	3.23	6.98	29-Aug
n=75	10.17	12.7	16.56	14.42	2.79	1.18	2.13	14.10
Lundy	02-Apr	9-Apr	15-May	5-Jul	8.26	3.26	6.96	27-Aug
n=33	9.00	9.71	9.14	8.13	1.85	0.69	1.40	9.71
Females	14-Apr	17-Apr	20-May	12-Jul	6.25	3.15	6.78	29-Aug
n=81	11.50	12.35	12.53	12.46	2.31	1.16	2.36	12.96
Males	11-Apr	15-Apr	15-May	11-Jul	8.26	3.05	7.13	01-Sep
n=78	11.95	11.3	16.61	11.83	2.76	1.11	2.71	9.88

There was a similar pattern in timing of the first day spent in the breeding burrow, with Lundy birds earlier (median date 9th April) than those on Rum (21st April). Testing a subset of the data for which sex of each bird was known, there was no significant difference between sexes in either of these dates (first night on the colony $F_1 = 2.096$, $P = 0.1526$, first day in the burrow $F_1 = 0.35$, $P = 0.5563$). For the dates of first arrival at the colony and day spent in burrow, colony explained a good proportion of the variation within the data (R^2_{fixed}= 0.211 & 0.104).

There were no differences between years (F_5= 2.281, $P = 0.0519$) or breeding colonies (F_5= 0.874, $P = 0.4829$, figure 5.7) in the date of first incubation stint. However males were significantly earlier in their first incubation stint than females (F_1= 4.404, $p = 0.0397$, R^2_{fixed}=0.046, table 5.2). The date of the last incubation stint differed across the six study years (2007-2012) (F_4= 6.214, $P < 0.001$, R^2_{fixed}=0.178; table 5.4, figure 5.5) but not between colonies (F_4= 1.432, $P = 0.2304$, figure 5.7). Sex did not further explain the variation in last incubation stint ($F_1 < 0.001$, $P = 0.985$).

There were no significant effects of year ($F_4 = 2.046$, $p = 0.1063$), colony ($F_3 = 1.255$, $p = 0.3024$) or sex (F_1= 0.196, $p = 0.6606$) on the last night spent at the breeding colony.

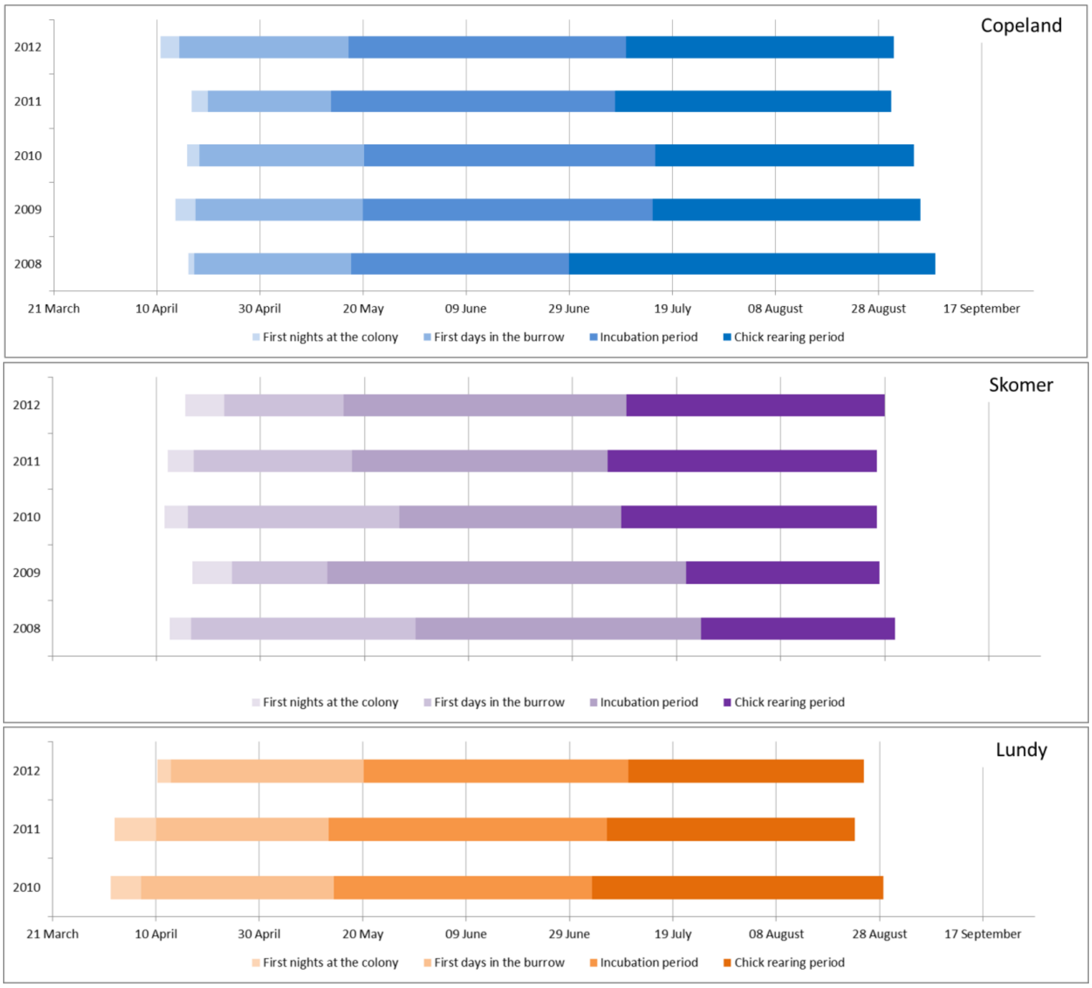

Figure 5.5. Median breeding season dates recorded from birds breeding on Copeland, Skomer and Lundy showing the variation between years. Only colonies where more than 5 birds were tracked for each year are included.

Table 5.4. Median date of last incubation stint during the different years of the study, showing 2008 and 2009 later than the following three years. Standard deviations are given in days.

	2008	**2009**	**2010**	**2011**	**2012**
Median	20-Jul	18-Jul	09-Jul	07-Jul	08-Jul
St. Dev.	16.43	12.39	9.10	10.01	10.21

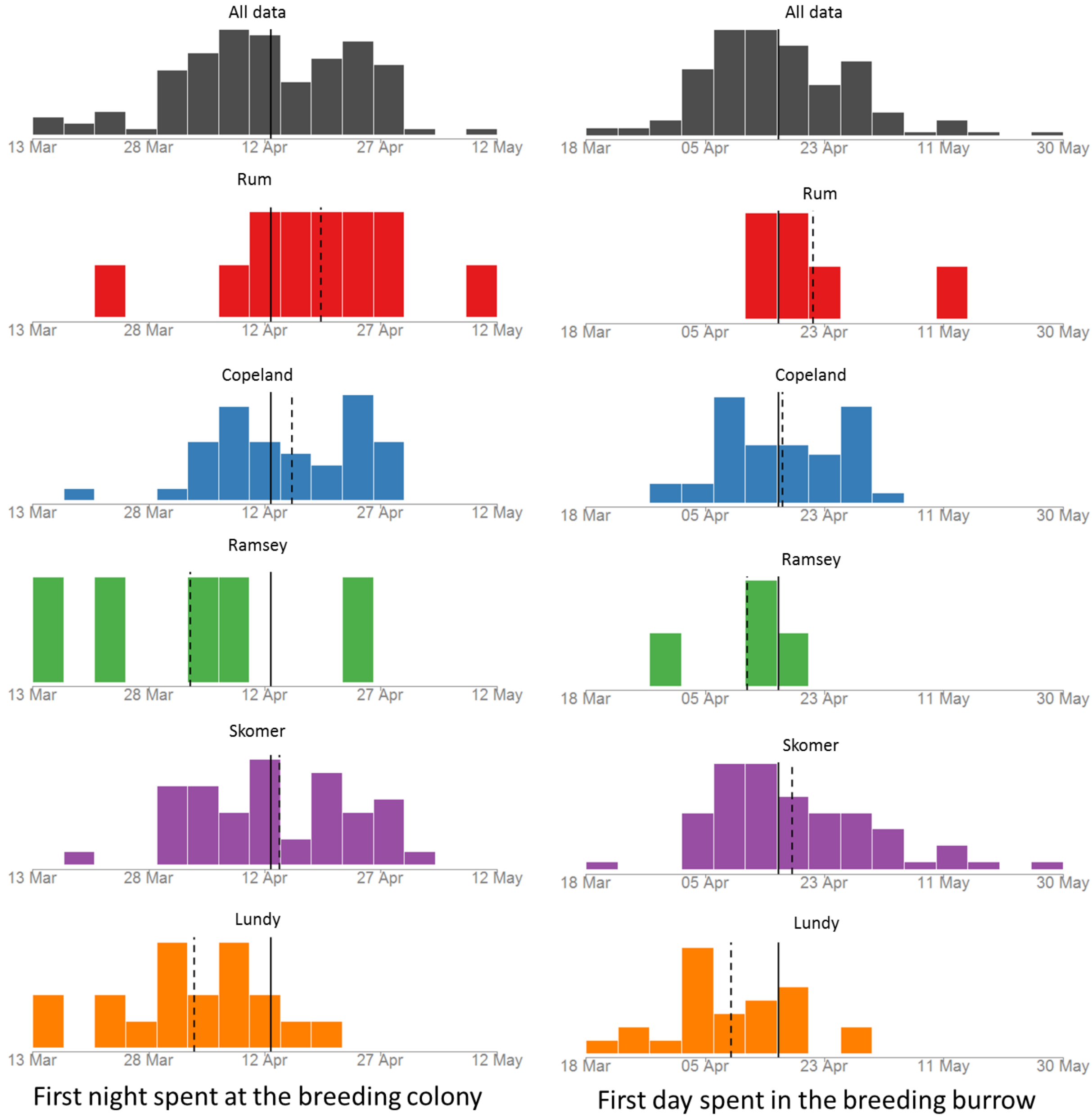

Figure 5.6. Inter-colony variation in colony arrival dates estimated from logger data: first night and first day spent in the burrow. Vertical lines indicate the colony level (dashed) and overall (solid) median dates. Colonies are plotted in order of latitude, with most northerly colonies at the top of the figure; birds from Lundy were than average in their return to the colony and birds from Rum were later.

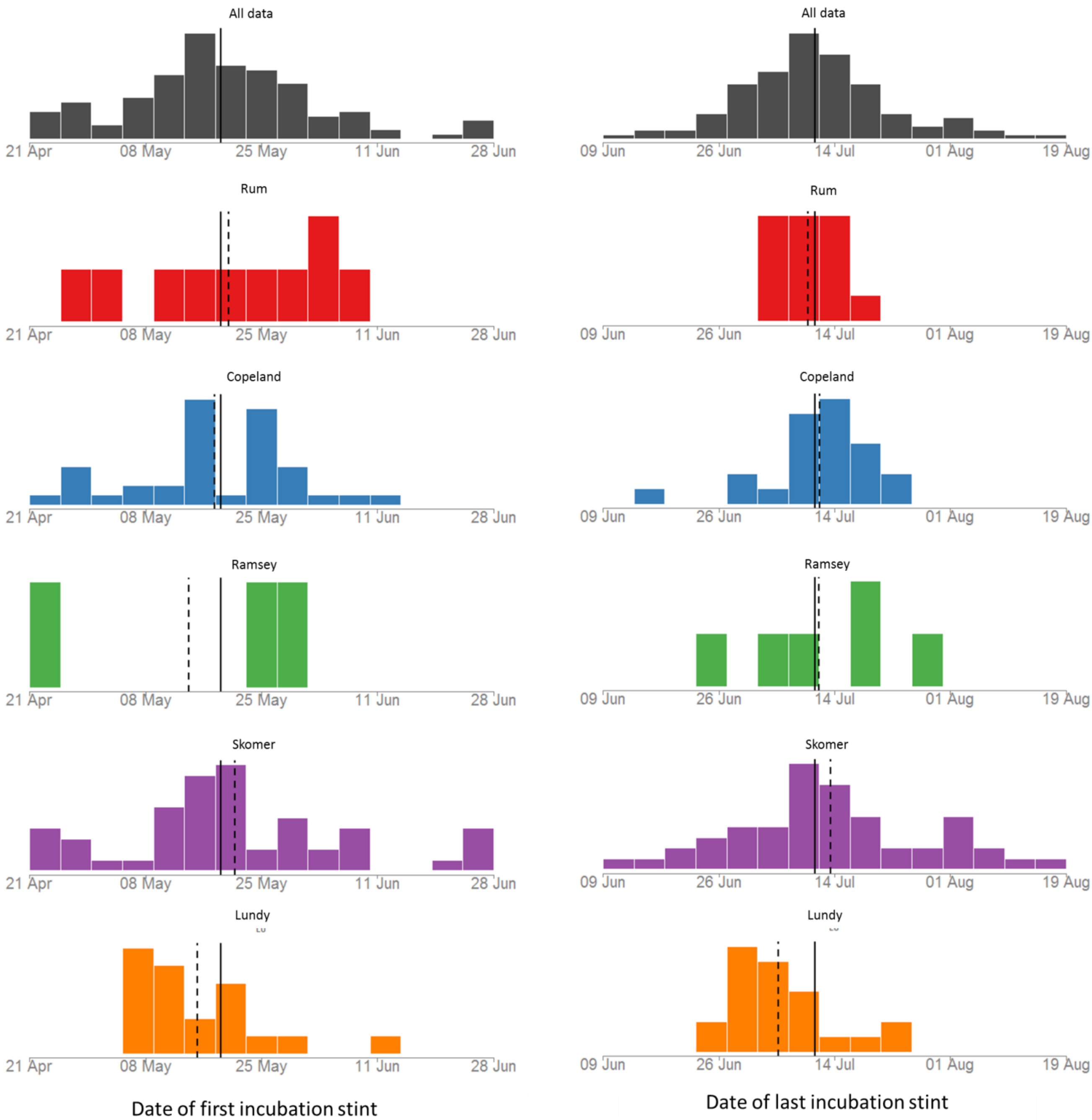

Figure 5.7. Inter-colony variation in timing of the incubation period estimated from logger data: start of the first incubation stint and end of the last incubation stint. Vertical lines indicate the colony level (dashed) and overall (solid) median dates. Colonies are plotted in order of latitude, with most northerly colonies at the top of the figure.

5.3.4 Individual repeatability

Investigating the effect of individual repeatability on the timing of key breeding season events identified significant individual repeatability in the date of first night spent on the colony (Rep = 0.343, SE = 0.152, p = 0.006), and the first day spent in the breeding burrow (Rep = 0.224, SE = 0.104, p < 0.001), see figure 5.8. There was statistically significant repeatability in the date of the first incubation stint (Rep = 0.064, SE = 0.079, p = 0.02) (figure 5.9). There was no significant individual repeatability in the date of the last incubation stint (Rep = 0.032, SE = 0.032, p = 0.084, figure 5.9), last night spent on the breeding colony, (Rep = 0.059, SE = 0.084, p = 0.545) or the number of incubation stints (Rep = 0.169, SE = 0.119, p = 0.124). Mean and max incubation stint length were not tested for individual repeatability as the sample size was too small (fewer than 3 repeated measures for each bird).

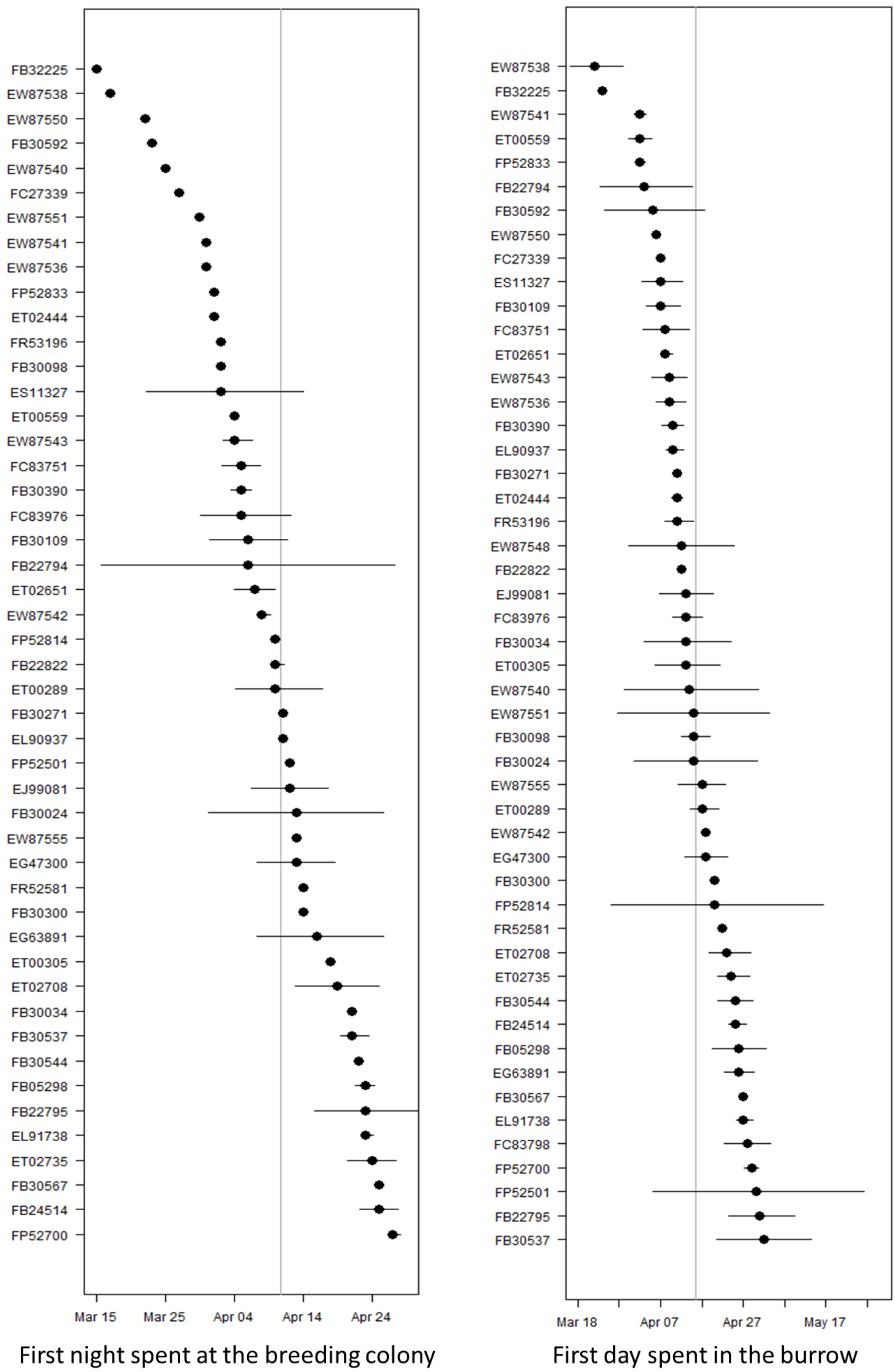

Figure 5.8. Individual repeatability in timing of first night spent at the breeding colony and the first day spent in the breeding burrow. Points give the mean date and bars indicate give a standard deviation either side of the mean for individuals tracked over three or more breeding seasons. The vertical line gives the overall mean.

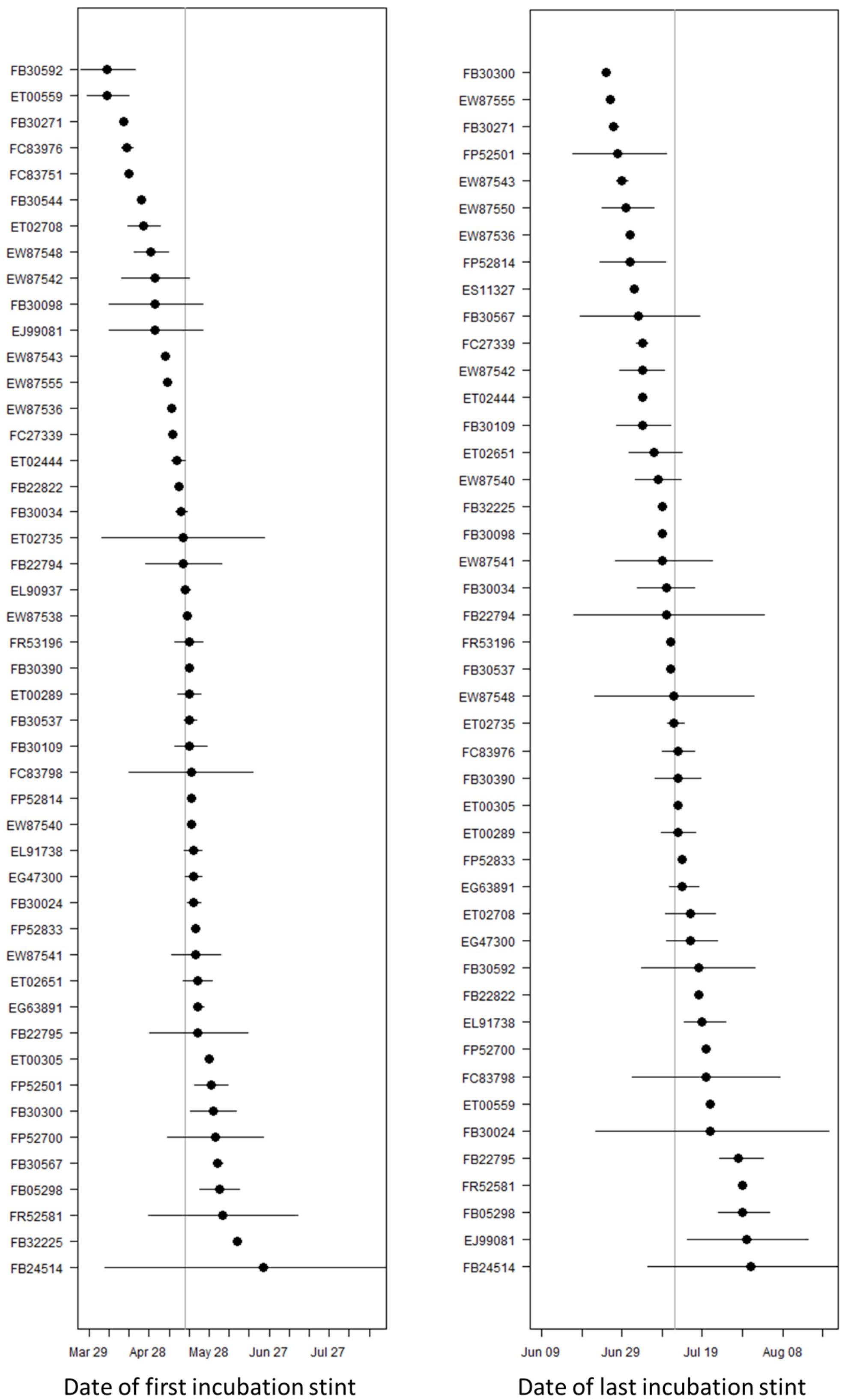

Figure 5.9. Individual repeatability in timing of start of first incubation stint and end of last incubation stint. Points give the mean date and bars indicate give a standard deviation either side of the mean for individuals tracked over three or more breeding seasons. The vertical line gives the overall mean.

5.3.5 Differences in incubation behaviour

Birds from different breeding colonies showed differences in the scheduling of incubation shifts and change-overs between partners. The total number of incubation stints a bird performed each season differed significantly between colonies ($F_4 = 6.052$, $p < 0.001$, $R^2_{fixed} = 0.173$, figure 5.10) but not years ($F_4 = 1.558$, $p = 0.193$). In general males also performed more incubation stints (mean = 8.26 stints) than females (mean = 6.25 stints) ($F_1 = 13.617$, $p < 0.001$, $R^2_{fixed} = 0.264$). Breeding colony also explained a significant proportion of the variation in mean ($F_4 = 5.559$, $p < 0.001$, $R^2_{fixed} = 0.170$) and maximum ($F_4 = 4.237$, $p = 0.0036$, $R^2_{fixed} = 0.135$) duration of individual incubation stints (figure 5.11). Year and sex did not explain any additional variance when added to the models for either mean stint length (year: $F_4 = 1.394$, $p = 0.2433$; sex: $F_1 = 0.139$, $p = 0.7109$) or maximum stint length (year: $F_4 = 0.713$, $p = 0.585$; sex: $F_1 = 0.186$, $p = 0.6676$).

