Long-distance movements in pelagic seabirds: at-sea behaviour and life-history consequences

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Thesis submitted for the degree of Doctor of Philosophy
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Abstract

Throughout their lives, animals have to make trade-offs between current and future events in their annual cycle. Long-lived migratory species in particular have to balance the cost of reproduction with adult overwinter survival, which is heavily dependent on migration. Behavioural plasticity, perhaps through experience and learning, may play a role in shaping individual variations in life-history decisions. The mechanisms by which such variations develop, and their potential effects on life-history traits, are poorly understood. This thesis uses two species of long-lived migratory seabirds, the Atlantic puffin *Fratercula arctica* and the Manx shearwater *Puffinus puffinus*, to address these questions, combining spatial tracking data with fine-scale measures of individual behaviour during long-distance at-sea movements.

At-sea behaviour (measured with estimates of daily activity budgets) varied amongst individuals of different sex, age, and colonies. Individual variations in non-breeding behaviour were affected by investment in the previous season, and such variations had important implications for individual fitness. Puffins which visited the Mediterranean Sea foraged more and had a higher breeding success than puffins which remained locally. In addition, females puffins which foraged more during the winter, regardless of their location, laid earlier (which is associated with higher fledging success) and had a higher breeding success. Shearwaters which invested more in reproduction and started fall migration later spent less time resting at the wintering grounds than in other years, laid later and had a lower breeding success the following season. Shearwaters which invested less in reproduction showed the opposite trend. These behavioural differences were reflected in the birds’ energy expenditure. Higher energy expenditure often correlated with higher fitness. Finally, pairs of puffins which followed similar migratory routes laid earlier the following year, why this was the case remained unclear.

Environmental conditions were likely drivers of individual variation in at-sea behaviour. Puffins from multiple colonies across their breeding range spent more time foraging when in colder and productive waters. Furthermore, puffins from colonies at higher latitudes foraged in colder waters, despite not necessarily remaining close to their colony; this suggests a local adaptation to temperature. In shearwaters, immature individuals foraged in less productive waters than breeding adults, which resulted in a lower foraging efficiency (mass gain per unit of time spent foraging).

Spatial segregation occurred between individuals of different age, sex, colonies and potentially individuals of different quality, often accompanied by differences in activity budgets. Although intra-specific competition was a likely driver of the observed segregated at-sea distributions - for example between immature and breeding shearwaters - it was unlikely to be the only factor. Spatial segregation between pair members in puffins in the months leading to the breeding season, accompanied with higher female foraging effort and breeding success, suggests that segregation resulted from different energy or nutritional requirements, perhaps related to egg laying.

Overall, this thesis highlights how the investigation of the behaviours underlying long-distance movements can be a powerful tool to study drivers of breeding and non-breeding distributions and migratory routes, and the important consequences that individual variation in behaviour may have on individual fitness, and ultimately on population dynamics and the evolution of life-histories.

Acknowledgements

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Author Contributions

All work in this thesis is primarily my own.

17 other people co-author one or more of the data chapters and their contributions are as follows:

Tim Guilford, Robin Freeman and Akiko Shoji contributed their ideas and feedback for all data chapters throughout the planning, data analysis and manuscript preparation, and participated in data collection in the field.

Chris Perrins contributed his ideas and feedback for all data chapters throughout the planning and manuscript preparation.

Holly Kirk contributed her ideas and feedback for manuscript preparation and participated in data collection in the field for chapters 2, 3 and 5.

Ben Dean contributed his ideas and feedback for data analysis and participated in data collection in the field for chapters 2 and 3.

Dave Boyle contributed his ideas and feedback for manuscript preparation and participated in data collection in the field for chapters 2 and 3.

Oliver Padget contributed his ideas and feedback for manuscript preparation and participated in data collection in the field for chapters 5 and 6.

Collaborators Tycho Anker-Nilssen, Kjell Einar Erikstad, Dave Fifield, Erpur Hansen, Mike Harris, Mark Jessopp, Tone Kirstin Reiertsen, Greg Roberston and Sarah Wanless all provided data for chapter 4.

A ma Maman

(to my Mum)

Despite our long familiarity with seabirds, there is much about them that we know or understand little. As we insulate ourselves ever more securely from the wild, wet and windy, the uncomfortable and the insecure, so nature becomes something remote from us, and we from it. Seabirds today are a part of everyday life for few but the patient inshore fisherman or long-distance sailor. As scientists, we may record every last feather and every slightest movement in our computers. We may digitise nest sites and telemeter heart rates, track them with satellites, probe them with ultrasounds and perform a thousand tests on their DNA. But, we too are becoming more distant from our subjects The constant insistence on the quantification of knowledge can tend to separate us from that sense of communion with our study subjects that characterised the generation of naturalists who first made watching birds not only a recreation but also a science.