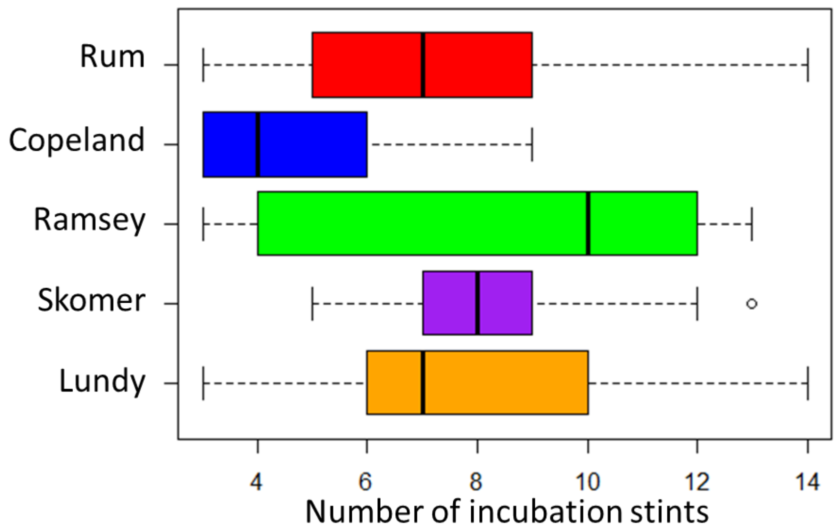

Figure 5.10. Inter-colony variation in the number of incubation stints observed in individual birds. Boxplots show the mean (bold line), interquartile range (box), 95% CI (dashed lines) and outliers (single points).

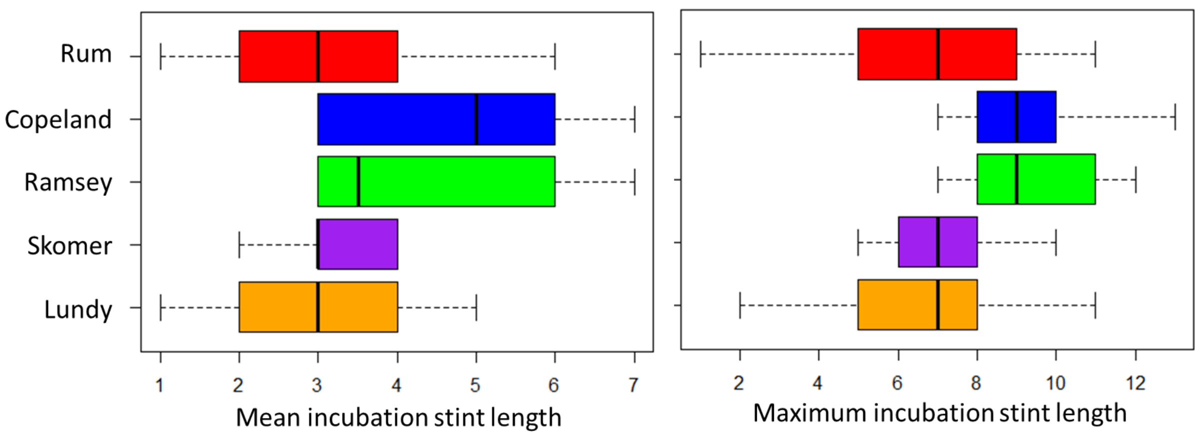

Figure 5.11. Inter-colony variation in mean and maximum incubation stint length, in days. Boxplots show the mean (bold line), interquartile range (box), 95% CI (dashed lines) and outliers (single points).

Examining the relationship between log-mean stint length and the log-total number of stints a bird undertook during each incubation period showed a strong, negative correlation (coefficient = -0.530, $p < 0.001$, accounting for individual-level effects). Birds with longer mean incubation stints had fewer stints (figure 5.12).

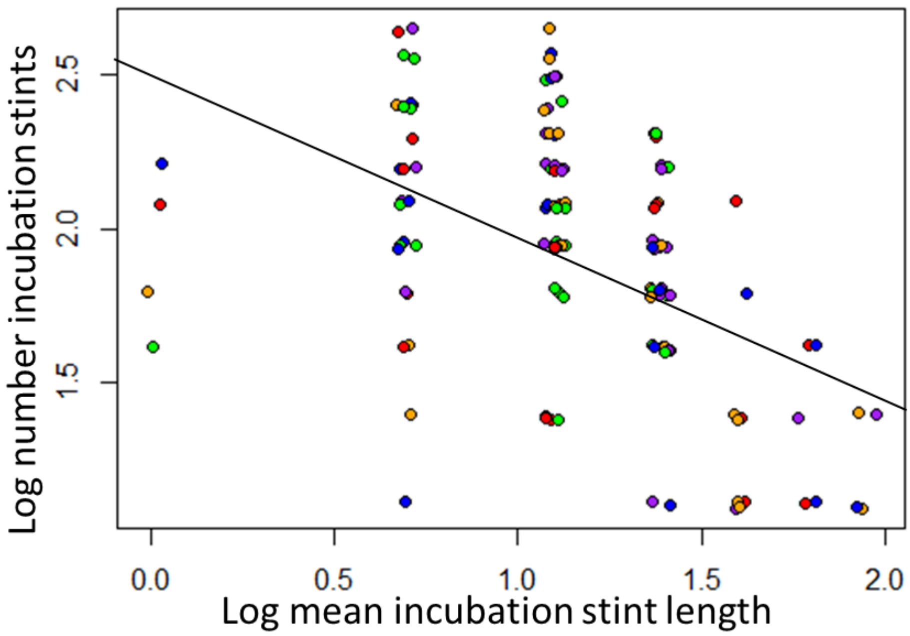

Figure 5.12. Relationship between the log number of incubation stints a bird undertakes in one season and the log mean length of those incubation stints. The points are coloured by colony and the black line represents the fixed-effect component of the linear mixed effect model. Points are jittered along the y axis to aid visualisation.

5.4 Discussion

This study used an automated procedure used to investigate the breeding behaviour of Manx shearwaters from 5 colonies in the UK. The main focus was on the timing of key events during the breeding season (timing of arrival at the breeding colony, the start and end incubation behaviour), particularly concentrating on inter-colony differences. Individual consistency in breeding phenology was also assessed, identifying an overall pattern of high repeatability in timing at the start of the breeding season and lower repeatability at the end.

5.4.1 Incubation behaviour

This is the first time that the timing of breeding behaviour has been compared across Manx shearwater colonies. The degree of variation between individual incubation regimes from fewer, longer incubation stints (3 seven-day stints) to many, shorter incubation stints (11 two-day stints) has not previously been reported. During breeding, synchrony (or mutual asynchrony) of behaviour in pairs is thought to be a determinant of breeding success (Mariette & Griffith, 2012; Sánchez-Macouzet, Rodríguez, & Drummond, 2014), and experienced pairs of Manx shearwaters have a higher reproductive success (Brooke, 1990). This may be important during the protracted incubation period of shearwaters since one of the main reasons for egg failure is being left unattended (Gaston & Powell, 1989; Brooke, 1990). The regulation of foraging trip length and incubation stint length during the incubation period has been the subject of studies on several seabird species, including albatross, giant petrels and Cory's shearwaters (Weimerskirch 1995; Mougin et al. 2000; González-solís 2004). These parameters are subject to conflict between foraging (which benefits individual fitness) and incubation (which benefits reproductive success, but usually causes loss of body condition) (Weimerskirch, 1995). This same trade-off could explain some of the variation in incubation strategies seen here. The mean length of incubation stint and the number of incubation stints a bird undertook over the breeding season were negatively correlated; individuals that exhibited longer incubation stints had fewer stints over the course of the incubation period. This relationship was consistent across all breeding colonies, but colonies differed significantly in mean incubation stint length and the total number of incubation stints. This suggests that differences in resource availability near to each colony may play a role in determining the optimal strategy in each location. If birds are able to forage successfully close to the colony, then the amount of time spent commuting to feeding locations and searching for food will be reduced (Ashmole, 1963; Warwick-Evans et al., 2016). Simultaneous GPS tracking of Manx shearwaters from Skomer and Copeland during the 2009, 2010 and 2011 incubation periods (Dean et al., 2015) detected inter-colony differences in foraging trip length. In this study, birds from Copeland foraged approximately 100km closer to the breeding colony than those from Skomer (2010 and 2011) (Dean et al., 2015). Copeland birds might therefore be expected to have shorter incubation stints since they do not need to fly as far in order to forage. However, in this analysis, birds from both Copeland and Skomer exhibited longer incubation stint durations than the other colonies during the 2010 and 2011. This suggests that foraging area during incubation does not necessarily determine the incubation behaviour undertaken by the breeding pair. Alternatively, shorter incubation stints may also mean that the general condition of the incubating individual does not deteriorate as rapidly, and therefore less foraging is required to return the bird to its previous condition. Shearwaters lose around 10g of mass for every day they spend incubating the egg (Brooke, 1990). Over the course of the mean stint length found here (approximately 4 days) a 500g bird would lose approximately 8% of its mass.

5.4.2 Individual repeatability

As documented in the earlier chapters of this thesis, Manx shearwaters display individual repeatability in various aspects of their migratory behaviour, both in terms of timing and use of space. Individual repeatability is also observed in a wide range of seabirds, across a range of breeding and non-breeding behaviours (Phillips, Silk, & Croxall, 2005; Guilford et al., 2011; Patrick et al., 2014; Ceia & Ramos, 2015; Dehnhard et al., 2016). Here, we found that individual repeatability continued during the breeding season, and was detected in the first night spent on the colony, the first day spent in the breeding burrow and the start of the first incubation stint (i.e. laying date). This concurs with the finding of the spatial analysis in chapter 2 that date of return to the breeding area after migration is highly conserved within individuals. The period between arrival and egg laying is when mature shearwaters establish (or re-establish) their breeding burrow, pair-bond and mate (Brooke, 1990). The female then departs on a pre-laying 'exodus', during which the male defends the burrow from competing pairs (Newton, 2011). These activities can only occur when both birds have returned from migration, hence the onset of incubation (date that the egg is laid) is conserved from one year to the next. An alternative explanation for conserved breeding dates across years could be that between season carryover effects are acting to maintain the timing across years. For example, late breeders may become stuck in later cycle (Gunnarsson, 2005). Inter-seasonal carryover effects on breeding phenology will be investigated in chapter 6 of this thesis.

The degree of repeatability in timing of events decreased as birds progressed through the breeding season, with no significant repeatability at the end of incubation and the chick-rearing period (date of last incubation stint and last night spent on the colony). This may be due to a combination of environmental factors (weather, temperature, marine productivity) and the degree of cooperation between the breeding pair, which will affect offspring development (Mariette & Griffith, 2012; Sánchez-Macouzet, Rodríguez, & Drummond, 2014). Once the egg hatches, the parents may be able to forage and return with a greater flexibility in timing than during the alternate windows of the incubation period. During this post-hatching period there may be a lower risk of breeding failure if the pair fall out of synchrony. However, chick growth rate will depend on the ability of the breeding pair to provide sufficient nutrition until fledging. Consequently, the duration of the chick provisioning period (and the date that the parent leaves the colony) may be dictated as much by the availability of food and the behaviour of the partner as by hatching date. As discussed above, for the parent there is also a trade-off between current and future reproductive success. Given that the timing of last night spent on the breeding colony is not repeatable between years, it seems that individuals may be more strongly influenced by the development of this year's offspring than the compulsion to leave the breeding colony early. This relationship and factors that dictate the duration of the breeding season will also be explored further in chapter 6.

5.4.3 Timing of breeding season events across years and colonies

The mean date of arrival from migration differed between colonies, both in the first night spent on the colony (mean difference of 17 days) and the first day spent in the breeding burrow (mean difference of 12 days). This concurred with differences in the timing of post-migratory arrival in the area around the breeding colony as quantified using spatial data in chapter 2, where more northerly colonies arrived later than those further south. Here a similar latitudinal gradient is evident, with birds from Lundy Island (the most southerly colony) consistently arriving at the colony approximately 10 days earlier than those breeding on more northerly colonies. This may be due to differences in behaviour during the pre-breeding migration.

In contrast, there was little evidence for such a latitudinal gradient in the date of first incubation stint, which could be expected to be positively correlated with date of arrival. Latitudinal variation in breeding phenology has been recorded in Atlantic puffin *Fratercula arctica,* black-legged kittiwake *Rissa tridactyla,* common guillemot *Uria aalge*, and Brünnich's guillemot *U. lomvia*, (Burr et al., 2016), but timing of egg laying could also be affected by body condition after migration (Bêty, Gauthier, & Giroux, 2003). Egg laying in this species is preceded by a distinct pre-laying 'exodus' during which the female leaves the colony for several days in order to forage and build up energetic and nutritional resources for egg laying. It may be that any initial colony differences in arrival time are then perturbed by environmental factors that govern this pre-laying behaviour, such as the availability and relative location of required resources (Bêty, Gauthier, & Giroux, 2003; Ramírez et al., 2016).

The date of the last incubation stint varied between years, with incubation ending around 11 days later in 2008 and 2009 than in the subsequent years (2010-2012). The number of birds tracked increased every year, and it is possible that during the earlier years where just birds from Skomer and Copeland were tracked the sample was skewed towards later breeders.

There were no evident differences between colonies, years or sexes in timing of the last visit to the breeding colony, suggesting that trends seen at the start of breeding are not carried forward across the chick-rearing period. This may be because timing of this event is more directly affected by food availability during the chick rearing period, and that this does not vary predictably between years or colonies.

5.4.4 Success of GMM methodology

This study used an automated method to investigate the breeding behaviour of Manx shearwaters on five colonies across their breeding range, studied inter-colony differences and tested for potential latitudinal effects on breeding phenology. Analysis of saltwater immersion data successfully identified key behaviours and events in the Manx shearwater breeding season. Some behaviours were immediately visible from the raw data without any further processing, particularly incubation stints. However, the unsupervised machine learning approach used here enabled automated and more objective identification of a wider range of behaviours and events.

Archival light and saltwater immersion loggers have been widely used to study the long distance movements of bird species, with the addition of using the immersion data to infer behaviour at sea (Bogdanova et al. 2011, Harris et al. 2009, Bost et al. 2009, Phillips et al. 2004; Carneiro et al., 2014; Gutowsky et al., 2014; Magnusdottir et al., 2014; Scales et al., 2015; Dias et al., 2016). However, few studies have used immersion data during the breeding season, and none to study behaviour on the colony during this period. Wider adoption of this approach could provide insights into the breeding behaviour of a range of seabird species, particularly those for which observational studies are impractical, such as sensitive or nocturnal species, or those breeding in inaccessible locations.

Comparing the estimated timing of breeding events with a subset of birds where the actual timing was known allows greater confidence in the capacity of this method to identify changes in Manx shearwater behaviour. The analysis automatically detected the date of the first 24 hours spent in the burrow, a useful proxy for the beginning of the breeding season since it confirms that the bird's pre-breeding foraging and burrow establishing behaviour has finished. For a subset of birds from Skomer, these estimated dates were compared with those collected by manual burrow inspection, confirming the accuracy of the automated procedure. Similarly, the analysis estimated the date of first arrival at the breeding colony. These dates are harder to record by manual inspection; when birds initially return to the colony they are unlikely to spend long periods in the breeding burrow. Estimates of this date using the GMM were all either on the same date, or earlier than observed on Skomer.

Egg laying dates and hatching dates were also directly observed on Skomer. Whilst it is not possible to estimate these dates directly from the behavioural classes identified here, they can be compared with the date of first incubation stint and date of last incubation stint respectively. The estimated dates of first incubation stint and last incubation stint did not align perfectly with egg lay and hatch dates. This is due to asynchronous scheduling between paired birds. Typically, male birds will take on the first incubation shift as the female leaves shortly after laying to forage and regain body condition (Brooke, 1990) When the chick hatches, whichever parent is present usually brood guard for the 4 days (Brooke, 1990). Since the pair incubates in turn and either may take the last incubation stint, it is not possible to determine whether the first incubation stint indicated egg laying, nor the last stint egg hatching, unless full tracks available for both birds in a pair. This was not possible for most birds, particularly on colonies other than Skomer. Nevertheless, the dates of first and last incubation stints were often within 1-10 days of the laying and hatching dates (Appendix 5A).

The chick fledging date was also recorded for some individuals on Skomer. Since breeding Manx shearwaters leave the colony before the chick fledges (between 1 and 23 days later; Brooke, 1990), an estimate of the date the bird left the colony should place a lower bound on the estimated chick fledging date. Indeed, the estimated last night spent at the colony was earlier than chick fledging date for all the observed birds (Appendix 5A).

5.4.5 Summary

In this chapter a novel analytical method was used to collect data on the breeding behaviour of a nocturnal burrow-nesting seabird the Manx shearwater. The timing of several key pre-breeding and breeding events from birds originating on 5 colonies were identified. Data collection over six years allowed the comparison of breeding phenology from individual birds, and individual consistency was uncovered during the start of the breeding season, but not at the end. Birds from different colonies differed in their incubation behaviour, and distinct strategies were identified in the scheduling of incubation.

The unsupervised classification enabled access to important life history information in situations where it would be time consuming and disturbing to the species to do daily nest inspections. This technique may prove invaluable for studying changes in the long term patterns of breeding phenology and strategies which may occur with changing climate and degradation of marine resources. The breeding phenology findings from this chapter are used in chapter 6 to investigate interactions between different parts of the Manx shearwater annual cycle.

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Chapter 6

The behavioural cycle of the Manx shearwater and potential carryover effects

6.1 Introduction

All long-lived species have an annual progression of life history events, which can vary according to the developmental stage of the individual (Senner, Conklin, & Piersma, 2015). Depending on the abiotic and biotic conditions to which a species has become adapted, the lengths of different parts of this cycle can vary. Bird species typically alternate between a breeding period and a non-breeding period, sometimes interspersed with a migratory phase. Whether and how the different parts of the annual cycle interact and potentially affect individuals' life-history decisions is poorly understood. The development of more sophisticated and longer-lasting tracking technology over the last decade has however enabled researchers to start addressing these questions by following individuals over the course of several seasons (O'Connor, *et al.,* 2014). The term 'carryover effect' describes instances where the timing or outcome of an event during one part of the annual cycle influences the timing or outcome of a subsequent event (Norris, 2005, Norris & Taylor, 2006, Harrison, *et al.* 2011). O'Connor et al. (2014) have further developed this to define carryover effects as instances where "an individual's previous history and experience explains their current performance in a given situation". Although the term has only recently been used in ecology (O'Connor et al., 2014), carryover effects have been identified in a wide range of bird species, including shorebirds and waders (Conklin & Battley, 2012; Duriez, et al., 2012), waterfowl (Norris & Taylor, 2006; Clausen, Madsen, & Tombre, 2015; Weegman, et al., 2016), passerines (Saino et al., 2012; Paxton & Moore, 2015) and seabirds (Sorensen, Hipfner, Kyser, & Norris, 2009; Crossin et al., 2012; Daunt et al., 2014; Szostek & Becker, 2015; Shoji et al., 2015; Perez, Granadeiro, Dias, & Catry, 2016). Similarly, the timing of annual routines and its effect on survival and reproductive success has been well studied for some time (McNamara & Houston, 2008). Despite this there are still many question to be addressed, including if carryover effects continue to be conveyed onwards throughout the annual cycle, and then into the next one. Cross year effects are investigated in this chapter.

Seabirds are some of the longest-lived animals on the planet (Froy et al., 2015). As such, their life-history strategy can be described as K-selected, with typically low annual reproductive output (one or two offspring), protracted development with late maturity and a high level of parental care (Ricklefs, 1990). Because of this, seabird reproductive value is perhaps best measured in terms of current *and* future reproductive output, and is therefore subject to a trade-off between expending resources to raise one season's offspring and retaining resources in order to survive until the next breeding season (Williams, 1966). The analyses presented earlier in this thesis identified significant individual behavioural consistency in migration behaviour, timing of breeding events, migration route and stopover behaviour. Given that individual reproductive value can be directly influenced by behaviour, this individual consistency may represent differing approaches to dealing with this trade-off. Individual strategies (such as minimising loss of condition during migration) in order to prioritise different parts of the lifecycle (for example, successful reproduction) may therefore lead to correlation in timing of key life history events and behaviour, which may appear similar to carryover effects (Senner et al., 2015).

Bird species that migrate long distances to geographically distinct non-breeding ranges, such as many seabirds, are likely to face a wide range of environmental conditions across the different phases of their lifecycle. They may therefore be subject to more intense environmental stochasticity than non-migratory species. These environmental differences can directly influence behaviour, physiology, and the timing of life history events (Arizmendi-Mejía et al., 2013). Stochastic environmental variation may also cause or heighten trade-offs in resource expenditure between different parts of the annual cycle (Schmidt-Wellenburg et al., 2008, Sanz-Aguilar et al., 2012).

Variation within a population in the timing of key events and in behaviour at different stages may be caused by recent environmental stochasticity or individual consistency of behaviour, or be the result of a carryover from an earlier event that has been influenced by environmental or individual effects. Identifying when and where in an individual's annual cycle carryover effects have the most impact necessitates controlling for these other potential explanatory factors. Previous studies have attempted to quantify the impact of specific carryover effects using experimental manipulation to investigate how events in one season influence events in the following season or annual cycle (Legagneux, et al, 2012; Catry, et al., 2013; Vincenzi, et al., 2015 and Fayet et al., 2016). Whilst these experimental studies provide robust evidence for carry-over effects, they can only evaluate those events that are amenable to manipulation, such as parts of the annual cycle that are accessible. For example, the impact of breeding can be manipulated by supplemental feeding of the chick or cross fostering young and old chicks. The moult period, or any at-sea behaviour is harder to manipulate.

By analysing multi-year tracking data, previous chapters in this thesis have disentangled the effects of individual consistency and inter-annual differences (as an indicator of stochastic events) on key life history events and behaviours. The same multi-year, full lifecycle dataset enables us to control for individual and environmental drivers of variation in order to identify carryover effects between different events across the whole lifecycle (Daunt et al., 2014; Szostek, Bouwhuis, & Becker, 2015). Moreover, by simultaneously considering the various events and behaviours in each stage of the annual cycle, we can identify the most likely causal pathways by which carry over effects influence key events. Questions addressed here include how behaviour during the two migratory periods (southbound and northbound) influences timing of arrival at the corresponding destinations, and whether this goes on to influence breeding phenology. Also addressed is whether breeding phenology has an effect on non-breeding behaviour. Variables determined from the previous chapters include the timing of main events during the migration and breeding season, inter-event durations, migratory routes, flight and stopover behaviour and travel distances. In this final chapter the relationships between these different components of the Manx shearwater annual cycle are investigated with the intention of identifying potential carry-over effects across non-breeding and breeding seasons, migrations and across years. Figure 6.1 illustrates the main annual cycle, with proposed interactions between intermediate variables, linking together all the events and behaviours that have been quantified. For a subset of birds breeding on Skomer Island, the arrival mass at the colony after northbound (pre-breeding) migration was also available, as a measure of body condition, a useful proxy for individual condition (Harrison et al., 2011). The main statistical analysis considers the three main sections of the annual cycle; post-breeding migration, pre-breeding migration and the breeding season. Structural equation modelling (SEM) is applied to identify the major pathways by which carry over effects influence key lifecycle events, and how they are mediated by behaviour. To my knowledge, this is the first study to use multi-individual, multi-year, multi-colony tracking data to investigate carry over effects across the whole annual cycle of a seabird species.

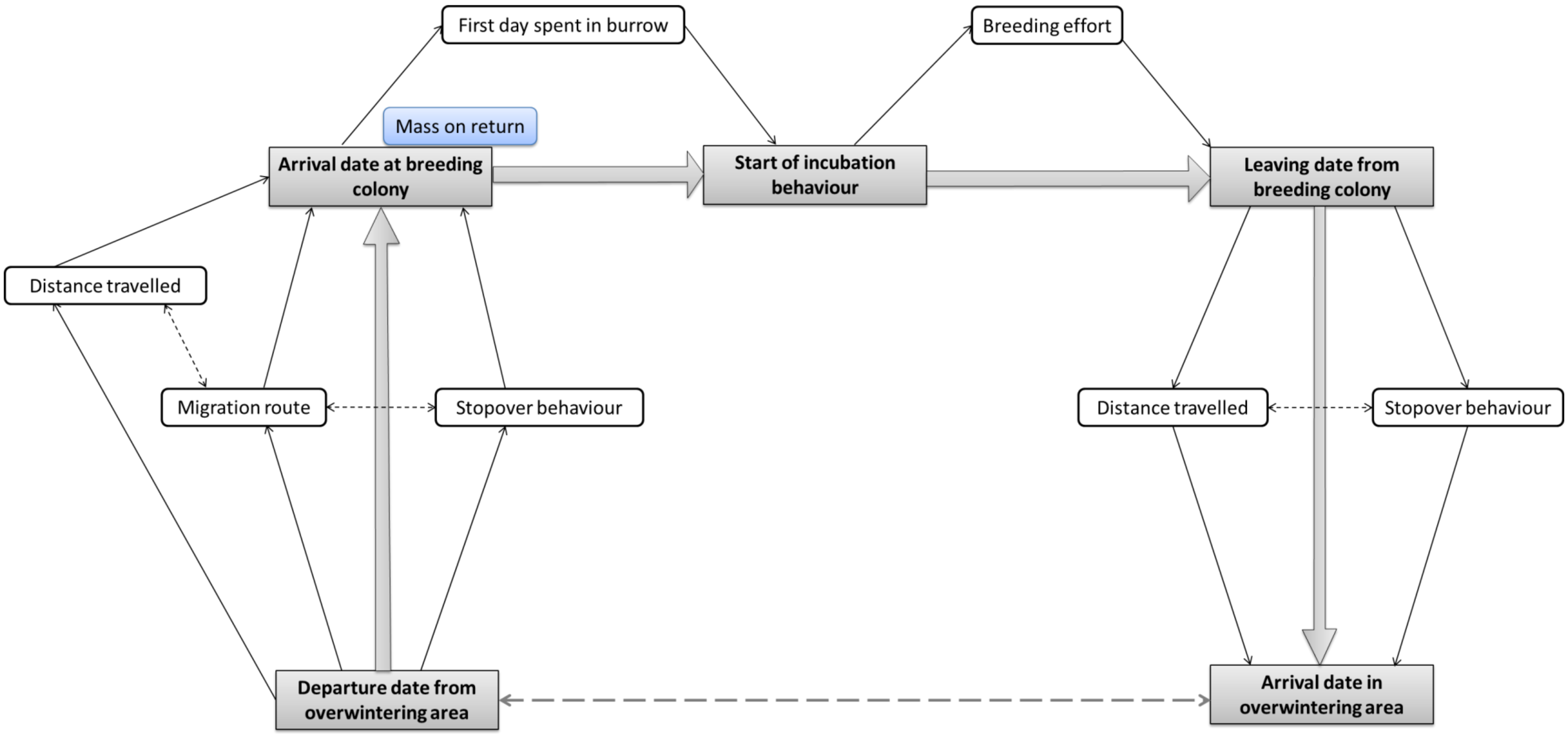


Figure 6.1. Hypothetical relationships between different parts of the Manx shearwater annual cycle. Grey boxes refer to major events and the blue box shows a variable only recorded from birds breeding on Skomer. White boxes and thin arrows show alternative pathways and interactions.

6.2 Methods

Data on migratory behaviour and the timing of life history and migratory events were compiled from the studies detailed in chapters 2 to 5. Additional data on post-migratory body condition was collected from birds breeding on Skomer Island. Path analyses were then conducted using piecewise structural equation models to investigate the links between these variables. The majority of data analysed here was collected using archival light and saltwater immersion loggers. For detailed methods on the data collection and processing methods see the relevant previous chapters of this thesis. Figures 6.2 shows the hypothesised pathways used in the structural equation models (see section 6.2.4 for more details).

6.2.1 Migration behaviour and timing

Dates of departure and arrival at the breeding and wintering areas for the post-breeding (southbound) and pre-breeding (northbound) migrations were determined from geolocation data (chapter 2). Date of arrival on the breeding colony was established using saltwater immersion and light data (chapter 5). The total great circle distances of each migration direction were calculated for each migration track in chapter 3, using smoothed and filtered data to remove any potentially erroneous locations. On the pre-breeding (northbound) migration, longitude crossed at latitude 40°N was used as a measure of the migratory route: a higher value representing a more easterly migration path (chapter 3). For both southbound and northbound migrations, the proportion of locations in the migration track that were classified as stopover behaviour was calculated using a machine learning classifier (chapter 4). 143 individuals were tracked over the course of six years, leading to 275 southbound and 275 northbound migration tracks.

6.2.2 Breeding phenology and behaviour

Chapter 5 details the methodology for extracting the timing of breeding season events from light and saltwater immersion loggers. In addition to the dates of arrival and departure at/from the breeding colony, the first day spent in the breeding burrow and the date of the first incubation stint were extracted. The proportion of time spent in flight behaviour (class three in chapter 4) across the breeding period was calculated for each individual as a proxy for the overall breeding effort (energy expended to maximise reproductive success). Breeding phenology was recorded from 59 individual birds, with a total of 89 full breeding seasons.

6.2.3 Post-migratory body condition

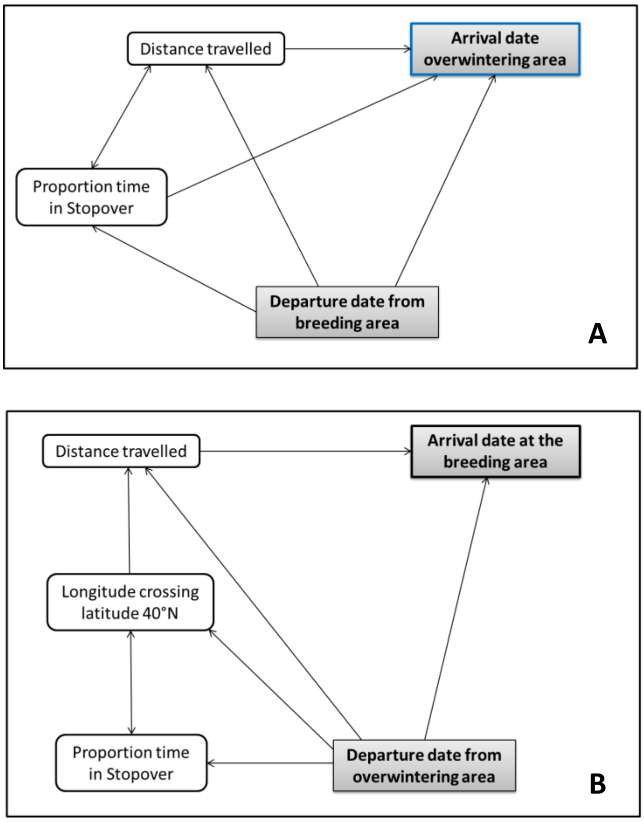
Manx shearwaters returning to established breeding burrows on Skomer Island during March and April 2010 and 2011 were caught and weighed on the first occasion that they were observed in each season. During the first month of the breeding season, burrows from which a pair had successfully raised a chick in the previous year were monitored at 30 minute intervals every night. When a returning bird carrying a geolocator was found in a burrow, it was captured using an access hatch built into the nest chamber. The ring number was then recorded and the individual weighed using a bag and a spring balance before being returned to the burrow. In total 21 birds were weighed in 2010 and 19 in 2011 (see appendix 6A for details).

6.2.4 Statistical analysis

Before undertaking the more complex path analysis, linear mixed effect models were used to investigate the relationships between the start and end events for the three main sections of the Manx shearwater behavioural cycle. These are as follows: dates of departure from the breeding area and arrival at the overwintering area (the southbound migration period), dates of departure from the wintering area and arrival at the breeding area (the northbound migration period) and dates of arrival at the breeding colony and departure from the breeding colony (breeding period) Arrival date at the breeding area was defined as first date a bird crossed the -10° longitude line, whereas arrival date at the breeding colony was determined using saltwater immersion data (first dry night). These six dates form the start and end points of the three pathways illustrated in figures 6.2. Linear mixed effects models were implemented in R, using the lme4 package, with individual nested within colony as a random effect, and both year and the predictor date as fixed effects.

In a second stage, the path analysis was conducted as follows. Three separate piecewise structural equation models (SEM) were built and analysed following the methods outlined in Lefcheck, 2015, using the R package `piecewiseSEM`. Each structural equation model corresponded with a key section of the annual behavioural cycle, and comprised a collection of component linear and generalised linear mixed-effects models representing the hypothesised pathways in each section. Birds from all colonies and years were included in each component model, so each of the component linear models included individual nested within colony as a random effect, and year as a fixed effect. Generalised linear mixed-effects models were employed for pathways with binomial response variables such as the proportion of time spent in flight or stopover behaviour; linear mixed-effects models were used otherwise (for date and distance response variables). The piecewise SEM approach facilitates examination of these component models (extracting path coefficients and quantifying goodness of fit via conditional and marginal R-squared values) as well as carrying out statistical tests over the collection of component models to assess goodness of fit to the whole dataset

(Shipley's test of directed separation – testing independence of residuals across the whole section, Shipley, 2009), and to test whether paths *not specified* in the hypothesised path diagrams appear to be important (via likelihood ratio tests).



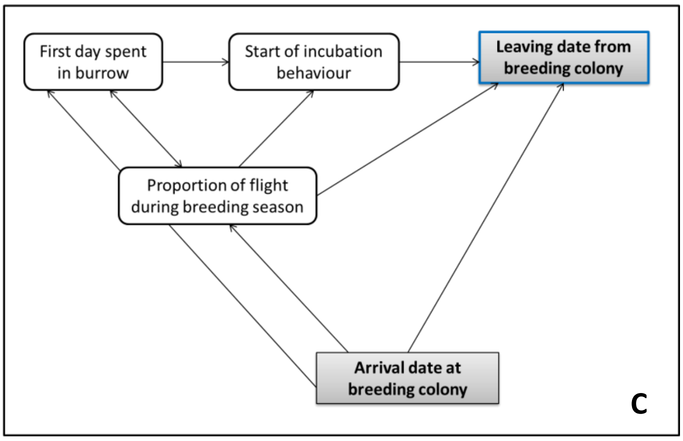


Figure 6.2 Path diagrams showing possible relationships between events and behaviours during the Manx shearwater breeding season. The annual cycle is split into three sections: A= southbound migration, B = northbound migration and C = the breeding season. The main response variable used in each SEM is outlined in blue.

In addition to the SEM, the effects of migration timing on return mass, and of return mass on breeding phenology were modelled on a subset of the data from Skomer Island using linear mixed-effects models. Linear mixed-effects models were also used to investigate effects between breeding and non-breeding phases; how events occurring in one annual cycle may be affect subsequent cycles. The possible inter-season effects considered were: the effect of departure date from the wintering area on the subsequent post-breeding date of departure from the colony; the effect of post-breeding departure date on the subsequent date of departure from the overwintering area; the effect of date of departure from the breeding area in one year on the date of arrival at the breeding area in the subsequent year; the effect of date of post-breeding departure from the breeding area on the duration of the subsequent overwintering period. The aim of these comparisons was to assess the overall impact of the timing of key events on subsequent phases in the annual cycle, rather than to attempt to further disentangle the effects via the pathways considered in the piecewise SEMs. Whilst it would be theoretically possible to disentangle these pathways by building a single piecewise SEM across the whole breeding season (and across multiple years), this was not practically possible using the data available. Since the piecewise SEM approach requires that all component models consider the same data points, only annual cycle records for which data are available for all events in the section can be included. Few annual cycle records (37 tracks in total) have reliable estimates for all events across the three sections, so this would have drastically reduced the statistical power of the analysis to detect key pathways.

6.3 Results

The first section of results summarises the dates for each of the key events of the Manx shearwater annual cycle. Figure 6.3 illustrates the median dates (and range) of the start and end of each part of the annual cycle, and how these differ between colonies.

The annual behavioural cycle was considered in three main sections: southbound migration (post-breeding), northbound migration (pre-breeding or return migration) and the breeding season. Figure 6.4 shows the relationships between the start and end dates for each of these sections. Significant positive relationships were detected between the start (departure from the breeding area) and end (arrival at the wintering area) dates of the post-breeding migration (t_{119}=10.720, $p<0.001$, R^2_M=0.362, R^2_C=0.536) and between the departure date from the wintering area and the subsequent arrival date at the breeding area (t_{119}=4.637, $p<0.001$, R^2_M=0.413, R^2_C=0.324). No statistically significant relationship was detected between the timing of arrival at the breeding colony and the following post-breeding departure date (t_{119}=0.984, p=0.330, R^2_M=0.168, R^2_C=0.474).

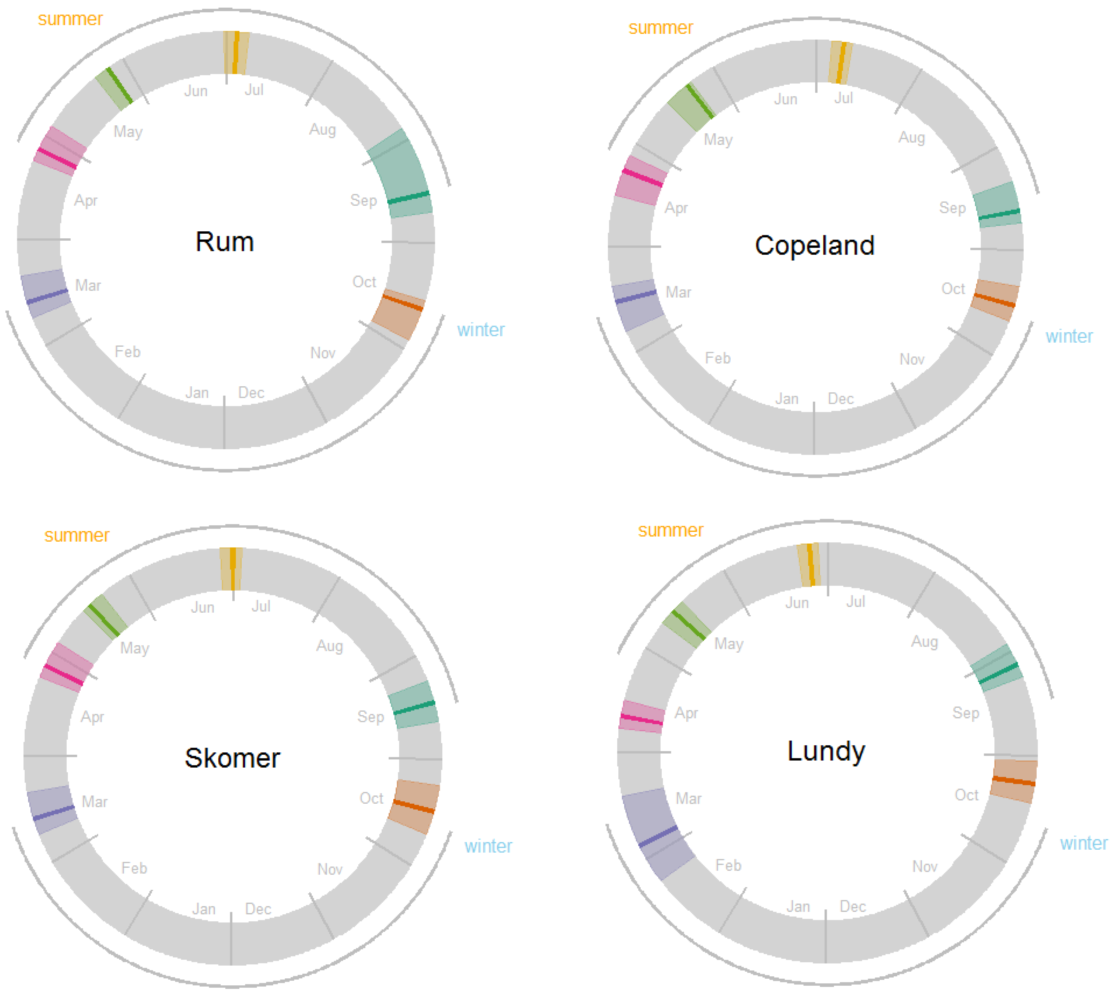


Figure 6.3. Timing of main behavioural events in the Manx shearwater life cycle. Bold coloured lines indicate the median date for each event across all records within each colony. The coloured region surrounding the median line shows the interquartile range. Pink = arrival date at the colony, green = laying date, yellow = hatching date, turquoise = departure from the colony, red = arrival at the overwintering location, blue = departure from the overwintering location. Ramsey Island is missing from this figure as there was not sufficient data to calculate all the variables.

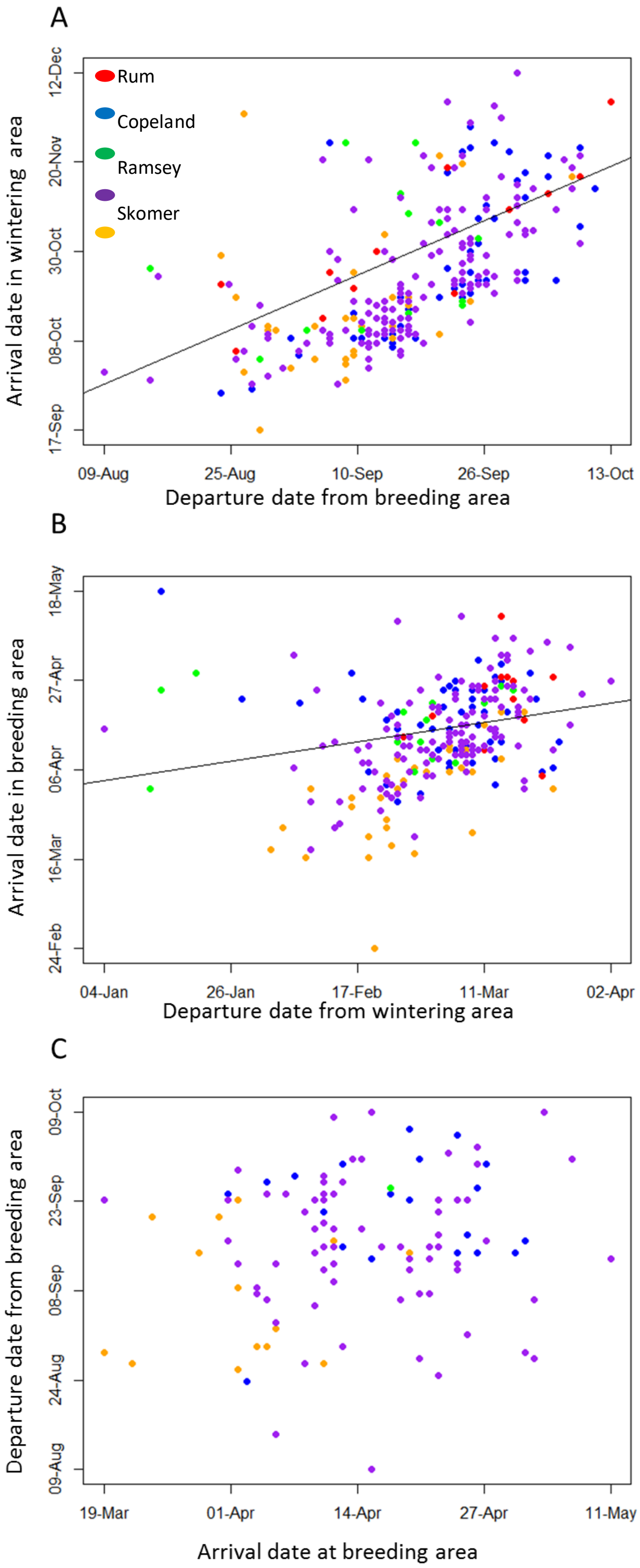


Figure 6.4. Scatterplots illustrating relationships between start and end dates for the three main sections of the annual cycle: post-breeding (southbound) migration (A), pre-breeding (northbound) migration (B) and the breeding season (C). The black line represents the overall trend from the corresponding linear mixed effects model and is only shown where the relationship is statistically significant. Points are coloured by breeding colony; Rum = red, Copeland = blue, Ramsey = green, Skomer = purple, Lundy = orange.

6.3.1 Southbound migration

Three of the causal pathways proposed in figure 6.2A were supported by the data (figure 6.5 and 6.6). Date of arrival at the overwintering area depended on the date of departure from the breeding area, with each day later departing corresponding to approximately a one day delay in arriving. Date of arrival also depended on the distance travelled on migration, with each additional 1000km travelled delaying arrival by approximately one day; after accounting for delays in departure. The distance travelled was in turn affected by the date of departure; each day delayed in leaving shortening the distance travelled by around 214 km. The two remaining hypothesised pathways both involved the proportion of time spent in stopover behaviour, and neither was found to be significant. Table 6.1 reports the estimated coefficients and results of significance tests for each hypothesised pathway.

Adding the missing (not hypothesised to have a direct causal link a priori) pathway - effect of proportion of stopover behaviour on arrival date – to the piecewise SEM did not significantly improve model fit (table 6.2). Similarly, Shipley's test of directed separation did not identify a violation of independence in the residuals of the SEM (X^2=4.62, p=0.160), indicating that all major relationships between events had been represented in the SEM.

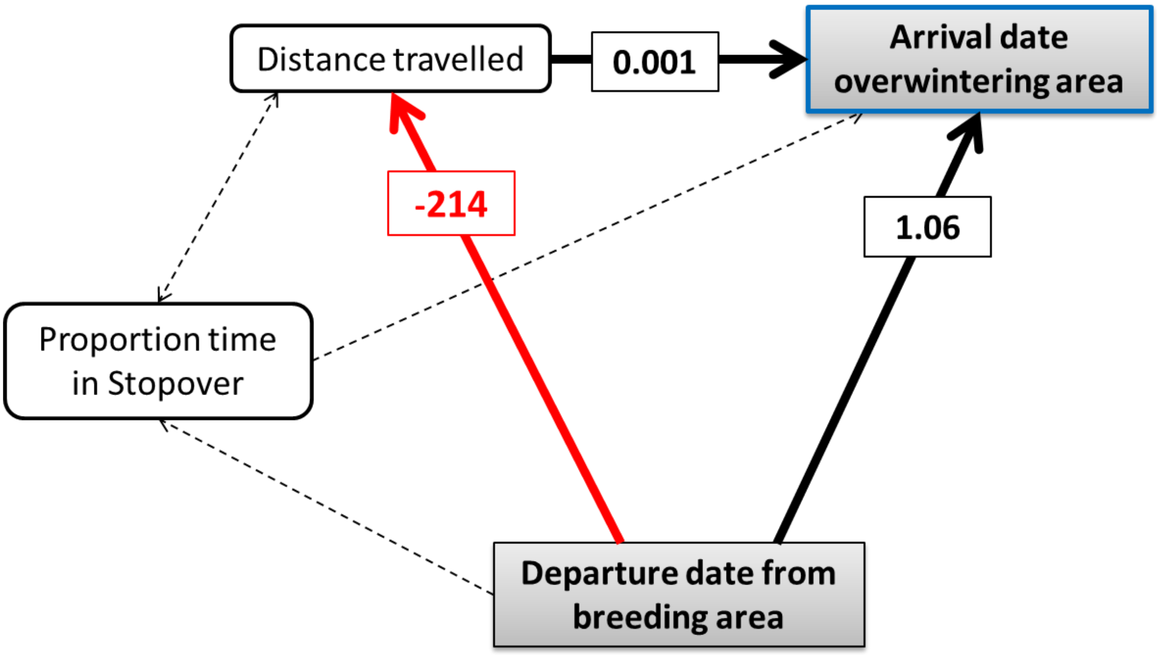


Figure 6.5. Path diagram representing the modelled causal structure of post-breeding (southbound) migration, estimated using a structural equation model. Hypothesised pathways are indicated by arrows. Statistically significant pathways are shown with a bold arrow; positive effects in black, negative relationships in red. Boxes give the estimated path coefficient. Non-significant paths are shown with a dashed arrow. Double-headed arrows indicate a hypothesised relationship without a direction of causality.

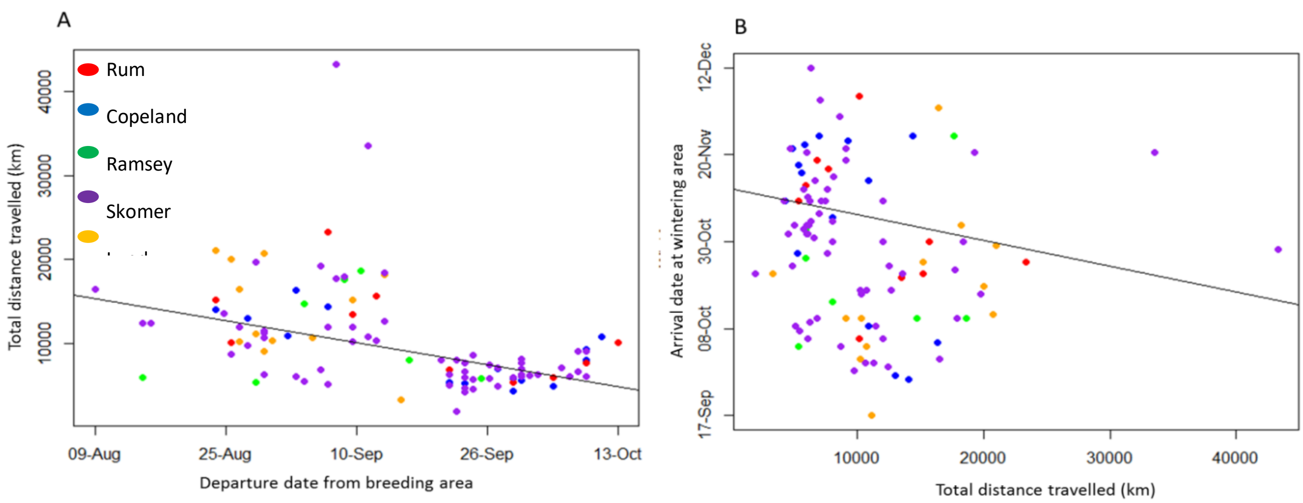


Figure 6.6. Scatterplots illustrating two of the significant pathways from the southbound migration SEM; effect of departure date on distance travelled (A) and effect of distance travelled on arrival date (B). The black line represents the overall trend from the corresponding linear mixed effects model. Points are coloured by breeding colony; Rum = red, Copeland = blue, Ramsey = green, Skomer = purple, Lundy = orange. The remaining significant pathway (effect of departure date on arrival date) is already illustrated in figure 6.4

Table 6.1. Results from southbound (post-breeding) migration SEM. Path coefficient is the raw estimated coefficient. Significant interactions are highlighted in grey. The main path is indicated in italics and boldface.