Anthony Gaston
Seabirds: A Natural History (2004)

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Chapter 1

General Introduction

Introduction

The life-history traits of organisms are shaped by natural selection to maximise fitness within the limits imposed by physical and ecological conditions (Lack 1954; Williams 1966). Animals must allocate finite resources to various crucial events in their life cycle such as reproduction (Bell 1980). The limited resources available to an animal during its lifespan result in trade-offs between present and future investment (Stearns 1989), and the latter requires adults to survive during the non-breeding season until the next breeding opportunity (Charnov and Krebs 1974). Despite extensive research on life-history theory since the mid-20th century (Stearns 1976; Roff 2002; West and Gardner 2013), whether and how behaviour during the non-breeding season affects the subsequent reproductive event(s) remains poorly understood (Norris and Marra 2007; Bowlin et al. 2010). It is, however, central to the understanding of the processes shaping life-history traits (McNamara and Houston 2008). Such mechanisms may also be important to understand which factors affect population dynamics and fitness (Clutton-Brock 1988; Stearns 1992).

The influence of non-breeding behaviour on animals' fitness is likely to be especially important in migratory species, whose survival during the non-breeding season relies on undertaking a long, energy demanding, and sometimes perilous return journey to a wintering destination with better resources (Sherry and Holmes 1995; Webster and Marra 2005; Norris and Taylor 2006). In these species, a sub-optimal non-breeding season may have a decisive impact on the outcome of the next reproductive event: a mistimed migration, a deviation from a migratory route or poor conditions at the wintering site may result in a more costly migration, a reduced body condition the next season, or even death (Sillett et al. 2000; Norris et al. 2004; Saino et al. 2004*a*; Saino et al. 2004*b*). In short-lived, *r*-selected migratory species which only have the opportunity to migrate a handful of times and where timing and direction of migration are most likely mainly genetically controlled (Helbig 1991; Berthold and Helbig 1992; Berthold 1996), flexibility in migratory strategies may be limited (Thorup et al. 2013). However in long-lived, *K*-selected migrants which repeat their migratory journey year after year, there is limited evidence for genetic control of long-distance movements (Meylan et al. 1990), and there may be scope for more behavioural plasticity, and the opportunity for learning and experience to play a role and shape age-related and individual variations in life-history decisions (Sutherland 1998; Mueller et al. 2013; Scott et al. 2014). The life-history consequences of such variations, as well as the mechanisms by which they develop, are currently poorly understood (Newton 2008; Bowlin et al. 2010; Chapman et al. 2011).

This thesis aims to explore the extent of individual variation in behaviour during long-distance movements, to understand why and how they develop and how they may affect individual life-history traits. These individual differences may ultimately influence population dynamics and the evolution of life-histories. More specifically, I explore the drivers of individual variation in behaviour during long-distance movements on large spatial and temporal scales (local to global and multi-year, day-in, day-out), and their life-history consequences at the pair, colony and global population level. I test for carry-over effects of reproduction on migratory behaviour, and assess the potential role of experience in driving at-sea intraspecific competition and segregation. Using seabirds as a study species, I address these questions by employing state-of-the-art methods to measure fine-scale individual variations in behaviour during long distance at-sea movements, in both natural and experimental settings.

Seabirds as model species

Seabirds are appropriate models to investigate the drivers and life-history consequences of individual variation in migratory behaviour. Despite a large range of size, they are all long-lived species, from the 45g Leach's storm-petrel *Oceanodroma leucorhoa* which can live for up to 36 years (Huntington et al. 1996) to the 9kg wandering albatross *Diomedea exulans* which can live for over 50 years (Weimerskirch and Jouventin 1987). They are also extraordinary migrants, most of them undertake yearly journeys of thousands of kilometers across open oceans, sometimes across hemispheres – such as the Arctic tern *Sterna paradisaea* which breeds in the Artic and winters in the Antarctic and holds the record for the longest animal migration (Egevang et al. 2010). The breeding biology of seabirds also makes them good models for life-history related studies. They are indeed highly philopatric to their breeding site, often breed in dense colonies, and engage in long-term pair bonds (Schreiber and Burger 2002). This makes it possible to study multiple birds at once, including pairs, and to monitor their breeding success and survival over multiple years. Compared to terrestrial birds they have a long, slow breeding season, and a long immature period before reaching breeding age.