Response	Predictor	Path coefficient	Std. Error	P-value
Arrival date at overwintering area	***Departure from breeding area***	***1.057***	***0.104***	***<0.001***
Arrival date at overwintering area	Distance travelled	-0.001	0.0003	0.004
Proportion of stopover behaviour	Departure from breeding area	0.002	0.016	0.879
Distance travelled	Departure from breeding area	-213.7	0.316	<0.001
Distance travelled	Proportion of stopover behaviour	0.131	NA	0.115

Table 6.2. Missing paths from the three SEMs used in this analysis.

SEM	Response	Predictor	Chi-squared	DF	P-value
Southbound migration	Arrival date at overwintering area	Proportion of stopover behaviour	1.759	14	0.100
Northbound migration	Distance travelled	Proportion of stopover behaviour	0.817	45	0.418
	Breeding arrival date	Proportion of stopover behaviour	-0.250	45	0.804
	Breeding arrival date	Distance travelled	-1.393	45	0.171
Breeding season	Date first incubation stint	Breeding arrival date	0.395	16	0.698
	Departure date from breeding area	Breeding arrival date	-0.114	15	0.911
	Departure date from breeding area	Date of first day in the burrow	1.466	14	0.165

6.3.2 Northbound migration

Two of the hypothesised pathways in the northbound migration found statistically significant support (figure 6.7 and 6.8). Delaying the date of departure from the overwintering area delayed arrival at the breeding season and shortened the distance travelled. The date of arrival was delayed by approximately one day for every three days the departure date was delayed, and the distance of migration was around 200km shorter for every day's delay in departure date. After accounting for these two pathways, none of the remaining hypothesised pathways were significant, with the migratory route (quantified as the longitude at which the individual crossed latitude 40) and the amount of stopover behaviour not significantly related to the other events. 6.3 reports the estimated coefficients and results of the statistical tests for each pathway.

Adding either of the two missing pathways (effect of migratory route or amount of stopover behaviour) did not significantly improve the fit of the model to the data (table 6.2) and Shipley's test for directed separation returned a non-significant result (X^2=5.726, p=0.455) indicating a lack of evidence to reject the SEM.

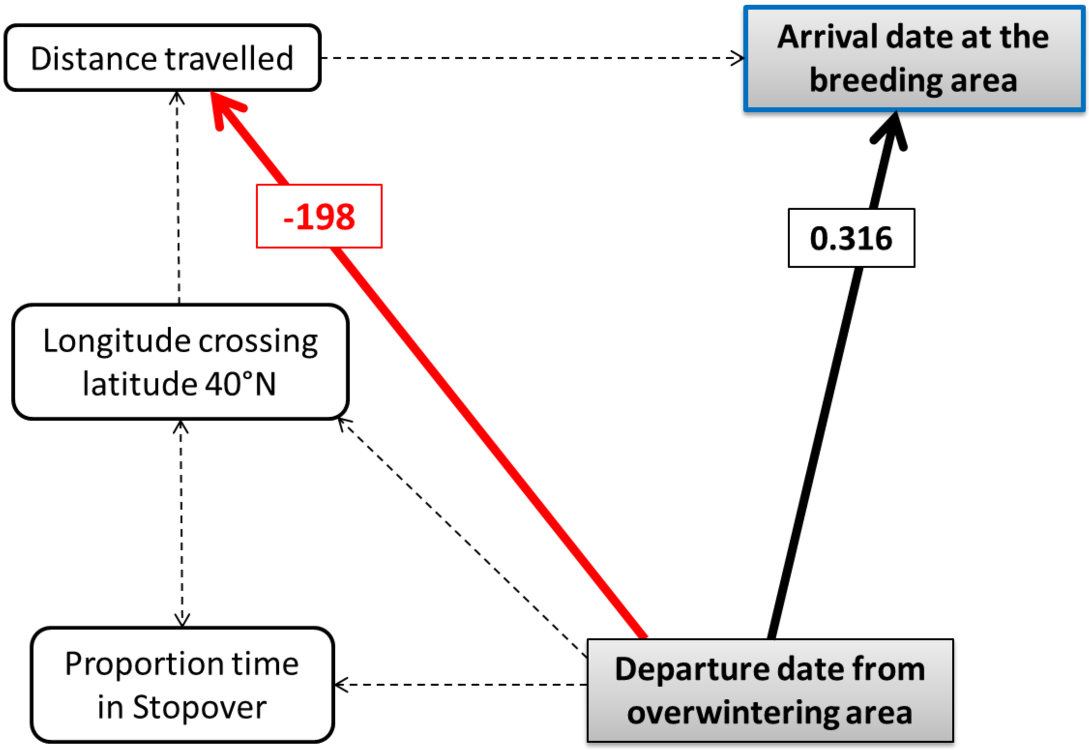


Figure 6.7. Path diagram representing the modelled causal structure of pre-breeding (northbound) migration, estimated using a structural equation model. Hypothesised pathways are indicated by arrows. Statistically significant pathways are shown with a bold arrow; positive effects in black, negative relationships in red. Boxes give the estimated path coefficient. Non-significant paths are shown with a dashed arrow. Double-headed arrows indicate a hypothesised relationship without a direction of causality.

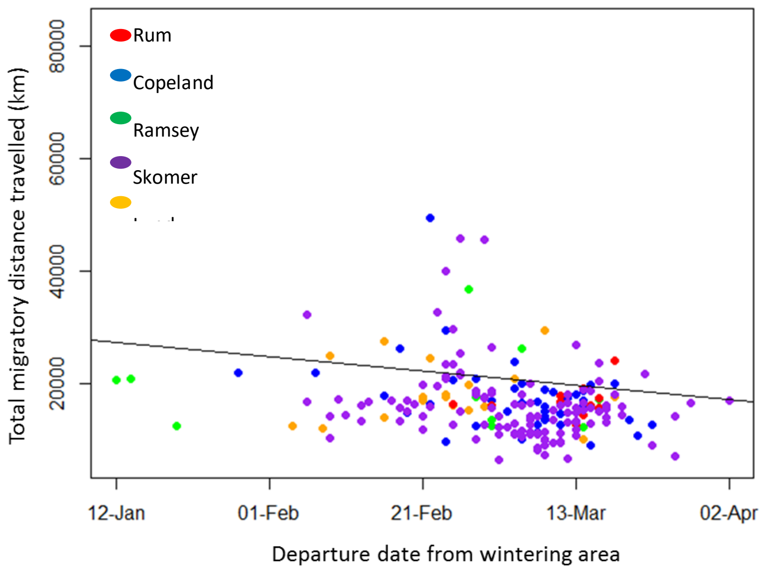


Figure 6.8. Scatterplot illustrating significant pathway from the northbound migration SEM; the effect of departure date on distance travelled. The black line represents the overall trend from the corresponding linear mixed effects model. Points are coloured by breeding colony; Rum = red, Copeland = blue, Ramsey = green, Skomer = purple, Lundy = orange. The remaining significant pathway (effect of departure date on arrival date) is already illustrated in figure 6.4

Table 6.3. Results from northbound (pre-breeding) migration SEM. Path coefficient is the raw estimated coefficient. Significant relationships are highlighted in grey. The main path is indicated in italics and boldface

Response variable	Predictor variable	Path coefficient	Std. Error	P-value
Breeding arrival date	***Winter departure date***	***0.316***	***0.065***	***<0.001***
Breeding arrival date	Longitude at latitude 40°N	-0.066	0.062	0.295
Longitude at latitude 40°N	Winter departure date	-0.055	0.087	0.53
Proportion of stopovers	Winter departure date	-0.007	0.017	0.639
Distance travelled	Winter departure date	-198.84	65.605	0.004
Distance travelled	Longitude at latitude 40°N	-30.758	61.344	0.618
Longitude at latitude 40°N	Proportion of stopovers	-13.462	NA	0.947

6.3.3 Breeding season

Three hypothesised pathways in the breeding season section of the lifecycle were statistically significant (figure 6.9 and 6.10). Date of arrival at the breeding area had a positive effect on the first day spent in the burrow; every four days delay in arriving resulted in a three day delay in the first day spent in the burrow (figure 6.10A). Both the first day spent in the burrow and the date of the start of the incubation period had a positive effect on the breeding season effort (proportion of time spent flying during the breeding season), later dates were associated with more flight effort (figure 6.10B and 6.10C). Neither the date of arrival nor the degree of breeding effort appeared to influence the date of departure, nor did the first day in the burrow influence the date of the first incubation stint. Table 6.4 reports the estimated coefficients and results of the statistical tests for each pathway.

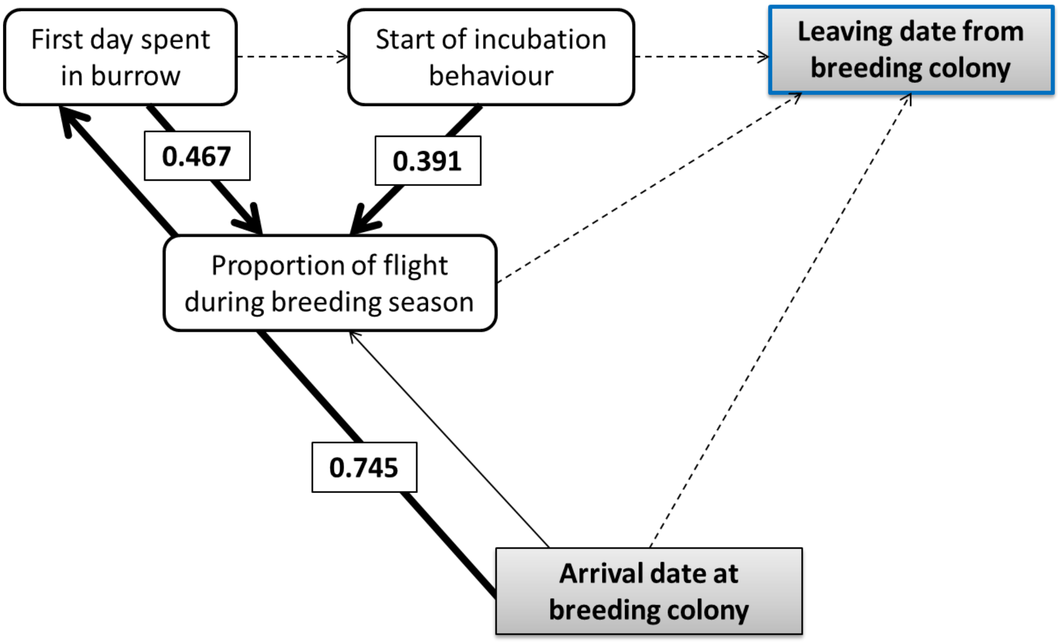


Figure 6.9. Path diagram representing the modelled causal structure of breeding season timing, estimated using a structural equation model. Hypothesised pathways are indicated by arrows. Statistically significant pathways are shown with a bold arrow; positive effects in black, negative relationships in red. Boxes give the estimated path coefficient. Non-significant paths are shown with a dashed arrow.

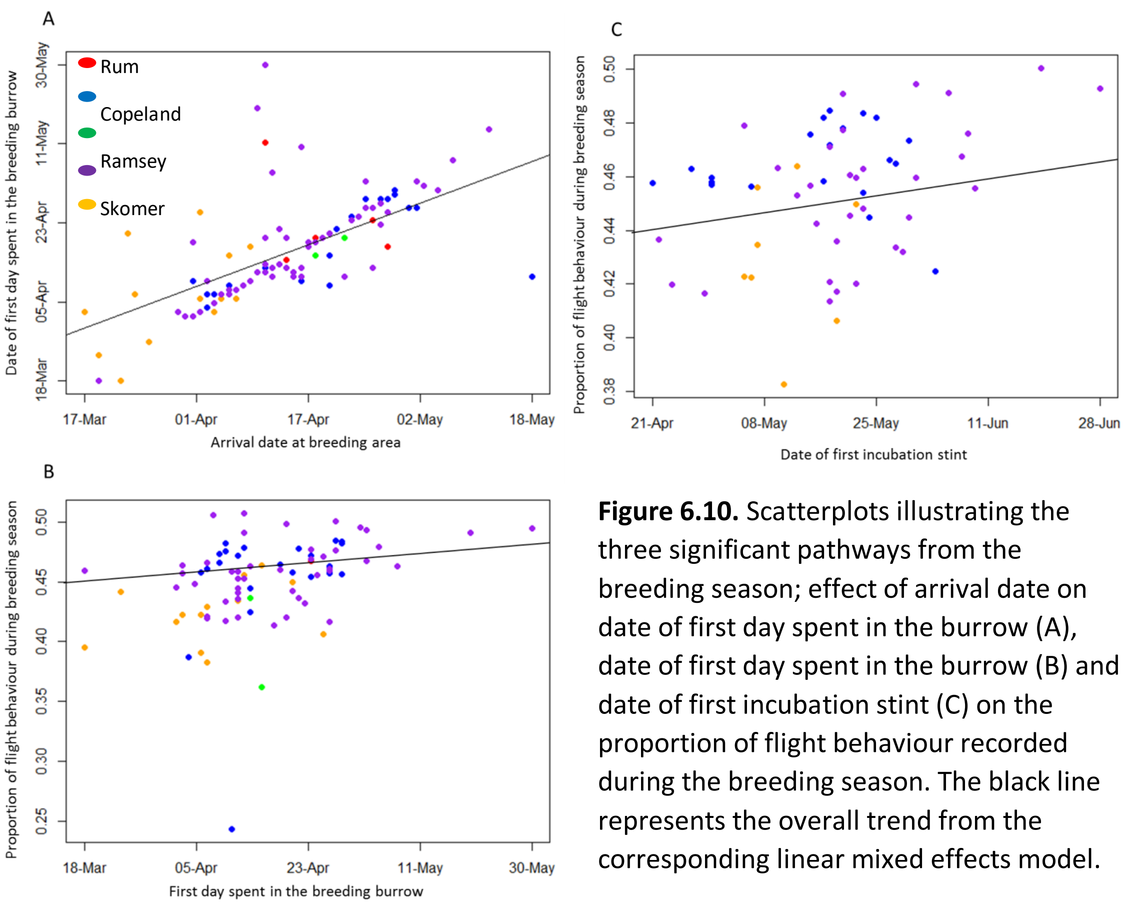


Figure 6.10. Scatterplots illustrating the three significant pathways from the breeding season; effect of arrival date on date of first day spent in the burrow (A), date of first day spent in the burrow (B) and date of first incubation stint (C) on the proportion of flight behaviour recorded during the breeding season. The black line represents the overall trend from the corresponding linear mixed effects model.

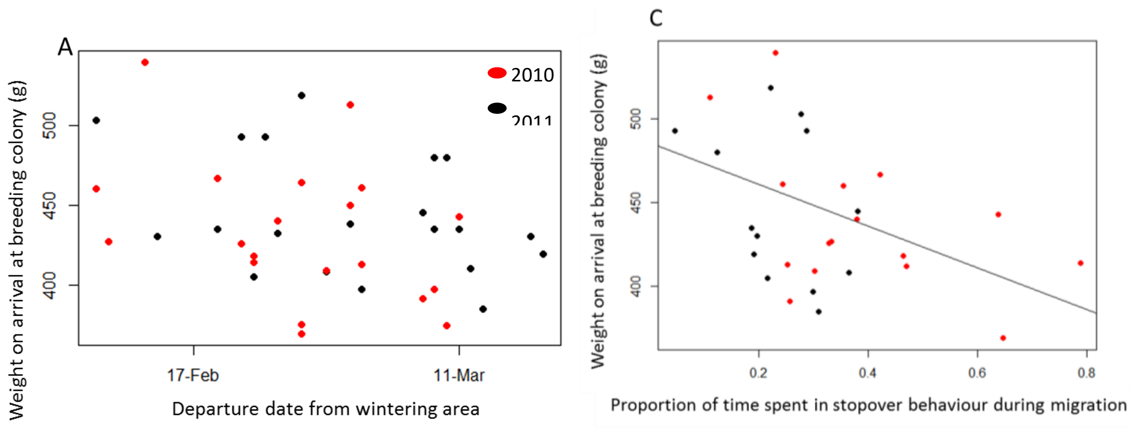
Table 6.4. Results from breeding season SEM. Path coefficient is the raw estimated coefficient. Significant relationships are highlighted in grey. The main path is indicated in italics and boldface.

Response	Predictor	Path coefficient	Std. Error	P-value
Departure date from colony	***Arrival at breeding colony***	***-0.141***	***0.099***	***0.172***
Departure date from colony	Proportion of flight behaviour	39.635	56.134	0.49
Date of first incubation stint	First day spent in the burrow	0.13	0.155	0.417
First day spent in the burrow	Breeding arrival date	0.745	0.127	<0.001
Proportion of flight behaviour	Date first incubation stint	0.391	NA	0.002
Proportion of flight behaviour	First day spent in the burrow	0.467	NA	<0.001

Adding either of the three missing pathways did not significantly improve the model fit to the data (Table 6.2). Shipley test of directed separation was non-significant (X^2=4.516, p=0.608), indicating a lack of evidence to reject the SEM.

6.3.4 Post-migratory arrival mass

Although there appeared to be a weak negative relationship between the date of departure from the overwintering area and the arrival mass of birds on Skomer Island (figure 6.11A), this was not significant when tested using a LMM (t_{28}=2.089, p=0.070, R^2_M=0.115, R^2_C=0.580). However, the date of arrival at the breeding area was significantly positively related to arrival mass, with later-arriving birds being lighter on arrival (t_{28}=2.483, p=0.038, R^2_M=0.169, R^2_C=0.174, figure 6.11B). The proportion of time spent in stopover behaviour also had a significant effect on arrival mass, with more stopover behaviour during the northbound migration corresponding to lighter birds on arrival (t_{28}=3.144, p=0.020, R^2_M=0.168, R^2_C=0.770, figure 6.11C).



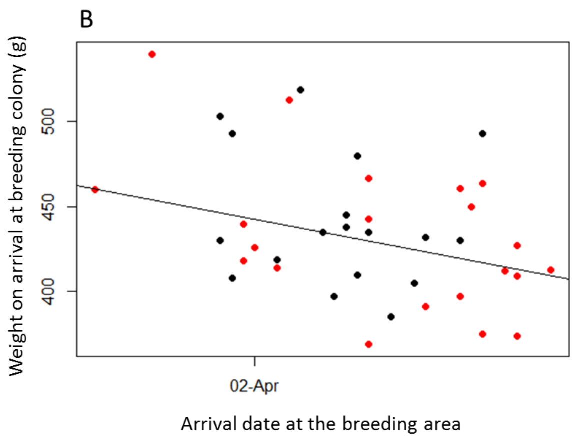
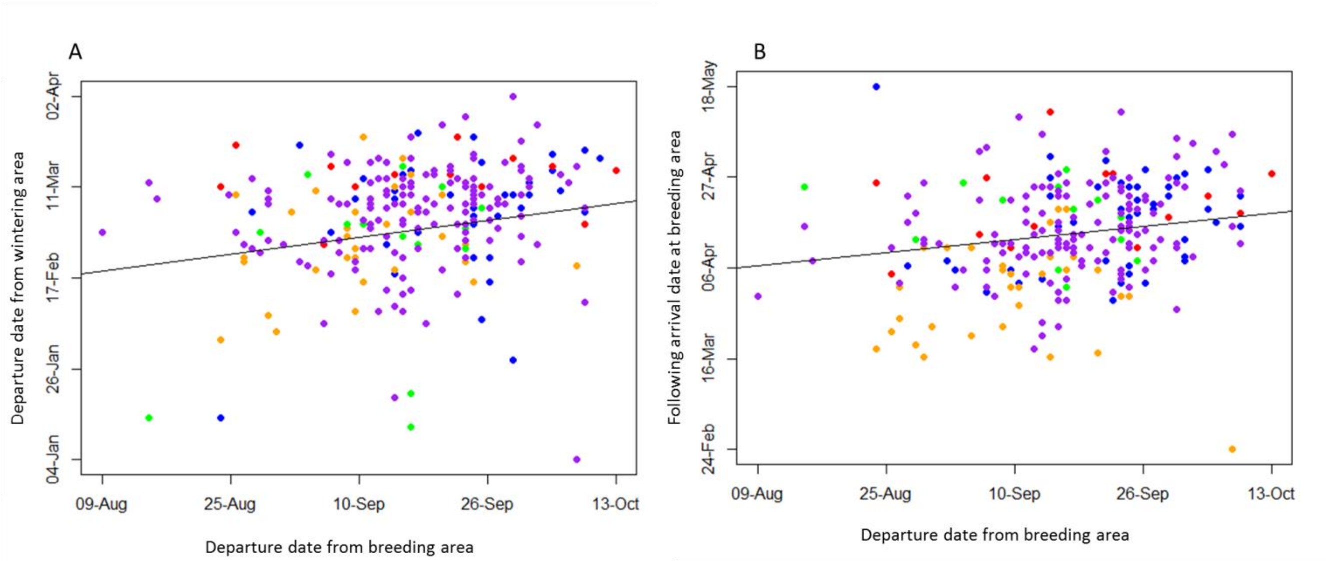


Figure 6.11. Scatterplots illustrating the effects of potential explanatory events on the mass of Manx shearwaters on arrival at Skomer (the only colony where weighing on arrival was possible): departure date from the wintering area (A) effect of arrival mass on the timing of the first night spent on Skomer (B) and the proportion of time spent in stopover behaviour (C). The black line represents the overall trend from the corresponding linear mixed effects model and is shown

6.3.5 Cross-seasonal relationships

Four cross-seasonal relationships were analysed using separate linear mixed-effects models and these are illustrated in figure 6.12. The date of departure from the wintering area had no apparent effect on the date of departure from the breeding area at the end of the subsequent breeding season (t_{119}=0.898, p=0.373, R^2_M=0.174, R^2_C=0.310). However, date of departure from the breeding area (start of southbound migration) was a strong predictor for the start of the following pre-breeding (northbound) migration (t_{119}=3.959, p<0.001, R^2_M=0.114, R^2_C=0.565) and the date of arrival at the breeding area in the next breeding season (t_{119}=2.962, p=0.004,

R^2_M=0.048, R^2_C=0.541) with birds leaving the breeding area later being later in these subsequent events (figures 6.12A and 6.12B). Later departure from the breeding area also lead to a shorter period of time spent in the overwintering area (t_{119}=4.814, $p<0.001$, R^2_M=0.141, R^2_C=0.514, figure 6.12C).



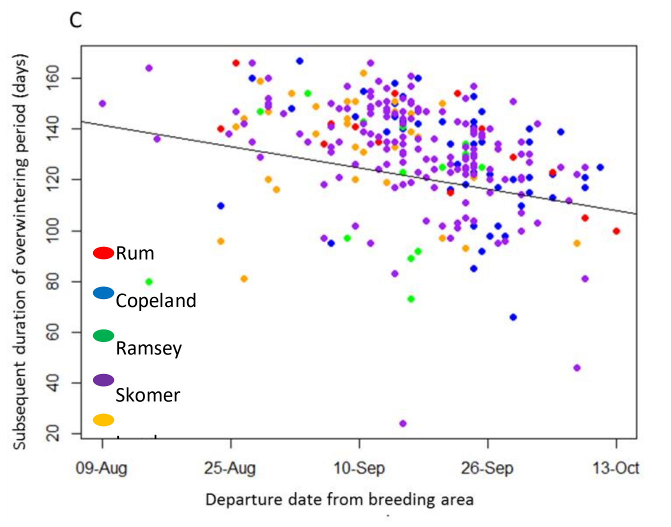


Figure 6.12. Scatterplots illustrating hypothesised cross-seasonal relationships; effect of breeding departure date on the subsequent date of departure from the wintering area (A), effect of date of departure from the breeding area on the date of arrival at the breeding colony the following year (B), effect of date of departure from the breeding area on the duration of the subsequent overwintering period (C). The black line represents the overall trend from the corresponding linear mixed effects

6.4 Discussion

In this study the complete annual cycle of a seabird species has been viewed as a 'joined-up' model, investigating the interactions between the different phases (breeding and non-breeding), and also looking across multiple years. The dataset used is complex, with several levels of variation, sometimes following individual birds for as long as five consecutive years. Despite this complexity, the SEM approach uncovered several key findings, with implications for the future direction of research in seabird behavioural ecology. For ease of analysis, the Manx shearwater annual cycle was initially divided into sections; southbound migration, northbound migration and the breeding season. The start and end dates for each of these sections were treated as the main pathways for each SEM, with the addition of other variables that could potentially drive the relationships seen across each period. These relationships are discussed in the following sections, initially addressing migration and breeding behaviour separately, before considering the effects occurring across different phases of the annual cycle.

6.4.1 Timing and behaviour on migration

The post-breeding migration of Manx shearwaters takes place from the end of September through to October or early November, with birds leaving the breeding colony before their offspring have fledged (Brooke, 1990). As described in chapters two and three of this thesis and by both Guilford et al., (2009) and Freeman et al., (2013), the southbound migration route from the UK to the coast of Argentina is relatively constrained with almost all birds crossing the Atlantic at the narrowest point between Africa and South America. However, the distance travelled by individual birds does vary, and plays a role in the timing of arrival in the southern Atlantic. It is likely that this variation comes from some birds flying to wintering areas further south (See chapter 3 and appendix 3C). Later departure from the breeding area results in later arrival in the sea off Argentina, but this is mediated by distance flown with later-leaving birds travelling shorter distances. Even after a delayed departure is accounted for, a greater distance travelled still leads to a later arrival time.

Birds leave the area off the coast of Argentina in February and arrive near the UK breeding colonies between mid-March and early April. As detailed in chapter 5, Manx shearwaters arrive in the seas around the breeding colony several days before they first spend time on the colony. The details of their behaviour during this period are the subject of ongoing research not addressed in this thesis. As with southbound migration, similar interactions between departure date, distance travelled and arrival date occur on the northbound migration. The timing of return to the breeding colony is also associated with the date of departure from the southern Atlantic. However, unlike the southbound migration, the migration route taken from the coast of Argentina back to the UK does vary, especially once birds have passed the Caribbean on their journey north. As shown in chapter three, the extent of westerly movement varied between individual shearwaters, with some birds taking a more direct route across the north Atlantic than others. Migration route lengths varied greatly, with a difference of over 10,000km between the longest and shortest. Despite this, the migration path taken had no effect on arrival time back at the colony. For every day a bird was later in departure, the distance travelled was 200km shorter. This suggests that individuals are compensating for later departure by flying a shorter migration path. For species breeding in temperate habitats there are time constraints on the completion of a breeding attempt while resources are plentiful (McNamara & Houston, 2008). This leads to pressure on an individual to have begun breeding by a certain time (McNamara & Houston, 2008). Therefore, for a migratory species, timing of arrival back at the breeding area may have a sizeable impact on reproductive success. In fact, the offspring of Manx shearwaters which start breeding earlier have a higher chance of survival (Perrins 1966). Optimal migration theory suggests that long distance migrants face a trade-off between minimising time and energy expenditure (Alerstam, Hedenstrom, & Susanne, 2003; Hedenström, 2008; Klaassen, et al., 2011). The results presented here show that although there are differences between individual migration strategies (some birds taking a more westerly route on the northbound migration) the distance travelled is shorter the later that a bird leaves the wintering area, possibly in order to ensure a timely arrival back at the breeding colony. Although the time constraints on post-breeding migration may not be the same, it seems that Manx shearwaters that leave the breeding colony later also take a shorter route to the southern Atlantic wintering area. This may ultimately be driven by environmental conditions, since birds may need to leave the northern hemisphere before weather conditions deteriorate and make their journey more hazardous (Richardson, 1990; Newton, 2006).

Surprisingly, on both southbound and northbound migrations, the proportion of time spent in stopover behaviour was not dependent on departure dates, nor did it affect timing of arrival. Additionally there was no relationship between the amount of stopover behaviour and the route taken during pre-breeding migration. Given the transient nature of pelagic resources on a variety of scales (Weimerskirch, 2007), it is possible that stopovers are not systematic, but instead opportunistic or driven by a bird encountering unfavourable flight conditions. Other shearwater species (Cory's shearwaters, *Calonectris borealis*) are not consistent in their stopover behaviour (Dias, Granadeiro, & Catry, 2013).

6.4.2 Post-migratory body condition

A key carryover effect from migration detected in this study was the effect of timing on return mass. Birds that arrived earlier from northbound migration returned to the breeding colony heavier than those that arrived later. Interestingly, birds heavier on return also spent less time in stopover behaviour during northbound migration. These two relationships appear contradictory, although perhaps heavier birds spend less time in stopover and lighter birds are forced to stop as they do not carry sufficient reserves to complete migration. However, as already discussed it is possible that stopover behaviour has more to do with necessary resting behaviour than a strategy to maintain body condition. If birds are forced to stop more frequently because of bad weather or inherently low quality this could lead to the negative relationship between stopping and return weight by forcing an individual to migrate for a longer period of time.

Other studies have found a strong positive relationship between Manx shearwater reproductive success and early breeding (Perrins, 1966; Shoji et al., 2015). It has been hypothesised that this is due to early birds being of higher quality (Brooke, 1990). My findings support this, indicating that those birds that start breeding earlier begin the breeding season in better condition (heavier), which is likely to have a positive influence on breeding success. What is less clear is exactly how this post-migratory body condition is achieved. Cory's shearwaters (*Calonectris diomedea borealis*) are known to feed intensively to gain body mass before they arrive at the colony, but after migration is completed (Arizmendi-Mejía et al., 2013). The same may be true for Manx shearwaters, and may be the main behaviour in the period of time between arrival in the breeding area and the start of breeding. In Cassin's auklet (*Ptychoramphus aleuticus*), the quality of the pre-breeding diet affected both the timing of egg laying and the size of the egg (Sorensen et al., 2009). However, Manx shearwaters, like other procellariiformes, perform a pre-laying exodus during which females build the egg (Phillips et al., 2006; Guilford et al., 2009; Catry et al., 2009), so diet before post-migratory arrival at the breeding colony may not be as important. Age related differences could also be responsible for the relationship between post-migratory body condition and date of arrival, as was found in common terns (*Sterna hirundo*) (Szostek et al., 2015).

6.4.3 Breeding season

Most Manx shearwaters lay eggs between late May and early June with eggs hatching from the middle of July. Incubation takes approximately 50 days, followed by 70 days of chick rearing (Brooke, 1990). With most birds having arrived back at the colony by April, the period before egg-laying is spent on burrow defence and maintenance, establishing the pair bond and mating.

Event timings of events at the beginning of the breeding season were tightly coupled, with date of arrival being a strong positive predictor of the first day spent in the burrow (four days delay in arrival resulting in three days delay in the first in-burrow stint). However, this coupling did not continue through the breeding season after this point, with no effect of the first day spent in the burrow on either the date of first incubation stint or date of leaving the breeding colony.

Consistent with the hypothesis that early birds are generally of better quality and more successful at breeding (Perrins, 1966; Perrins, 1969; Price, Kirkpatrick, & Arnold, 1988;

Kokko, 1999; Shoji et al., 2015), the earlier that birds started breeding the lower the proportion of flight behaviour recorded during the breeding season. This suggests that later birds may be less efficient at foraging, or may have to spend more time in flight to make up for beginning breeding later (perhaps having missed key peaks in productivity or important resources).

6.4.4 Cross-seasonal effects

Whilst there was a positive relationship between timing of key events during migration, this was not the case across the breeding season, where early arrival at the breeding colony did not appear to lead to early departure. Similarly, there was no relationship between the date of departure from the wintering area and the date of departure from the breeding area after the subsequent breeding season. It is possible that the drivers of breeding phenology (environmental conditions, offspring growth, and synchronisation with the breeding partner) have a greater effect on the timing across the breeding season than the schedule of the individual bird. This hypothesis is supported with experimental work by Fayet et al., 2016, where the chick rearing period of Manx shearwaters was artificially lengthened or shortened. Birds with a longer breeding period left the breeding area later, however those finishing earlier did not actually leave on migration any earlier.

The end of breeding in one year did however strongly influence the start of pre-breeding migration in the following year. Birds departing the breeding season later had both a shorter wintering period and a later arrival date in the subsequent breeding season. This further supports the theory that, in this species, events during the breeding season strongly carryover to affect things that occur 'down-stream' (the migration to and from the wintering are), although these effects do not last more than one annual cycle, becoming ‘reset’ during the subsequent breeding season.

6.4.5 The role of individual variation

It is unclear from this analysis to what extent the relationships observed between key events in the annual cycle were driven by individual behavioural plasticity from year to year (for example compensating for a delayed departure by reducing the number of stopover events or taking a shorter migration route) versus longer term behavioural adaptations resulting in individual strategies. Individual consistency in behaviour has been identified in many seabird species. This includes annual phenology (Thorup et al., 2013; Yamamoto et al., 2014), route stereotypy (Raine, et al., 2012), wintering areas (Carneiro et al., 2016), foraging specialisation (Patrick & Weimerskirch, 2014) and breeding behaviour (Daunt et al., 2005). However, other seabird species also show flexibility in behaviour, including switching migratory destinations and routes (Quillfeldt, Voigt, & Masello, 2010; Dias, et al., 2011).

This thesis has identified individual consistency in timing of breeding and migration events, route choice, stopover behaviour and overwintering destination. Individual-level effects were responsible for more of the variation in these key events and behaviours than was the effect of year (as an indicator of environmental variation). The findings in this chapter suggest that individual variations in timing have strong carryover effects from one year to the next, especially during the non-breeding period. However, without further experimental work and measures of individual fitness, it may be hard to fully understand if and how birds are compensating for these carryover effects (Conklin & Battley, 2012).

6.4.6 Limitations of structural equation modelling

The statistical analyses in this chapter were enabled by the recent development of structural equation modelling procedures based on generalised linear mixed-effects modelling, enabling the models to account for the complex, nested nature of the dataset. This analysis compared alternative pathways for carryover effects within each of three main stages of the annual cycle. Ideally, these analyses would have been combined into a single SEM covering the entire annual cycle. Such an approach would enable direct comparisons of links between events in different sections of the lifecycle. However, such an analysis would require the fitting of a very large number of models, representing all possible links among key variables. Statistical tests would have to be carried out to evaluate the strength of evidence for each one of these links, and the evidence for including possible missing links. Such a large model would be very susceptible to inflation of the overall false positive rate (type I errors): the analysis would be likely to consider links important even if the apparent relationship occurred by chance alone. Another hurdle to analysing the data in a single SEM is the need to analyse a dataset where each observation (here, variables in a single annual cycle for a bird) has a value for all variables. Even though this study comprised data on over 300 annual cycles for 143 individuals, due to limitations of the logging technology (occasional device failure, and high positional uncertainty at certain times of the year), only a small number of tracks (37) had information for every single variable. Applying a very large model to such a small dataset would have led to vastly reduced statistical power to detect effects. Using prior biological knowledge about the most likely pathways for carryover effects enabled me to split the analysis into distinct sections, and make meaningful inference into their importance. As datasets increase in size, techniques such as these which aggregate a large number of variables to compare competing hypotheses across whole annual cycles will become more and more useful.

SEMs formalise comparison between competing hypotheses about causal pathways (Shipley, 2009). As well as providing a coherent quantitative framework for formulating these hypotheses, statistical methods have been developed to analyse the overall goodness of fit of the whole SEM. Whilst useful, it is important to bear in mind that the direction of these tests is different to standard hypothesis testing. Tests such as Shipley's test of directed separation evaluate the strength of evidence to reject the *alternative* hypothesis (that the proposed SEM is correct), rather than the null hypothesis (that there are no causal pathways). Where a model is incorrect, but where little data are available to reject it, the resulting non-significant result will be misleading. Rather than assessing how good the final model is, or the strength of evidence for the existence of causal pathways, SEMs are better suited to comparing between alternative competing pathways. When used in this way they help to formalise comparisons between direct and indirect pathways in a way that is not possible in other modelling frameworks (Lefcheck, 2015).

6.4.7 Conclusions

This chapter brings together the main findings presented in other sections in an attempt to understand how different parts of the Manx shearwater annual cycle interact, and if these interactions can explain some of the documented variation. Timing of key events during the two phases of migration are examined in relation with breeding phenology, both within single annual cycles and across years. Strong relationships are found between the timing of migration departure and the distance travelled, with later birds flying a shorter distance. The timing of arrival at the breeding colony was influenced by the timing of migration, but subsequent breeding phenology was not affected by migration. Birds which arrived at the breeding colony later were in poorer condition and generally spent more of the breeding season in flight behaviour.

Cyclical relationships bring another level of complexity to an analysis, and SEMs provide a useful tool for addressing this. While it was beyond the scope of this study, it would be possible to build similar SEMS including environmental records in conjunction with logger data.

Despite the difficulty of working with this cyclical data, now that we are beginning to follow individuals for the duration of their annual routine, the importance of this technique for understanding population dynamics and ecological interactions should not be underestimated (Marra, et al., 2015). This is especially true for migratory species, where conservation strategies may need to be applied at several points in the annual cycle (Hostetler, Sillett, & Marra, 2015).

6.5 References

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Chapter 7

Discussion

7.1 Key findings

This thesis sought to quantify behaviour and the timing of key events throughout the entire annual cycle of the Manx shearwater, and to investigate inter-colony, inter-sex and inter-year differences, and individual consistency in these behaviours and events. Disentangling the relative impact of these drivers was made possible by the unprecedented volume and scope of the data set. A total of 275 non-breeding periods (migrations and overwintering, from 143 individuals) and 89 complete breeding seasons (from 59 birds) were recorded across 6 years (2006-2012) from individuals breeding on five colonies. Archival logger data enabled quantification of behaviour during the oceanic phases of the annual cycle, when Manx shearwaters are otherwise very hard to observe. By estimating behavioural states and the timing of key events from these data for each individual, this thesis was able to answer investigate the differences in and links between sections of the full annual cycle in a way that no previous studies have.

There was a noticeable pattern of individual consistency and behavioural variation among birds from different breeding colonies. Individual shearwaters were consistent in their migration and breeding phenology and also spatially consistent in their non-breeding phases. There was particularly marked individual repeatability in migration route and the locations of the overwintering area and migratory stopovers. The multi-colony data presented here demonstrated that birds breeding at colonies separated by a few hundred kilometres exhibited clear differences in behaviour. These inter-colony differences occurred in the timing of migration and the flight paths followed across the Atlantic Ocean. Incubation strategy also differed, with more southerly colonies taking more, shorter incubation stints and more northerly colonies opting for fewer, longer incubation stints. The strength of interactions between different parts of the annual cycle was quantified by combining variables determined in chapters 2 to 5 in a path analysis. This analysis showed that delays in the timing of key events in the life cycle lead to delays in the timing of subsequent events during the non-breeding (i.e. migratory and overwintering) period, but that these carry-over effects appear to reset over the breeding season.

7.2 Multi-colony tracking

Inter-colony differences in timing were most apparent between shearwaters breeding at opposite ends of the latitudinal range of breeding colonies. Birds from more northerly colonies were generally later than southerly colonies their timing of migration and also incubation. Birds from different colonies were also idiosyncratic in their use of space during the non-breeding phase, with birds from the same colonies being more similar in their migration routes and the locations of both overwintering areas and migratory stopovers.

Migratory behaviour has been shown to be under genetic control in other bird species (Peter Berthold, 1991; Berthold et al., 1992). It therefore seems likely that genetics plays at least some role in explaining the distinct behaviours of individual Manx shearwaters. Genetic dissimilarity between colonies may therefore also play a role in the marked inter-colony differences in timing, migration route, and overwintering locations observed here.

The degree of inter-colony breeding, and therefore genetic relatedness between colonies, in the global Manx shearwater population is unknown. Manx shearwaters exhibit natal philopatry (returning to their colony of birth, Brooke, 1990). Ringed individuals have been recaptured outside their colony of origin (Brooke, 1990), though it is unclear how frequently and how often it is associated with breeding. Many other seabird species exhibit a surprisingly low level of genetic diversity between different breeding populations (Genovart et al., 2013; Wojczulanis-Jakubas et al., 2014). A phylogenetic study of the shearwater population breeding on these five colonies in this study could enable a better understanding of inter-colony connectivity, and the role of genetic relatedness in explaining inter-colony differences.

Other multi-colony tracking studies have found even greater differences in migration route (Fifield et al., 2014; Winden et al., 2014; Fayet et al., 2016) and wintering destination (Dias et al., 2011; Weimerskirch et al., 2015) than those observed in this study. The studies presented in this thesis tracked a large sample of birds from some of the main Manx shearwater breeding colonies in the UK. All but one of these birds migrated to the same general wintering area: a region of the South Atlantic Ocean off the coast of Argentina. Confirmation that this area is used by shearwaters from so many breeding colonies emphasises the importance of this region for the global population of this species. This has important implications for the conservation of this species, since it implies susceptibility of the population to localised environmental stochasticity and potential anthropogenic impacts in this area (such as oil spills).

7.3 Behavioural variation and individual consistency

The mechanisms that control when an individual leaves on migration, the path taken, and where to overwinter are complex and variable (Alerstam, 2006). Answers to some of the questions regarding the migration strategy of a species can be found by studying multiple migration trips within individuals (Wiltschko & Wiltschko, 2012). The identification of significant individual consistency in Manx shearwater migratory behaviour implies that intrinsic factors must play a major role in governing behaviour in this species. Individual consistency has similarly been observed in several other shearwater species (Cory's shearwater (*Calonectris borealis*, Dias et al., 2013); Scopoli's shearwater (*Calonectris diomedea*, Müller et al., 2014); streaked shearwater (*Calonectris leucomelas*, (Yamamoto et al., 2014); Balearic shearwater (*Puffinus mauretanicus*, (Meier et al., 2015) and related procellariiformes (Phillips, Silk, & Croxall, 2005; Deppe et al., 2014; Ramírez et al., 2015). The presence of significant individual behavioural repeatability in these species also raises more questions about the mechanisms governing these behaviours. For example, how do individual birds follow specific routes across the North Atlantic on their pre-breeding migration? And what cues do individuals use to judge the timing of departure on migration or the start of breeding? Whilst progress has been made in understanding mechanisms enabling broad-scale navigation at the species-level (Guilford et al., 2011; Dell'ariccia et al., 2014; Pollonara et al., 2015), our current understanding is insufficient to explain the navigational precision required for individuals to follow distinct routes year on year.

In addition to understanding how individuals navigate consistently, considering the evolutionary drivers of behaviour can provide insights into why different strategies are adopted, and repeated. Both heritability of behavioural traits (such as migratory timing and route) and persistence of these traits in the population are directly linked to how a strategy or type of behaviour influences individual fitness and survival (Senner, Conklin, & Piersma, 2015). This thesis used on weight on arrival at the breeding colony (available only for a subset of individuals), and amount of flight activity during the breeding season as proxies for fitness and reproductive effort. Understanding how these individual differences in behaviour relate to fitness directly will require even longer term tracking, linked with comprehensive data on reproductive success.

The behavioural strategies recorded here could be considered evidence for individual specialisation, a term that is frequently used to describe foraging consistency (Bearhop et al., 2006; Bodey et al., 2014; Ceia & Ramos, 2015; Ramírez et al., 2015), but is less commonly applied to other behaviours. The observed variation in migratory behaviours (both spatial and temporal) could be classified into different strategies, such as: "late and fast" (departing on migration late, and shortening the migration period) versus "early and slow" (leaving early and spending longer on migration). This might allow easier study of behavioural variation in the context of individual fitness. High correlations between two or more behaviours (i.e. observed simultaneously) are sometimes considered as 'behavioural syndromes'. This is defined as "behavioural traits that vary consistently across functionally different contexts" (Adriaenssens, Johnsson, & Sih, 2012 and Dingemanse & Dochtermann, 2013). A somewhat similar approach to considering individual variation is research on 'personality' in animals, including seabird species (Patrick, Charmantier, & Weimerskirch, 2013; Patrick & Weimerskirch, 2014). It may be useful to investigate Manx shearwater behavioural consistency using this framework. A personality study might score individual shearwaters according to a gradient of (for example) 'boldness/shyness' (Samantha C. Patrick & Weimerskirch, 2015). It may be that the differences in behaviour that we see here can be explained by similar inherent behavioural traits.

Much has been made of the use of seabirds as indicator species for the functioning of marine ecosystems (Shaffer et al., 2006; Parsons et al., 2008; Guilford et al., 2009; Gaston et al., 2011). To use a seabird species as an indicator requires a baseline understanding of the species' utilisation of different marine areas, in order to see how that is changing. Given the large degree of individual, inter-colony and inter-year variation in utilisation of marine areas (for overwintering and stopover) in the Manx shearwater (as identified in this thesis) and many other shearwater species, establishing that baseline may not be straightforward (Grémillet & Charmantier, 2010). Multi-year, multi-colony studies of spatial utilisation such as those in this thesis will be crucial to doing so. Relatedly, this high degree of behavioural variation between individuals may make the global population of Manx shearwaters more resilient to environmental shocks, as climatic conditions continue to change and drive fluctuations in productivity and the spatio-temporal distribution of resources (Frederiksen & Daunt 2008; Hipfner 2008; Freeman et al. 2013).

7.4 Carryover effects and the annual cycle of behaviour

The importance of studying behaviour as part of an annual cycle was underlined in chapter one. Not only can this help to explain variation in behaviour observed at an individual level, but it also allows a better understanding of how differing behavioural strategies affect fitness and breeding success (McNamara & Houston 2008; Harrison et al. 2010). Chapter 6 detected interactions between the timing of key events throughout the non-breeding poriton of the Manx shearwater annual cycle. However, the breeding season appears to act as a 'reset' point in the annual cycle. Whilst the timing of the end of an individual's breeding season influences the subsequent migration, and migration influences the start time of breeding, timing of the start of breeding was unrelated to timing of the end of breeding. Whilst clear, these relationships should not be considered carryover effects in their own right, since they could simply be indicators that carry-over effects may be present. No direct measure of individual fitness or reproductive success was made to prove the significance of the relationships identified in chapter 6. The examination of fledging success or long-term measures of individual mass during the breeding season would provide direct evidence to assess whether carryover effects are present.

Studying animals throughout their annual cycle, and focussing on how experiences during one phase influence outcomes in another, is especially important from a conservation perspective. Models of climate change impacts will need to account for how individuals within a species react to environmental variability in order to make accurate predictions about future populations (O'Connor & Cooke, 2015; Marra et al., 2015). For the Manx shearwater, this could mean further studying of the coupling between breeding phenology and subsequent migration in the context of environmental change.

7.5 Limitations and future directions

This study predominantly used data collected by archival light and saltwater immersion loggers. Location estimates derived from light data are subject to large statistical error in both longitude and latitude. This is due to shading by the bird or habitat, cloud cover, movement between records and uniform day length during the equinox (as detailed by Phillips et al, 2004; Fudickar et al., 2012; Lisovski et al., 2012; and Bridge et al., 2013). This uncertainty has the potential to obscure detail in migratory routes and timing, and mask important differences in these behaviours between colonies, years and sexes. However, since all tracks are measured in the same way and are all subject to the same errors, independent of potential explanatory variables, this noise did not lead to bias in any of the tests conducted in this study. If the positional estimates from long-term, lightweight loggers could be made more accurate, this could vastly increase the power of statistical analyses.

This study employed immersion data to sort periods of time into different behavioural classes, in order to identify the timing and locations of key at-sea behaviours. Since these behaviours take place at sea, direct observations of behaviour were not available to train the classifiers. Instead, I used unsupervised classification methods, paired with prior knowledge of behaviour. By pairing these saltwater immersions loggers with other data collection devices, it would be possible to calibrate classifiers against direct observations of at-sea behaviour; enabling assessment of, and potentially improving, classification accuracy. Tracking with combined loggers has been successfully used in several seabird species (Peron et al., 2010; Cleasby et al., 2015; Meier et al., 2015; Warwick-Evans et al., 2015) . Dive loggers or miniature cameras could be employed to verify foraging behaviour inferred from immersion data. Whilst these devices could not be deployed across a full annual cycle (due to size and battery constraints), paired deployment during breeding-season foraging trips could be used to better train models to infer behaviour from long-term deployment of immersion recorders (as in Freeman et al., 2013 and Dean et al., 2012). However, such an approach would first require classification of behaviour from an alternative type of logger, which whilst more precise may still propagate errors into the model. This approach also relies on an assumption that at-sea behaviour during the migratory period is the same as at-sea behaviour during breeding.

A major assumption made by all biologging studies is that deployment and continued presence of the logging device does not substantially alter the animal's behaviour. The use of small archival loggers in this study minimises the impact on study birds, relative to larger devices such as GPS recorders and platform transmitter terminals (PTTs). Nevertheless, it is likely that there were some negative effects on the birds in this study, however small (Wilson & Vandenabeele, 2012). Deployment of similar devices on other species has caused variability in survival (Costantini & Moller, 2013; Casas et al., 2015); flight activity and energy expenditure (Vandenabeele et al., 2011; Chivers, Hatch, & Elliott, 2016); and body condition (Igual et al., 2004). However, small loggers do not seem to affect immediate reproductive success (Carey, 2011; Kim et al., 2014) but the effect on lifetime reproductive output in long-lived birds may be harder to quantify. The likely population-level impacts of tracking studies can be assessed by quantifying individual survival and reproductive success of tracked birds. In this study, it was hard to quantify impacts on individual survival across all colonies as many were only visited for a short period of time once per year. However, on Skomer the re-sighting rate of tracked birds the year after logger attachment was 75% (131 birds re-sighted out of 176 deployments). In a concurrent study on Skomer, there was no apparent effect of GPS deployment on growth rate of the chicks of tracked birds; a proxy for reproductive success. Given that GPS loggers are much heavier than geolocators and deployed during the most energetically demanding phase of breeding, it is unlikely that geolocator deployment had a significant impact on reproductive outcomes. More recently, Shoji et al., (2015) showed that data collected using the same methods (running partially parallel to this study) had no impact on the number of chicks raised by tracked birds when compared to controls.