Advances in bio-logging technology (described below) have made it possible to track animals and collect data on their movements and behaviour remotely (Ropert-Coudert and Wilson 2005). Seabirds, compared to many terrestrial migratory birds, tend to be large enough to carry tracking devices during long journeys at sea, sometimes over multiple years (Müller et al. 2014; Yamamoto et al. 2014). This enables researchers to collect longitudinal data, which is invaluable to study interactions between events of the annual cycle and their potential life-history consequences (Daunt et al. 2014). Furthermore, seabirds live in a unique binary environment. Apart from short periods when they visit land to incubate their egg or feed their chick, seabirds are either flying over the sea or are on the sea surface (or beneath it). By measuring the patterns of contact with salt-water, it is possible to estimate directly the activity of the birds at sea, remotely, thereby allowing for estimations of foraging effort and energy expenditure (Weimerskirch et al. 1997; Elliott et al. 2008; Freeman et al. 2013). This would be challenging in terrestrial species (but not impossible, for example with the use of accelerometers, Robert et al. 2009, and doubly-labelled water methods, Speakman and Krol 2005). These datasets, combined with appropriate analytical techniques, can provide remote estimations of behaviour with an unprecedented resolution, and bring a unique insight into the at-sea behaviour of seabirds.

Tracking animal migration

Animal migration has always fascinated mankind. Aristotle wrote about “animals […] quitting the cold countries after the autumn equinox to avoid the approaching winter” (Aristotle 343AD). However, studying migration is not easy. It is only after the invention of bird metal rings in the late 19th century that the extent of bird migration started to be unveiled (Alerstam 1990). However, the likelihood of ringing recoveries depends greatly on the accessibility of the wintering grounds of the species. Recovery rates of some species are < 0.1%, meaning a single recovery requires ringing more than 1,000 individuals (Robinson et al. 2009). The recovery rates of seabirds are among the lowest (Walker et al. 2014), given the low likelihood of recovering a bird whose death occurred far from the coast. Furthermore, it is often difficult to know what recovered birds died from and whether they are representative of the whole population, for example they could have got lost and died as a result (Bairlein 2001). Nonetheless ringing has provided useful information about the wintering destinations of some seabirds (Harris and Tasker 1999). At-sea surveys by boat and plane tried to compensate for the lack of seabird ringing recoveries, but they too can be inaccurate, focus on small sections of the ocean, and do not provide information on the origin of the observed birds (Schneider and Duffy 1985). As a consequence, seabird migration remained poorly understood until tracking technology revolutionised the field in the late 20th century (Burger and Shaffer 2008).

The first remote-sensing loggers for marine animals were depth-loggers developed 50 years ago and deployed on Weddell seals *Leptonychotes weddellii* (Kooyman 1965), a few years later on penguins (Kooyman et al. 1971; Kooyman et al. 1982; Naito et al. 1990), and finally on flying seabirds (Croxall et al. 1991). Simultaneously, in the 1990s, other types of devices were developed and deployed on large seabirds, including satellite-tracking devices (Jouventin and Weimerskirch 1990; Prince et al. 1992), activity loggers (Prince and Francis 1984; Wilson et al. 1995*a*; Weimerskirch et al. 1997) and stomach probes (Wilson et al. 1995*b*). It had become possible to track the at-sea movements of seabirds. The continuing miniaturisation of devices allowed researchers to track smaller birds during their foraging trips (e.g. Guilford et al. 2008, Paiva et al. 2010; see reviews in Wakefield et al. 2009, Tomkiewicz et al. 2010). At the same time, the invention of geolocators, small archival light-loggers inferring bi-daily approximate position from light-levels combined with saltwater-immersion loggers (Afanasyev and Prince 1993; Wilson et al. 1995*c*; Afanasyev 2004), allowed the tracking of seabirds during entire migration cycles (Weimerskirch et al. 2000; Croxall et al. 2005; Phillips et al. 2005; Shaffer et al. 2006; Gonzales-Solis et al. 2007; Guilford et al. 2009). More recently, researchers have started to use miniature cameras and accelerometers to investigate the fine-scale at-sea behaviour of seabirds (Elliott, Vaillant, et al. 2013; Watanabe and Takahashi 2013; see reviews in Ropert-Coudert and Wilson 2005, Wilson and Vandenabeele 2012).