The causes of spatial variation in stopover and overwintering behaviour, and of temporal variation in timing of key events, could be investigated in more detail by comparison with detailed data on environmental conditions. Spatial information on remotely sensed proxies for marine productivity, such as Chlorophyll A concentration and sea surface temperature (Yen et al., 2006; Peron et al., 2010; Neves et al., 2012; Deppe et al., 2014; Passuni et al., 2016), or tidal fronts and bathymetry (Phillips et al., 2006); Paiva et al., 2010; Dias, Granadeiro, & Catry, 2012; Cox, Scott, & Camphuysen, 2013; Drew, Piatt, & Hill, 2013; Carneiro et al., 2016) could be used to test whether overwintering or stopover locations are targeted toward more productive areas. Temporal information on these same metrics could be used to investigate whether timing of arrival at the breeding and overwintering areas coincides with peaks in productivity, as seen in both marine and terrestrial species (Reed et al., 2012; Thompson et al., 2012; Lany et al., 2016; Ramírez et al., 2016; Regular et al., 2014). Other environmental variables may also be of interest for this species. Wind speeds and directions during migration are also likely to have an impact on the choice of flight strategy, as has been detected in passerines and raptors (Klaassen at al., 2010 Chapman et al., 2015) as well as seabirds (Felicísimo, Muñoz, & González-Solís, 2008; González-Solís et al., 2009; Mateos-Rodríguez & Bruderer, 2012). Several individuals in this study repeatedly overwintered in an area of sea into which fluvial deposits from the Rio de la Plata are added. This region also contains a major continental shelf that causes regular upwelling. Both of these sources of primary nutrients may lead to transient local increases in marine productivity that could be a key resource for Manx shearwaters overwintering in this area. More detailed investigation of the at-sea activity of wintering birds could be used to determine whether their locations coincide with these increases in productivity at a fine spatial scale.

7.6 Concluding observations

Occupying the position of top predators in the marine food web, seabirds are often regarded as useful indicators of ocean "health" (Parsons et al., 2008), and certainly during their spectacular migrations they sample a wide range of habitats (Shaffer et al., 2006). However, like many other species, seabirds are currently facing a diverse array of problems, many human-induced. Issues caused by climate change (such as ecological mismatching and increased environmental stochasticity) need to be understood within the framework of individual variation in long-lived species (Sydeman & Bograd, 2009; Saino et al., 2010; Zador et al., 2013). Additionally, Procellariiformes are some of the most at risk seabird groups from conflict with fisheries (Delord et al., 2008; Jiménez et al., 2014; Genovart et al., 2016), plastic pollution (Petry et al., 2008; Wilcox et al., 2015) and colony based predation by invasive species (Jones et al., 2008).

It is my hope that by increasing our understanding of Manx shearwater migration and implications for breeding behaviour, the work in this thesis will better prepare us to implement effective policies (such as marine protected areas, and no-take zones for fisheries) for the protection of this species, both at the breeding colonies and the overwintering area (Lascelles et al., 2012; Hays et al., 2014). I also hope that the simple techniques outlined here for identification of key behaviours from archival loggers will prove useful for other seabird species.

7.7 References

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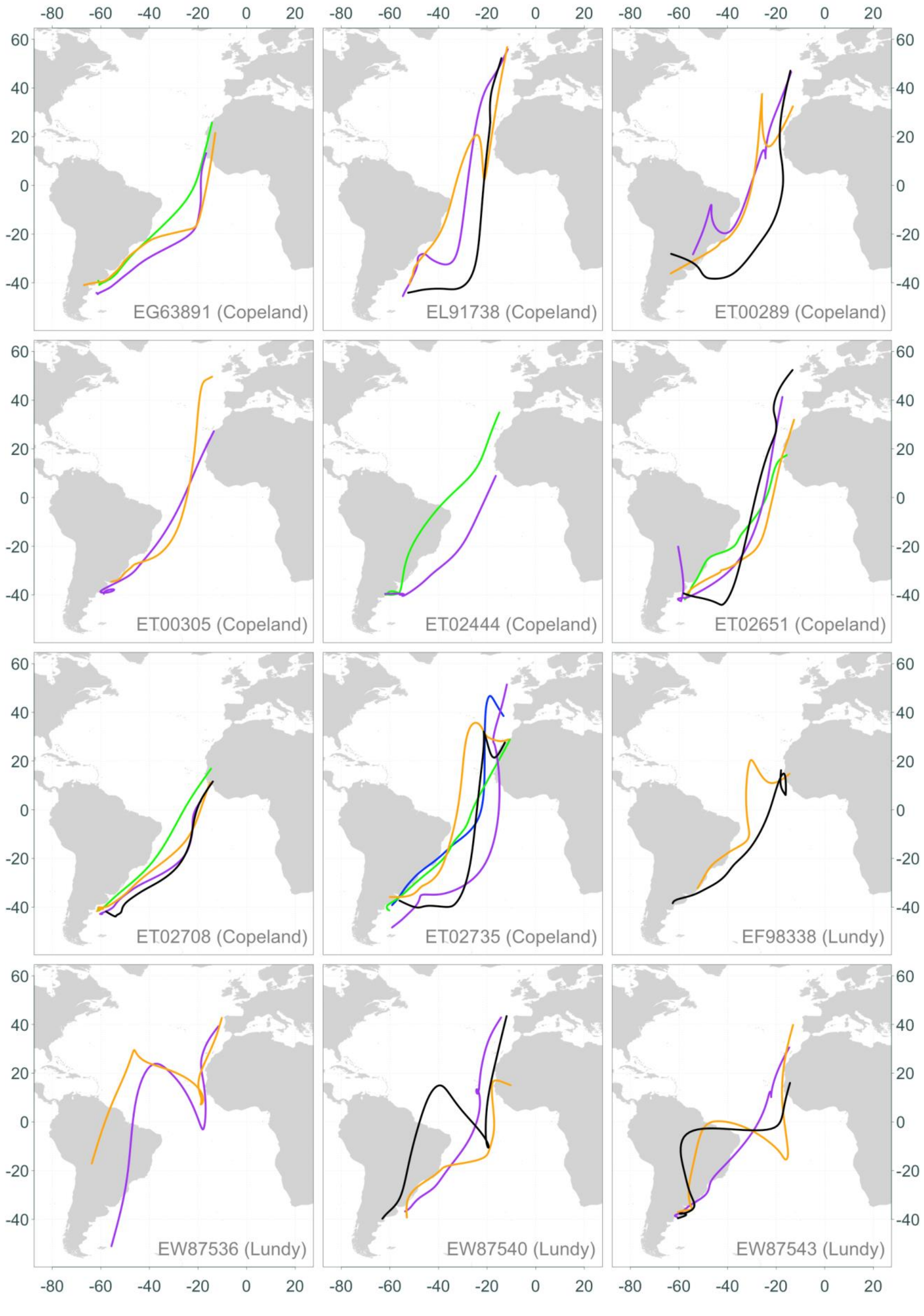
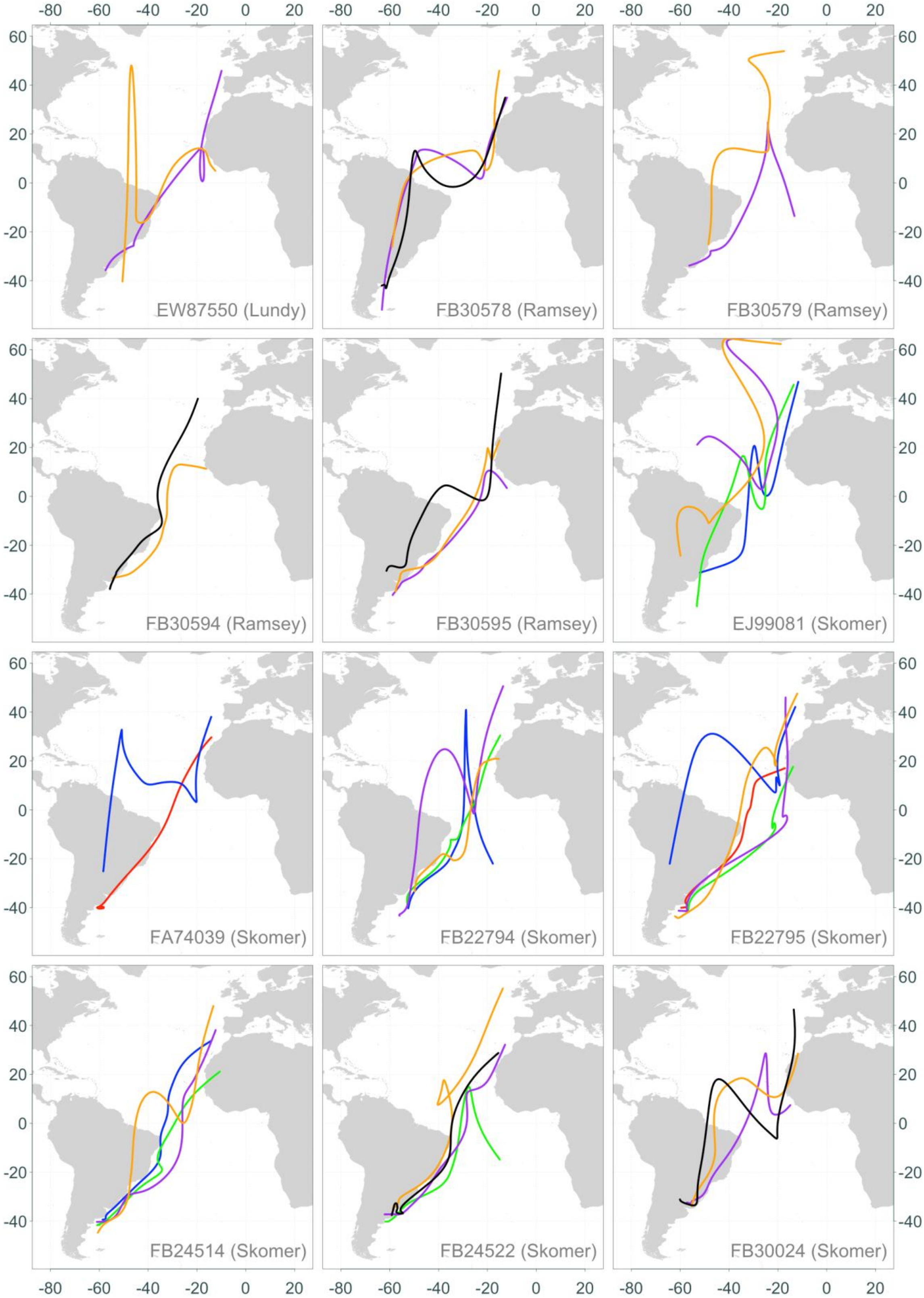
Appendices

Appendix 3A

Individual repeated southbound migration routes from Manx shearwaters breeding on five different UK colonies. Tracks are smoothed using a cubic spline with 10 degrees of freedom. One bird is plotted per panel, with multiple years. Line colour indicates year data were collected (on return to the breeding colony): Red = 2007, Blue = 2008, Green = 2009, Purple = 2010, Orange = 2011, Black = 2012.

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FB22794 (Skomer)
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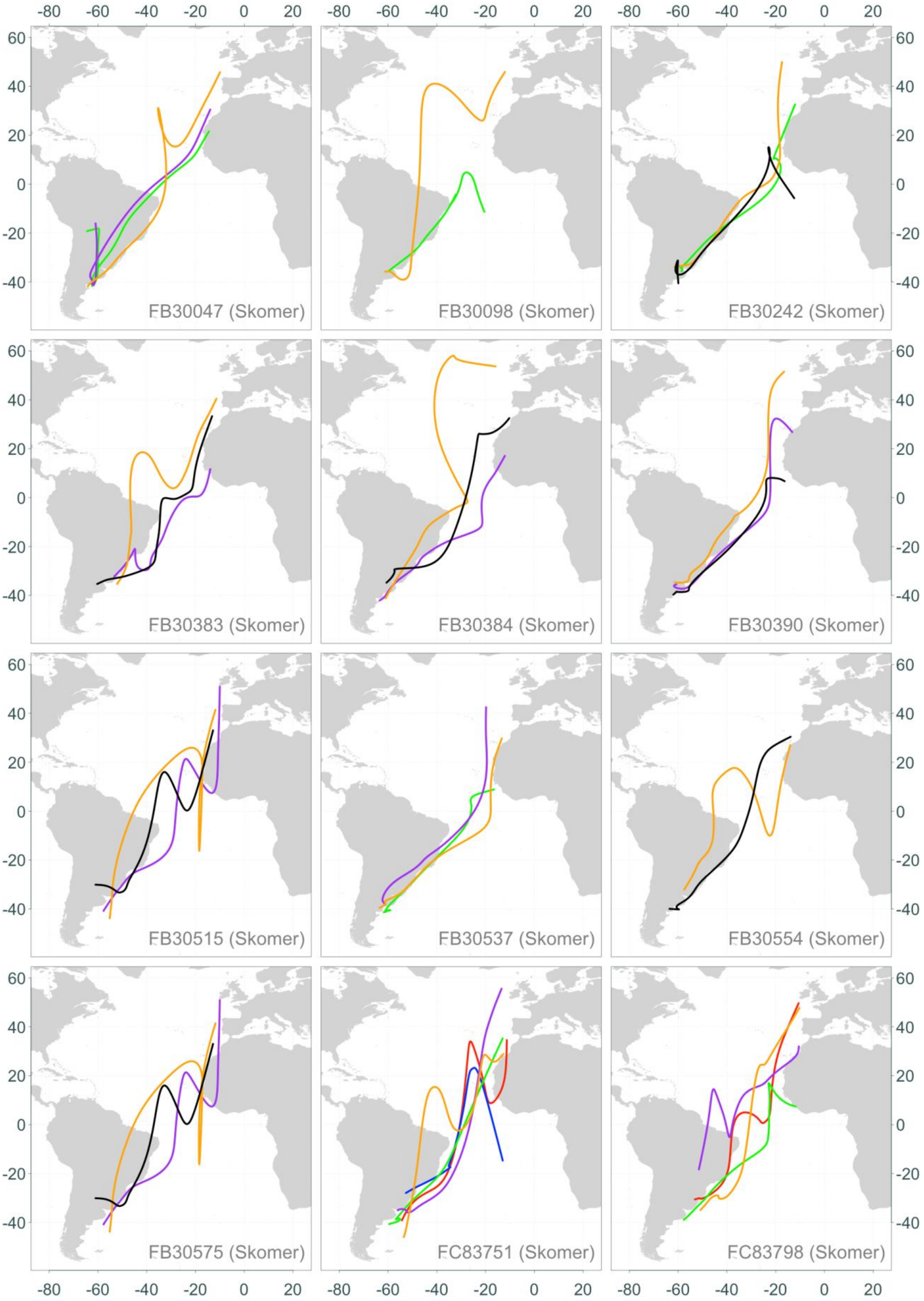
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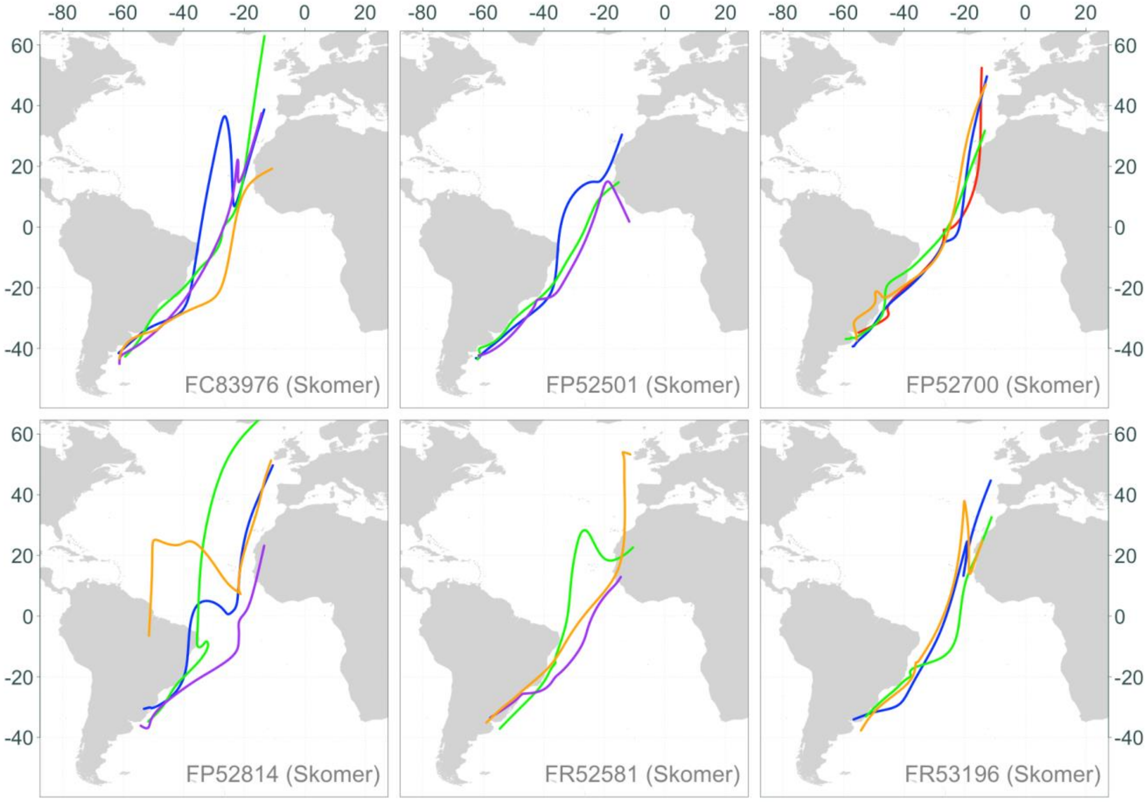

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20
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-20
-40
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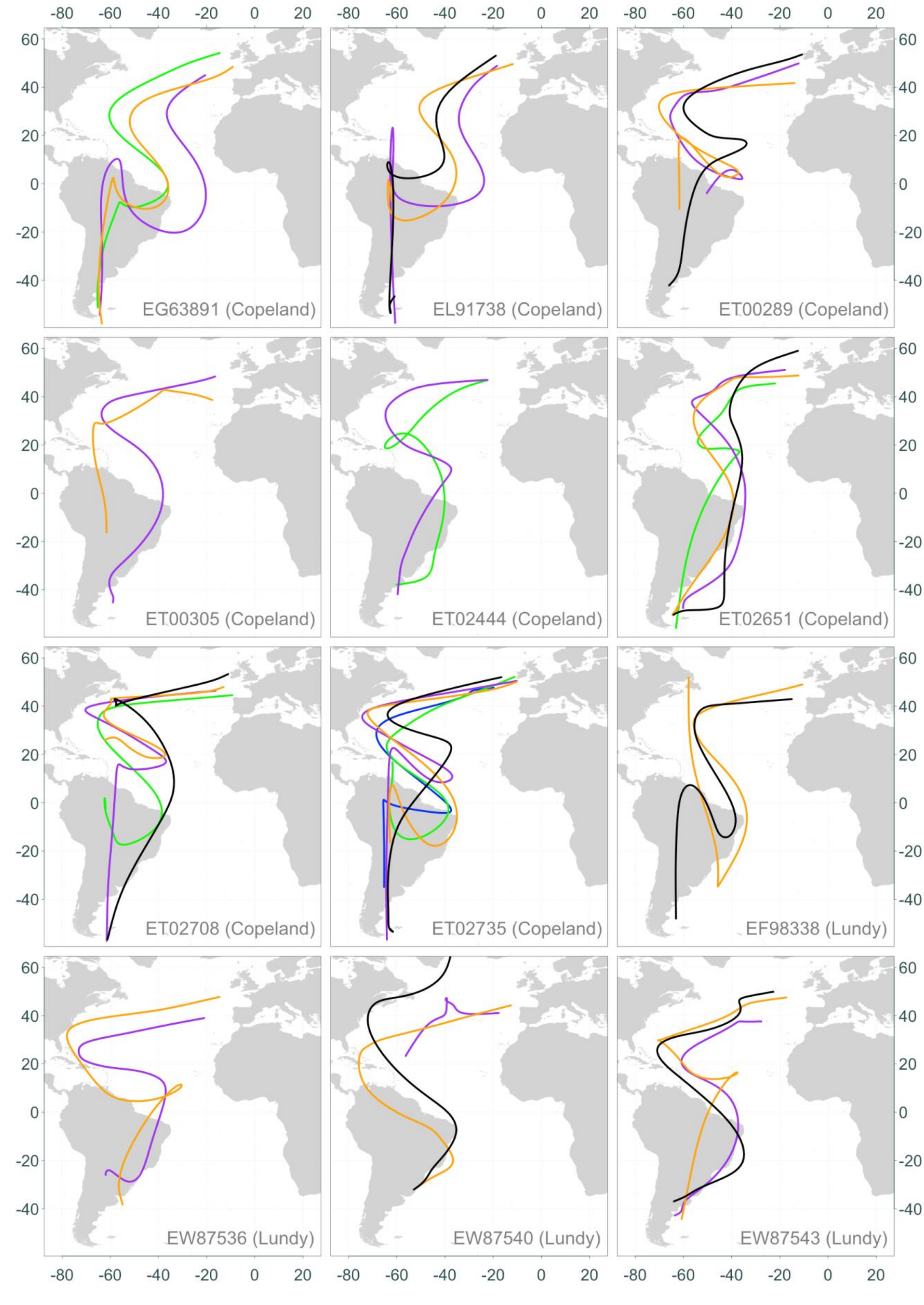
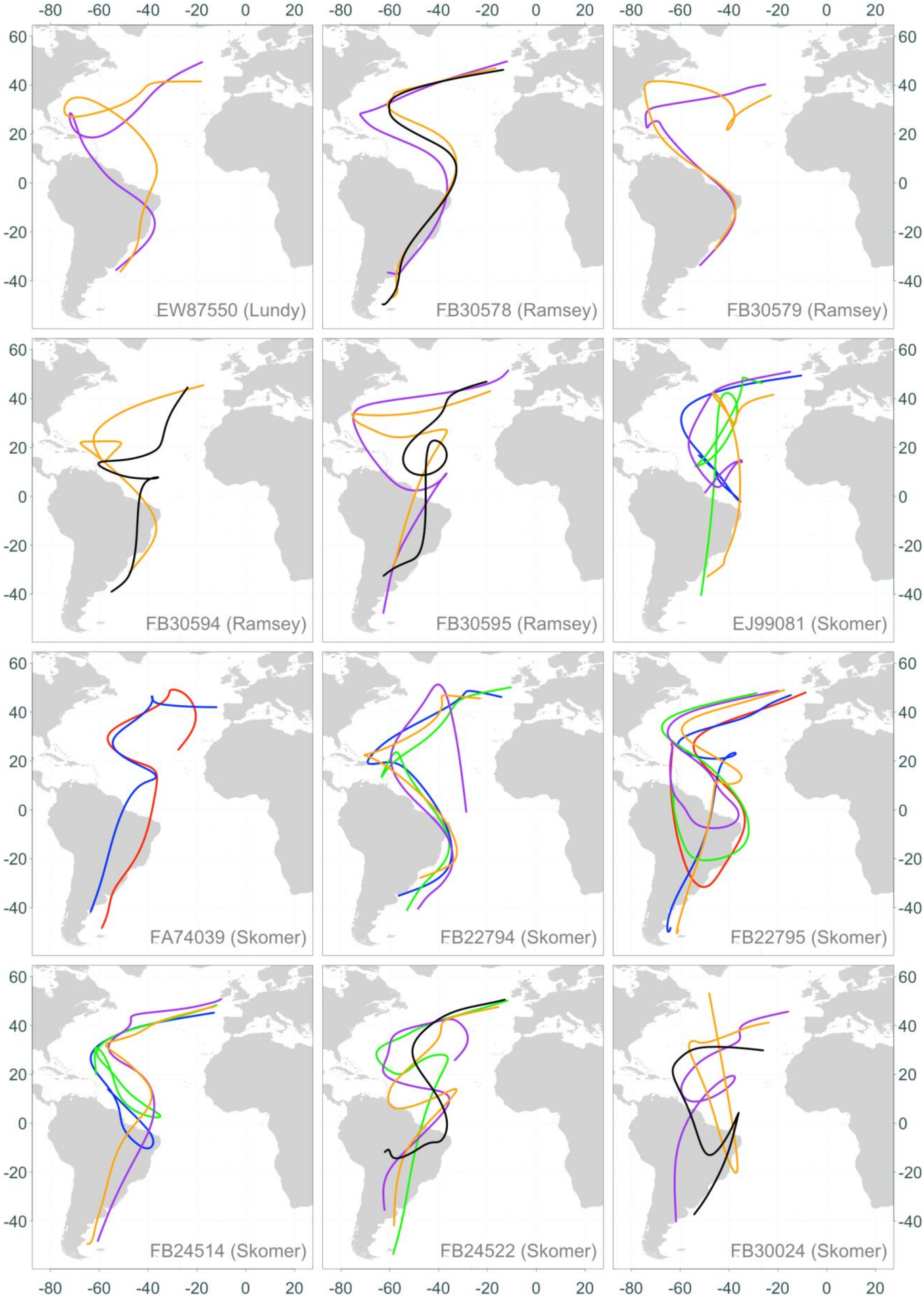
FP52700 (Skomer)
FP52814 (Skomer)
FR52581 (Skomer)
FR53196 (Skomer)

Appendix 3B

Individual repeated northbound migration routes from Manx shearwaters breeding on five different UK colonies. Tracks are smoothed using a cubic spline with 10 degrees of freedom. One bird is plotted per panel, with multiple years. Line colour indicates year data were collected (on return to the breeding colony): Red = 2007, Blue = 2008, Green = 2009, Purple = 2010, Orange = 2011, Black = 2012.