Although these loggers enable the collection of a wealth of information on the at-sea behaviour of seabirds, they have drawbacks which need to be carefully considered. First, the disturbance caused by capturing and handling the bird, and by the extra weight of the device, can alter the natural behaviour of the animal and create a bias in the data, especially in sensitive species such as auks (Wilson et al. 1986; Vandenabeele et al. 2014; Heggoy et al. 2015). Such impacts are discussed in more detail in Chapter 7. Second, many devices do not transmit data and so require the recapturing of birds, which, depending on the species, can be challenging and cause additional disturbance. As a result, more devices have to be deployed in the hope of recovering a large enough sample. This leads to the third and last main drawback of tracking devices: their cost. Devices, especially those which transmit data, are expensive. This results in small sample sizes which may not reflect the whole population representatively and jeopardize statistical power (Soanes et al. 2013). Furthermore, more expensive devices like satellite transmitters are also often attached with harnesses to avoid losing the devices within a few weeks after deployment; this can also be more disturbing for the animal (Phillips et al. 2003) and condemns the animal to carry the extra weight for long periods of time, in some cases for all of their lives. Finally, the large amount of data collected during tracking studies, often noisy and with a large number of points for a small number of individuals, can be challenging to analyse without appropriate analytical techniques (tracking a single bird with a geolocator during an 8-month migration can result in around 500 positions and more than 30,000 records of saltwater-immersion activity data).

The majority of the data presented in this thesis were collected by either geolocators or GPS-loggers. All my work was conducted after ethical approval by the appropriate institutions (British Trust for Ornithology Unconventional Methods Technical Panel, Natural Resources Wales, Skomer Island Advisory Committee and the University of Oxford’s Local Ethical Review Process). Precautions were always taken to minimise disturbance and handling time. Geolocators did not exceed 1% of the birds’ total body mass and GPS-loggers did not exceed the 5% limit (and were only deployed for a maximum of 2 weeks). The attachment of GPS loggers (attached to back feathers with tape) was designed to fall off naturally after a few weeks in cases where we did not recapture the bird. During the entire study period, breeding success was monitored and compared with that of non-tracked birds on the same colony. Similar techniques were used by our research group on these species for several years and no significant negative effect was detected on breeding success and adults' return rate (Guilford et al. 2011; Dean et al. 2015; Shoji, Aris-Brosou, et al. 2015).

Estimating at-sea behaviour

Although the most obvious and primary aim of tracking data is to establish the spatial movements of animals, it can reveal much more than simple positions. For example, high-resolution GPS data, or a combination of spatial and saltwater-immersion data, can be used to identify and locate different types of behaviours. The behavioural classification can be done by looking at patterns of wet/dry transitions or variation in speed and turning angle (Patterson et al. 2008; Schick et al. 2008; Jonsen et al. 2013). This approach was first used 20 years ago to unveil the foraging patterns of albatrosses (Weimerskirch et al. 1997). It gained more momentum with recent advances in analytical techniques, and has been used to uncover the behaviours underlying seabird movements, and to reveal important information such as important foraging locations, stopovers or foraging activity patterns (Yamamoto et al. 2008; Guilford et al. 2009; Lecomte et al. 2010; Dean et al. 2012; Dias et al. 2012; Péron et al. 2013). It is now sometimes referred to as predictive etho-informatics (Freeman et al. 2013).

All five research chapters of this thesis rely on identifying and classifying behaviour from tracking data, either using saltwater-immersion data collected by geolocators or high-resolution GPS data. A range of analytical techniques exist to estimate behaviour from such datasets. Here I shall only give a brief overview of these techniques, and more detail will be given further in the thesis. Saltwater-immersion data consist of a time series with each data point corresponding to the proportion of time spent dry during a 10-min period, or a suite of transitions between wet and dry states (Afanasyev and Prince 1993). One of the simplest methods consists of measuring a variable (or combination of variables) extracted from the data, which gives information on the bird's activity. For example, researchers have used the number and duration of dry bouts (Dias et al. 2012), or the number of wet/dry transitions in the data (Yamamoto et al. 2008) to measure the number and frequency of take-offs and landings. Alternatively, the data can be classified in different classes using thresholds (Lecomte et al. 2010). The "mostly wet" state corresponds to the birds sitting on the water, the "mostly dry" state corresponds to sustained flight, and the "intermediate" state corresponds to a foraging-related activity, with birds alternating short bouts of flights and short wet bouts (sitting on the surface and diving). Studies of shearwaters combining dive or GPS data with saltwater-immersion data showed that the intermediate state is strongly associated with foraging activity (Dean et al. 2012; Freeman et al. 2013). This classification method was used in a range of seabird species (Lecomte et al. 2010; Mattern et al. 2015, Shoji et al. 2015). Here I use it for the first time in auks in three research chapters.