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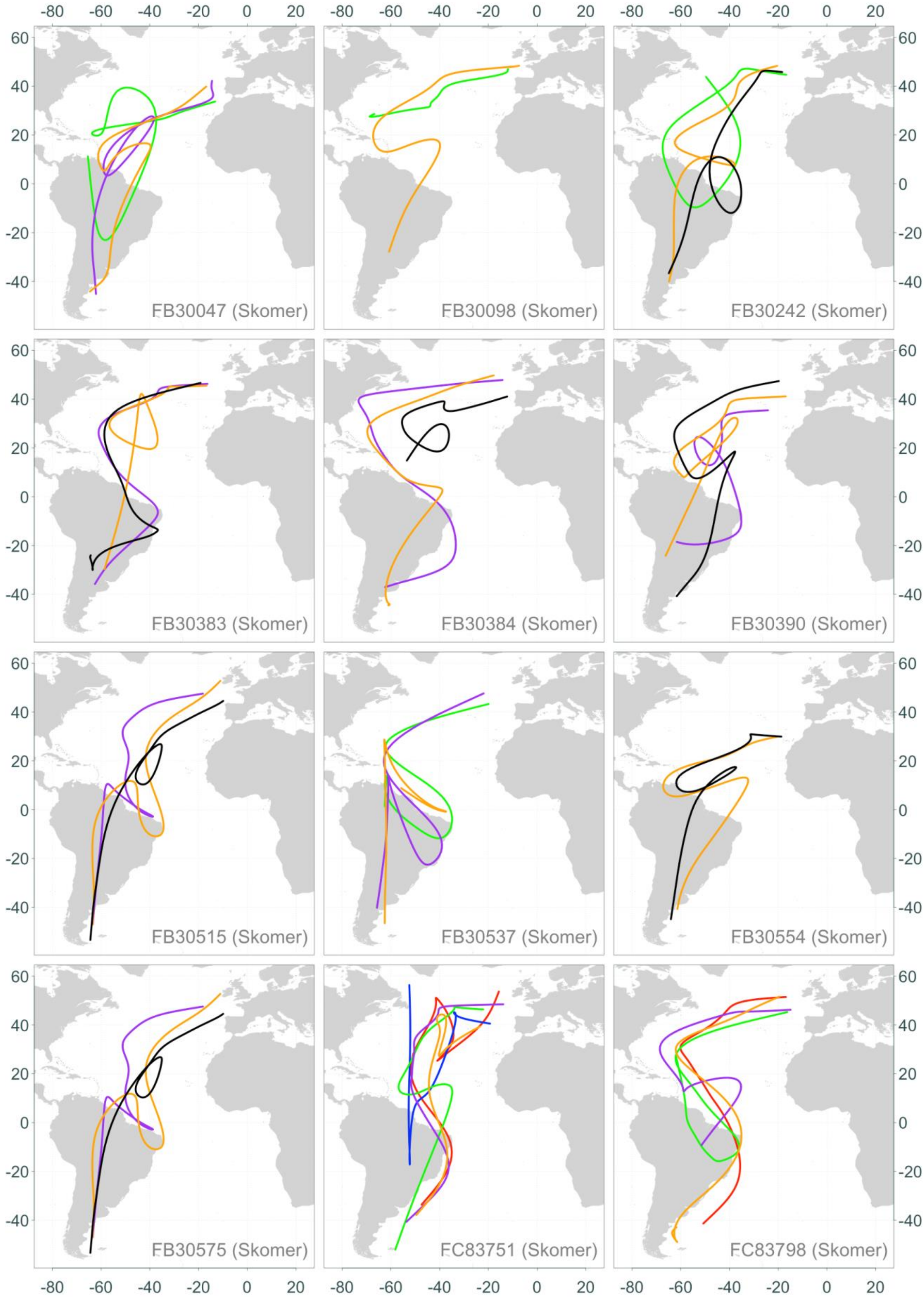
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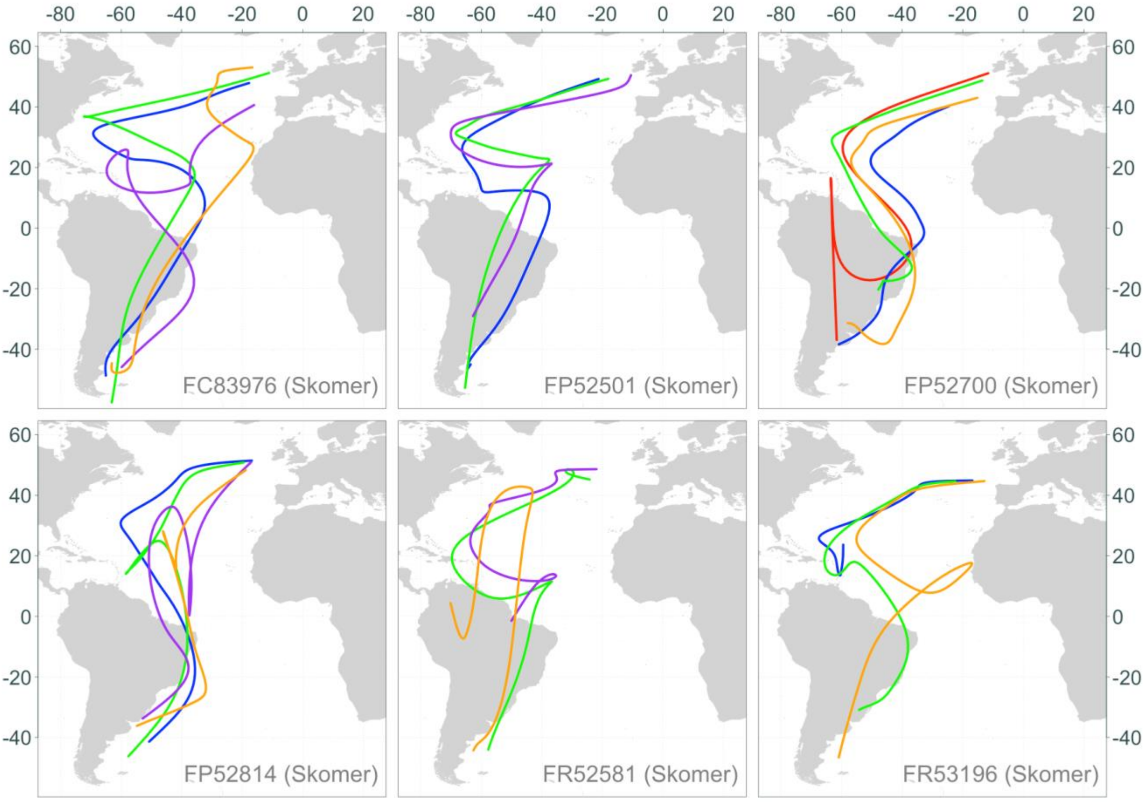
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FR53196 (Skomer)
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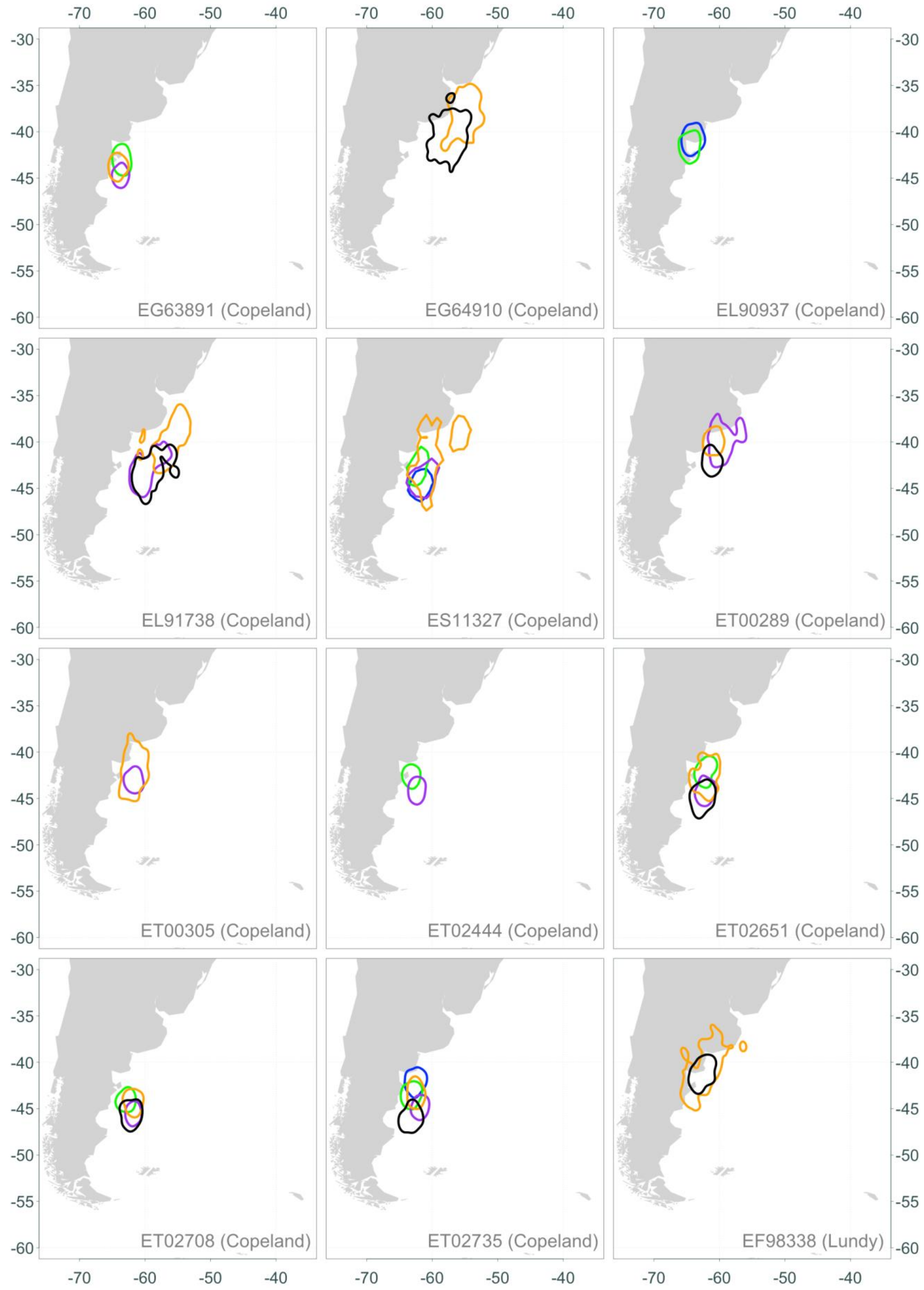
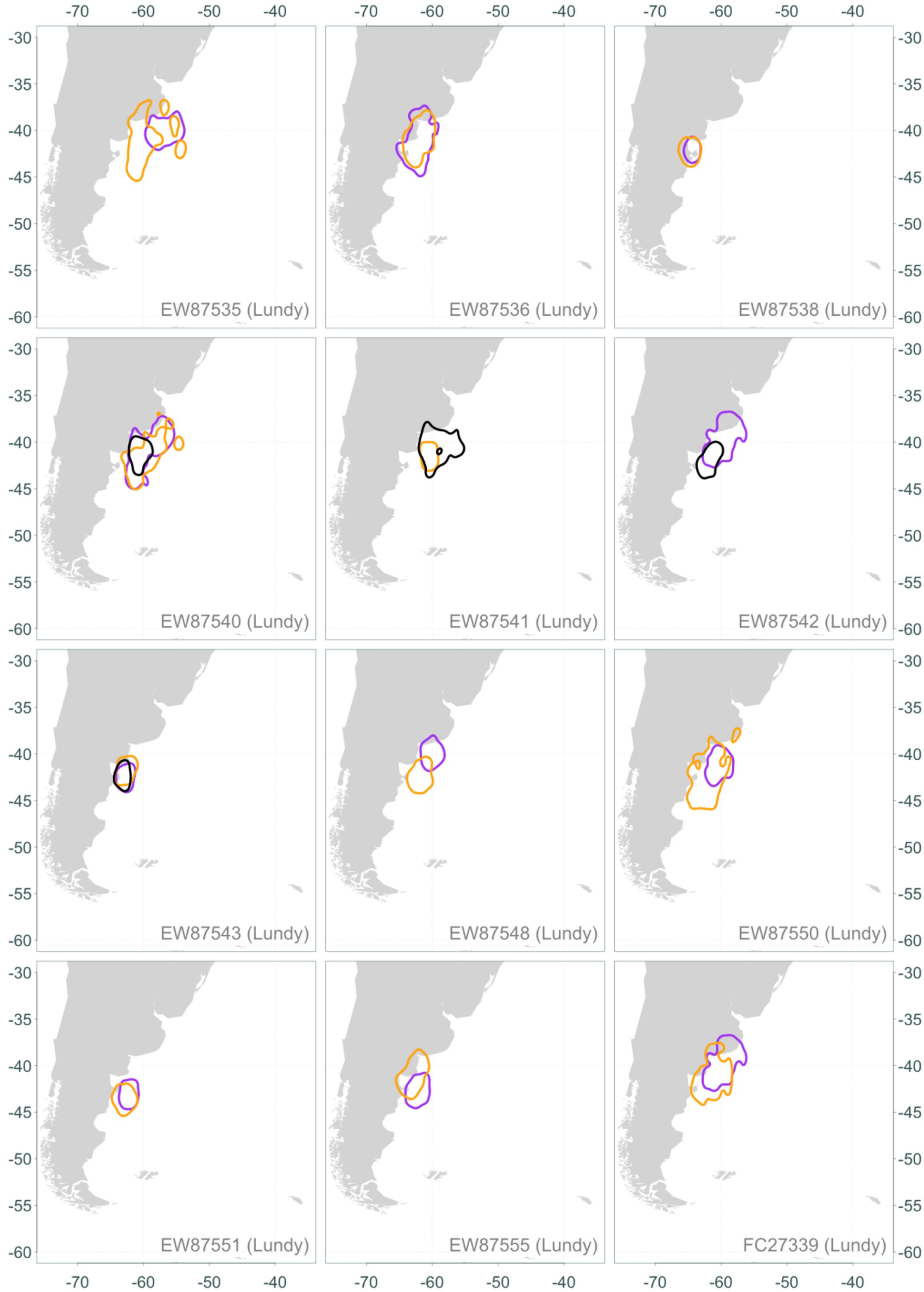
60 40 20 0 -20 -40

Appendix 3C

Individual wintering areas from Manx shearwaters breeding on five different UK colonies. 75% Kernel density estimates, showing one bird plotted per panel, with multiple years. Line colour indicates year data were collected (on return to the breeding colony): Red = 2007, Blue = 2008, Green = 2009, Purple = 2010, Orange = 2011, Black = 2012.

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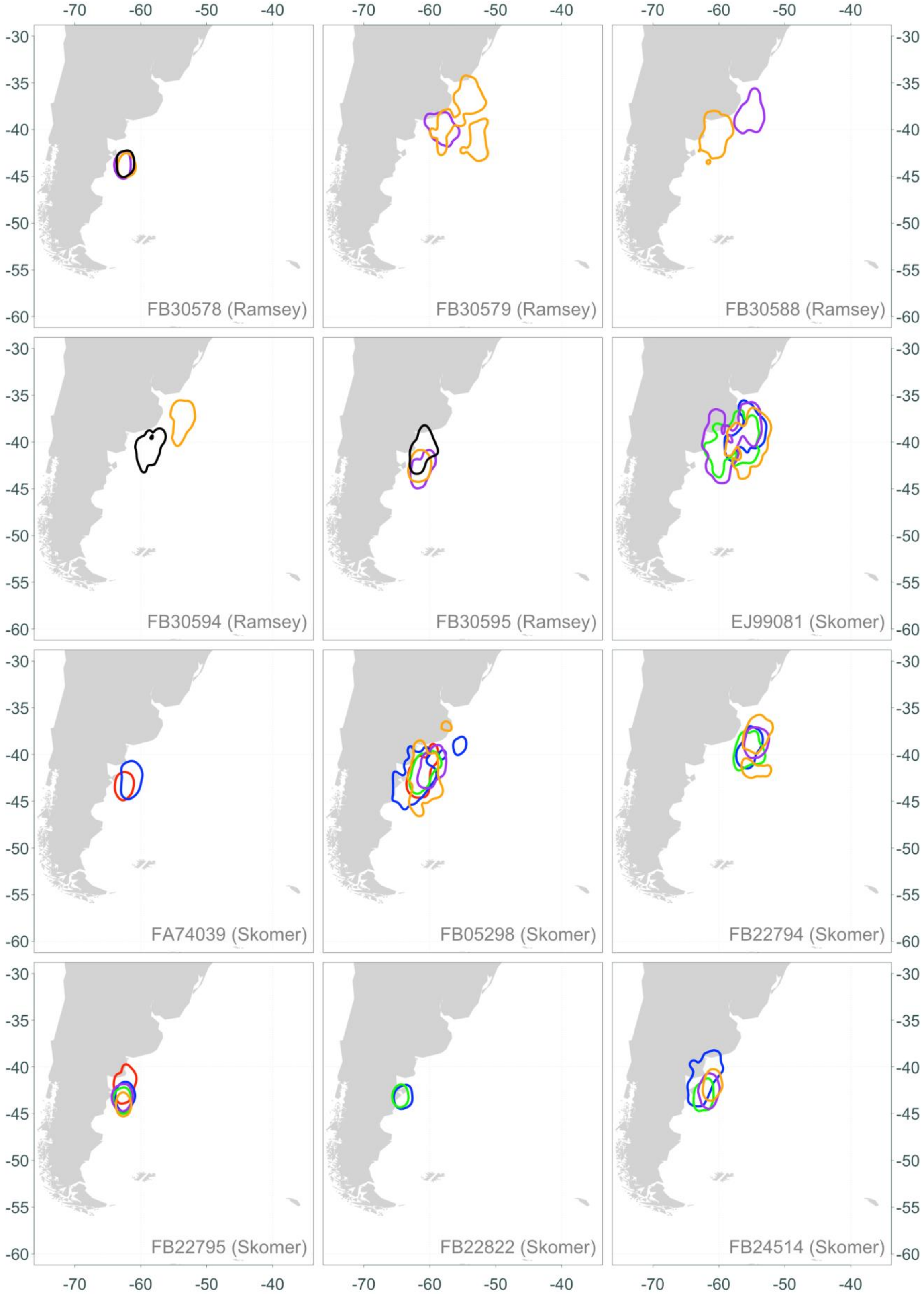
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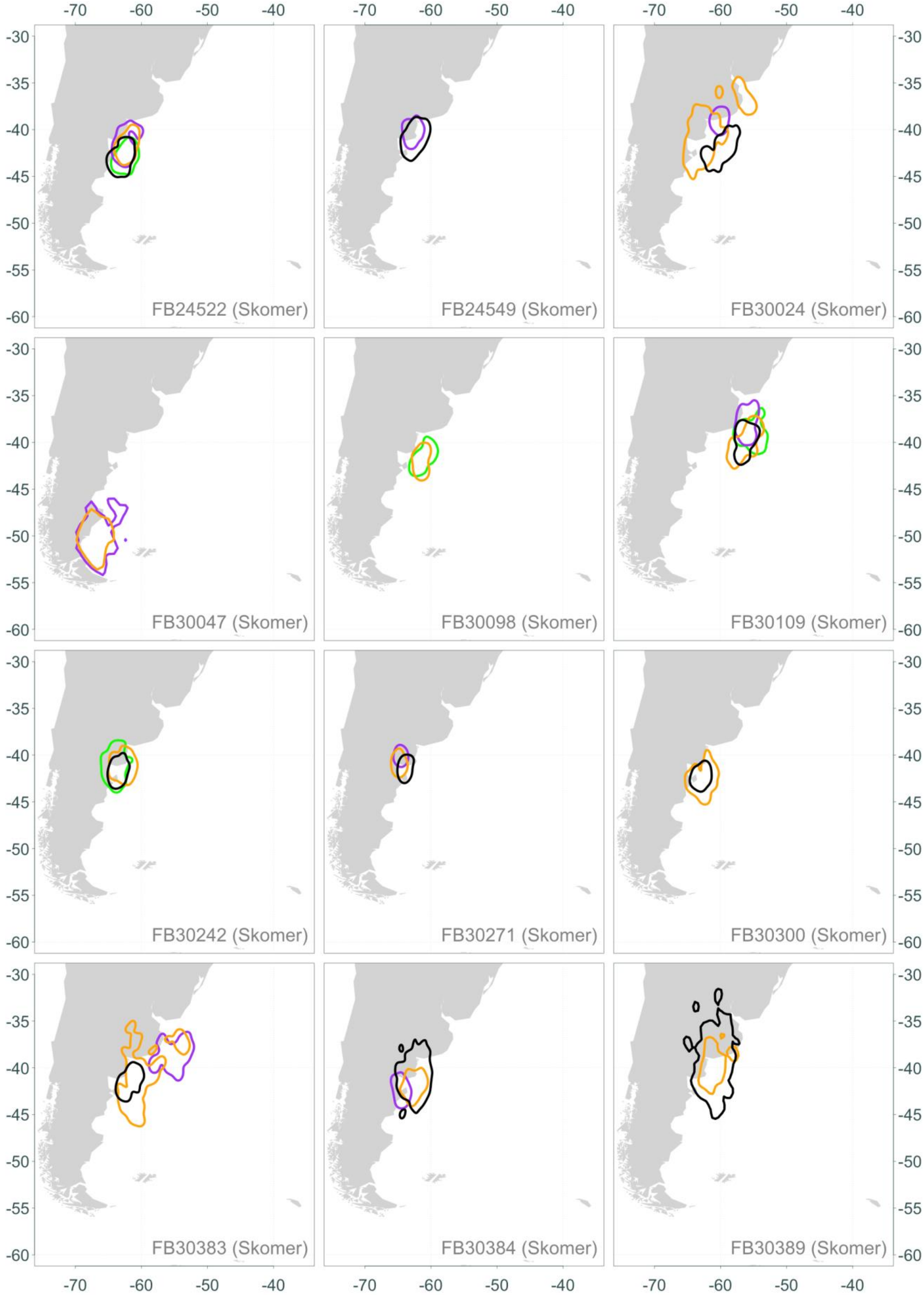

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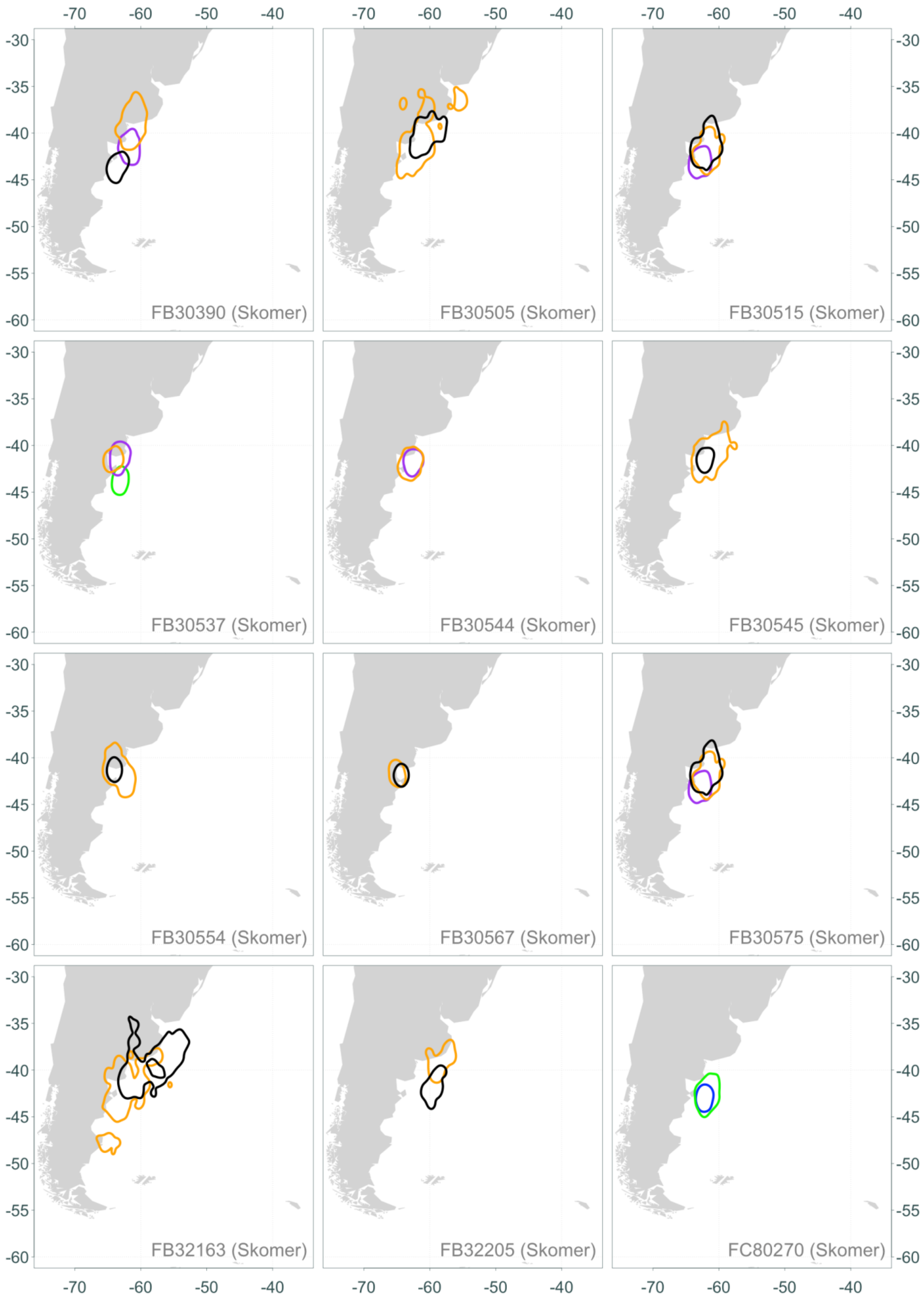
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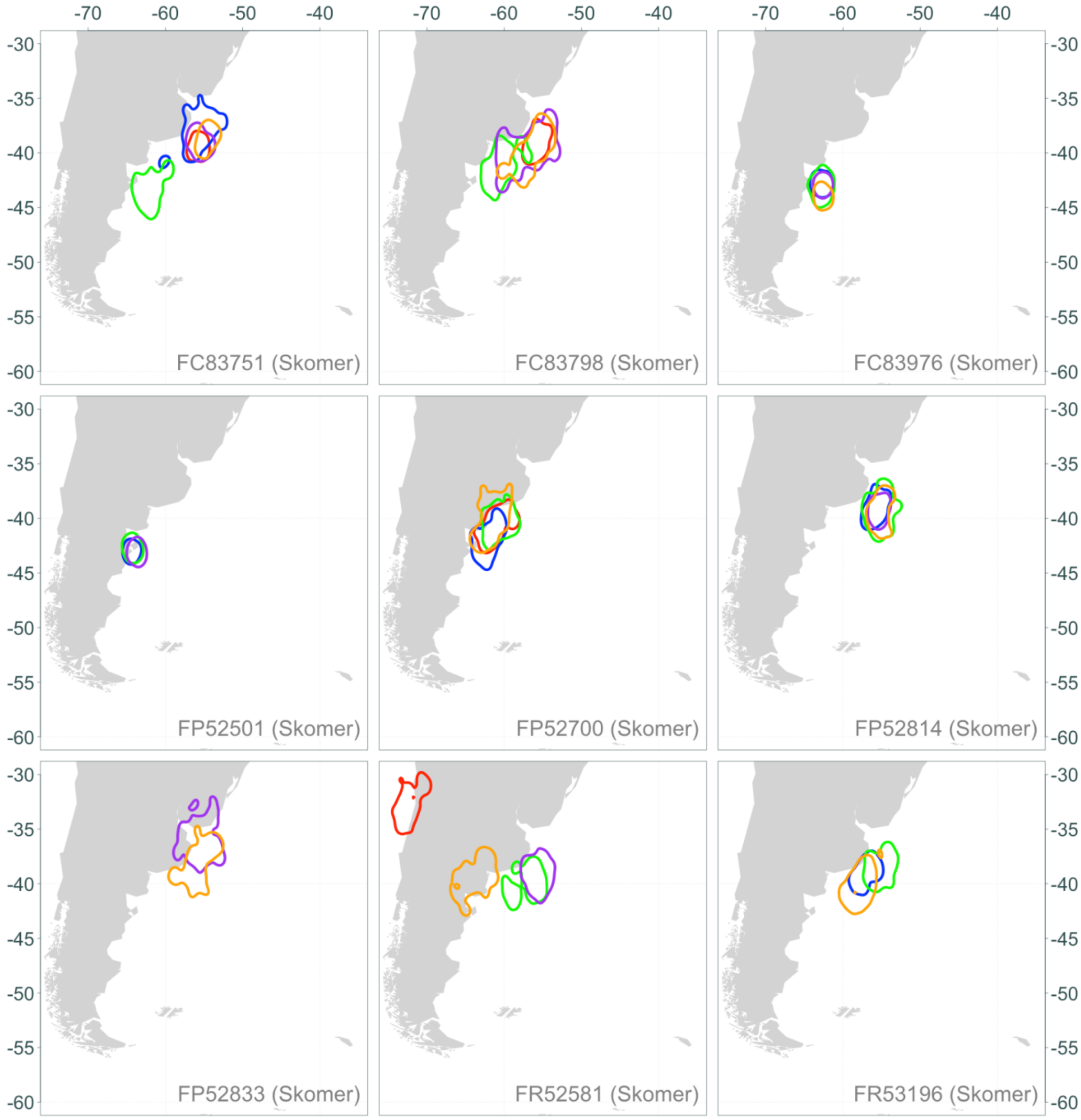
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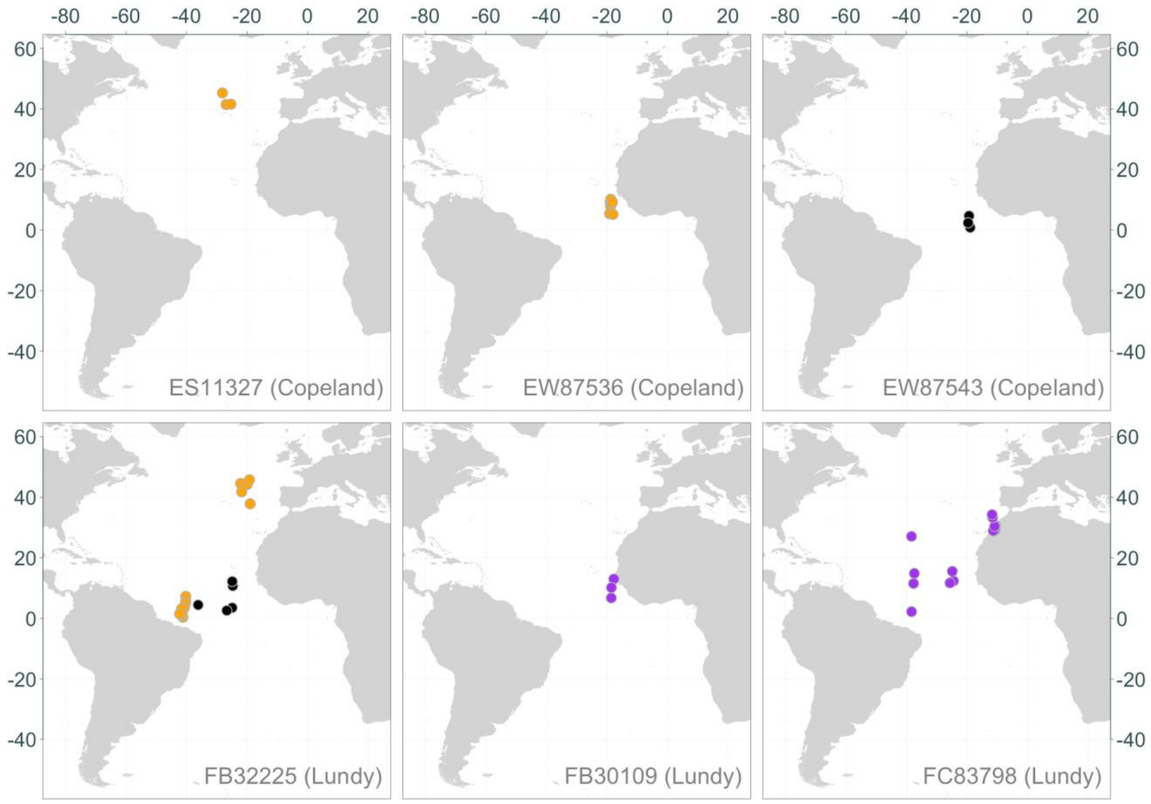
FP52833 (Skomer)
FR52581 (Skomer)
FR53196 (Skomer)

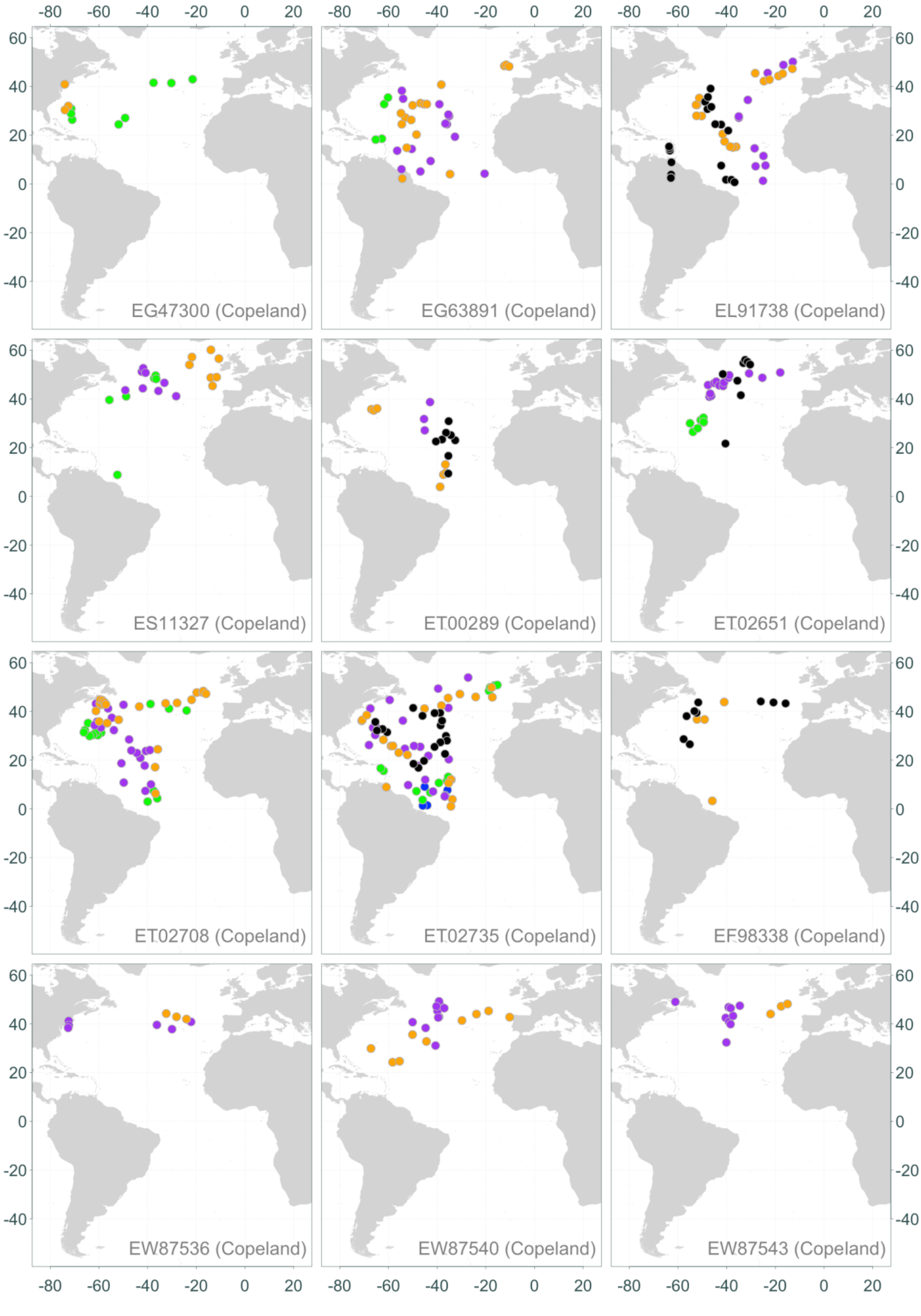
Appendix 4A

Individual stopover locations during southbound migration from Manx shearwaters breeding on five different UK colonies. One bird is plotted per panel, with multiple years. Point colour indicates year data were collected (on return to the breeding colony): Red = 2007, Blue = 2008, Green = 2009, Purple = 2010, Orange = 2011, Black = 2012.

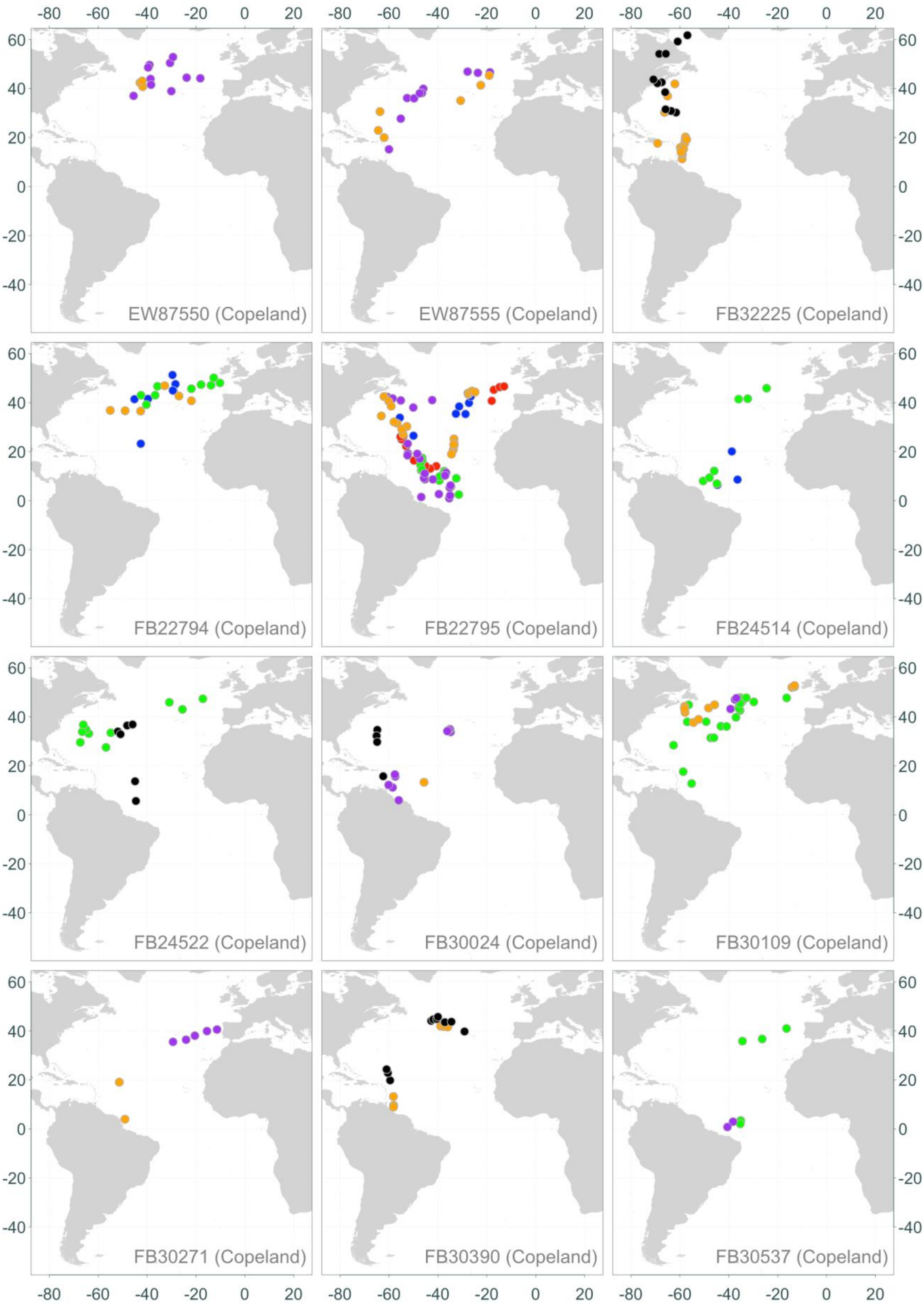


Appendix 4B

Individual stopover locations during southbound migration from Manx shearwaters breeding on five different UK colonies. One bird is plotted per panel, with multiple years. Point colour indicates year data were collected (on return to the breeding colony): Red = 2007, Blue = 2008, Green = 2009, Purple = 2010, Orange = 2011, Black =



2012.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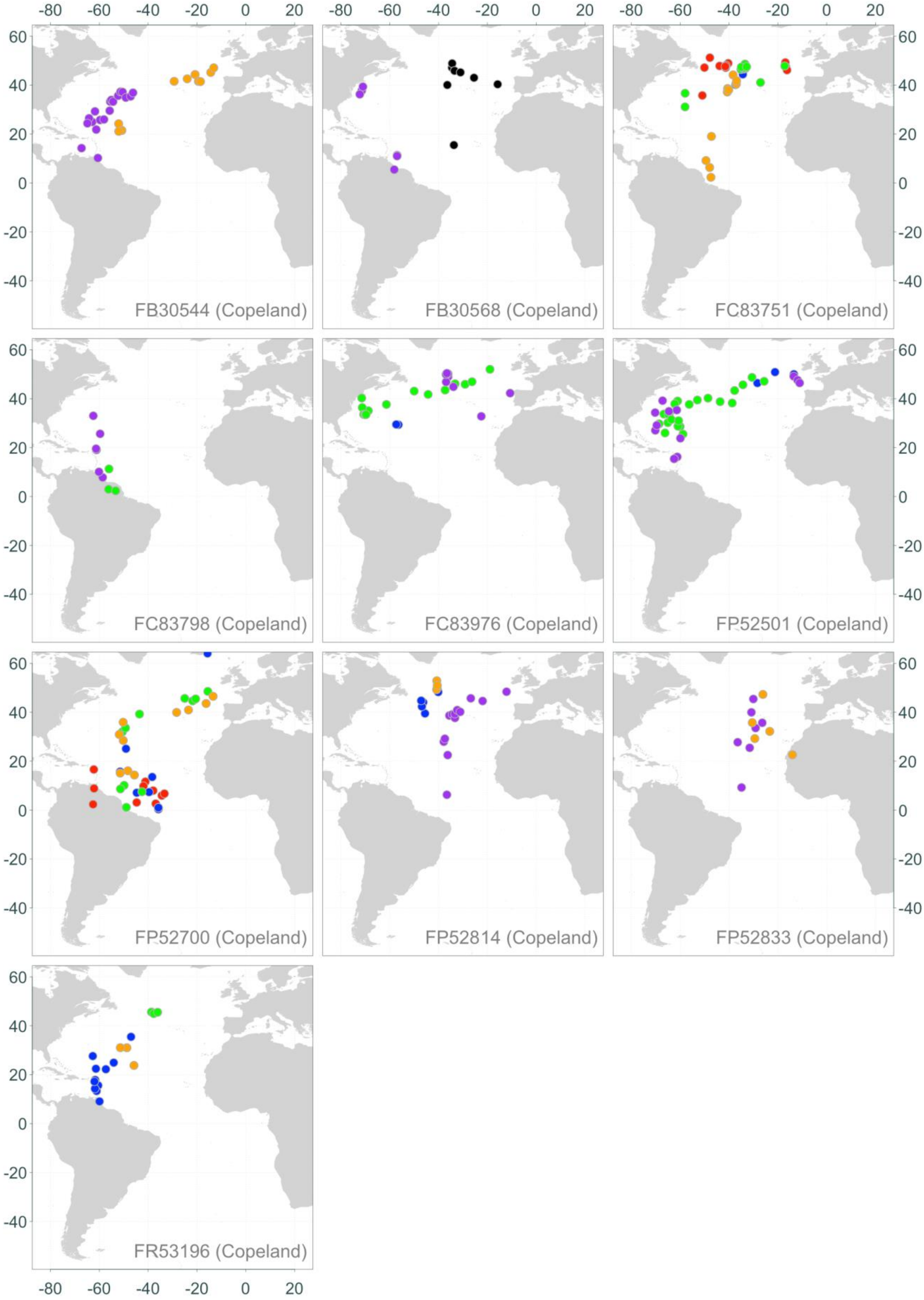
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FP52814 (Copeland)
FP52833 (Copeland)
FR53196 (Copeland)
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Appendix 5A

Timing of breeding events collected by burrow inspection on Skomer, compared to corresponding events determined from saltwater immersion and light loggers (blue columns).

Year	Bird	Burrow	Sex	First seen on the colony	First day spent in burrow	Lay date	Date of first incubation	Hatching date	Date of last Incubation shift	Fledging date	Last night on colony
2009	FB24514	B01	M			16-May	10-May	16-Jul	13-Jul	10-Sep	31-Aug
2009	FB30098	B01	F			16-May	18-May	16-Jul	19-Jul	10-Sep	
2009	FB30537	B50	M			18-May	20-May	07-Jul		>20-Sep	30-Sep
2010	FB30024	B120	F	24-Apr	22-Apr						
2010	FB30034	B46	M			17-May	16-May	05-Jul	13-Jul	10-Sep	29-Aug
2010	FB30109	B14	F	02-Apr	02-Apr	13-May	15-May	02-Jul	01-Jul	07-Sep	30-Aug
2010	FB30271	B70	M	30-Apr	11-Apr	11-May	12-May	29-Jun	28-Jun	30-Aug	
2010	FB30390	B50	F	26-Apr	06-Apr	22-May	21-May	12-Jul	17-Jul	17-Sep	08-Sep
2010	FB30537	B50	M	26-Apr	23-Apr	22-May	21-May	12-Jul	11-Jul	17-Sep	26-Aug
2010	FC83976	W22	M	05-Apr	30-Mar						
2011	FB30024	B120	F	07-Apr	04-Apr						
2011	FB30109	B14	F	10-Apr	10-Apr	18-May	28-May				
2011	FB30300	B01				17-May	22-May	07-Jul	30-Jun	12-Sep	01-Sep
2011	FB30390	B50	F	12-Apr	04-Apr	15-May	22-May	05-Jul	09-Jul	14-Sep	11-Sep

Appendix 6A

Mass (g) on return to the breeding colony, recorded from birds breeding on Skomer Island in 2010 and 2011.

2010			2011		
BTO Ring	Date	Bird Weight	BTO Ring	Date	Bird Weight
FB22794	25/03/2010	460	FB30380	29/03/2011	389
FB30551	25/03/2010	540	FP52833	30/03/2011	430
FR53196	30/03/2010	466	FB30551	31/03/2011	515
FP52833	01/04/2010	440	FP52814	31/03/2011	493
FB30109	02/04/2010	426	EJ99081	02/04/2011	408
FB30568	05/04/2010	427	FC83751	03/04/2011	503
FC83976	05/04/2010	418	FB24518	06/04/2011	466
FB30390	06/04/2010	513	FB30527	06/04/2011	443
FB30526	06/04/2010	402	FB30552	06/04/2011	398
FB30527	06/04/2010	478	FB22794	07/04/2011	519
FP52814	06/04/2010	414	FB30024	07/04/2011	419
FB30271	10/04/2010	467	FB30049	09/04/2011	447
FB30380	11/04/2010	362	FB30109	09/04/2011	397
FB24517	12/04/2010	443	FB22822	10/04/2011	416
FB30300	12/04/2010	460	FB30271	10/04/2011	493
FB30544	12/04/2010	369	FC83661	10/04/2011	439
FB30127	18/04/2010	429	FB24549	11/04/2011	383
FP52501	18/04/2010	391	FB30568	11/04/2011	438
FB30044	19/04/2010	435	FB30034	12/04/2011	515
FB24522	20/04/2010	450	FB30390	12/04/2011	480
FB30047	20/04/2010	375	FB30554	12/04/2011	445
FB30075	20/04/2010	410	FB30633	12/04/2011	480
FB30034	21/04/2010	461	FC83976	12/04/2011	405
FB30383	21/04/2010	397	FP52501	12/04/2011	415
FR88595	22/04/2010	363	FB30127	13/04/2011	475
FC83751	23/04/2010	464	FB30383	13/04/2011	410
FB22822	24/04/2010	378	FB30384	13/04/2011	432
FB30024	24/04/2010	413	FB30505	13/04/2011	435
FB30032	25/04/2010	391	FR52581	14/04/2011	435
FB30381	25/04/2010	412	FB30069	16/04/2011	375
FB30537	26/04/2010	409	FB30509	16/04/2011	355
FB30515	27/04/2010	374	FB05298	21/04/2011	385
			FB30545	21/04/2011	430
			FB30547	21/04/2011	480
Median	**15/04/2010**	**426.16**	**Median**	**11/04/2011**	**439.65**