More complex methods of classification of behaviours in tracking data rely on detecting patterns in the data, often unidentifiable with the naked eye, with pattern recognition techniques using machine learning algorithms derived from the field of artificial intelligence (Bishop 2006). These techniques can be supervised (i.e. the algorithm is first trained on a subsample of the data) or unsupervised (the algorithm only uses unlabelled data and looks for hidden patterns). They identify different states in the data, which are equivalent to behaviours (e.g. flying, foraging) (Patterson et al. 2008; Jonsen et al. 2013). Different variants of machine learning techniques have been successfully used to identify the behaviour of seabirds on foraging trips or on migration (Péron et al. 2013, Freeman et al. 2013). The two last research chapters of this thesis rely on two of these techniques (Gaussian mixture models, Gaffney and Smyth 1999, and Hidden Markov models, Rabiner 1989).

The Atlantic puffin

One of the two species studied in this thesis is the Atlantic puffin *Fratercula arctica*. The species is described in great detail in the excellent book on the species by Harris and Wanless (2011), which is the main reference in this short summary of the life-history of puffins. Puffins are small auks (around 370g) breeding across the North Atlantic Ocean. Main colonies are found in Iceland and Norway, but smaller colonies reach as far south as French Brittany. Although over 90% of the world population is believed to breed on the east Atlantic coast, puffins also breed on the west coast of the Atlantic, in Canada and along the coast of Maine in the US. Estimates of the world population of puffins are difficult due to the remote location of the main colonies in the northern part of their breeding range, however most recent estimates are around 3-4 million breeding pairs, which makes it one of the most common seabirds in the North

Atlantic. Steady but inexplicable declines have occurred in many European colonies in the last few decades; recently leading the IUCN to classify puffins as endangered on its European Red list (European Red List of Birds 2015).

However, although well studied during the breeding season, puffins remained elusive during the winter and their migration patterns remained mostly unknown until the first tracking studies in the late 2000s. Flocks of puffins are rarely witnessed offshore in winter, and prior to the mid-1950s only six sightings were made during 101 crossings of the Atlantic (Aikman 1958). Recent tracking studies revealed that puffins seem to have surprising migration patterns. While birds nesting on the east coast of Scotland remain mostly in the North Sea, birds from southwest Wales and Ireland are very dispersive, with birds nesting a few metres from each other wintering thousands of miles apart (Harris et al. 2010; Guilford et al. 2011; Jessopp et al. 2013). Tracking puffins with (larger) higher resolution satellite devices attached to back feathers or harnesses proved disturbing for the birds and led to abnormal behaviour and nest desertion (Anker-Nilssen and Aarvak 2009; Harris et al. 2012). Therefore little is known about the foraging movements of puffins during the breeding season.

Like other seabirds, puffins are long-lived (around 25 years, although 30-year-old birds have been recorded), do not breed before 4-5 years old, and form long-term monogamous bonds. They are highly philopatric to their natal colony and their nest, nest in burrows or crevices, and raise a single chick each year. On Skomer Island in Wales (51°44’ N, 5°17’ W), the main study colony in this thesis, puffins breed between April and July. Most lay an egg in their burrow between mid-April and mid-May, which partners incubate in turns of short (<24h) shifts for around 41 days. Parents provision their chick for ~40 days by carrying beakfuls of sandeels *Amomodytes spp*. to their burrows several times a day (Figure 1a). In the last few days before fledging, chicks (Figure 1b) come out of their burrow in the evenings and practise flapping their wings. Fledging occurs at night. Chicks walk out of their burrows until the nearest cliff and disappear at sea. Where juvenile and immature puffins go in their first few years before returning to the colony is unknown. After their chick has fledged, adult puffins remain on the colony for a few more days/weeks before setting off on an eight-month migration, the object of over half of this thesis.

Puffins are very sensitive to disturbance at the nest (Rodway et al. 1996), and react very badly to large devices attached to their backs (Anker-Nilssen and Aarvak 2009; Harris et al. 2012). They are relatively poor flyers with high flight costs (Elliott, Ricklefs, et al. 2013), but excellent wing-propelled divers which can dive up to 40m (Shoji, Elliott, et al. 2015). In this thesis, to minimise disturbance to the birds, we only tracked puffins with small (< 2g) geolocators (Figure 1c). Each bird was caught only once per year to replace its logger, and indirect estimates of laying date and breeding success were made when possible.

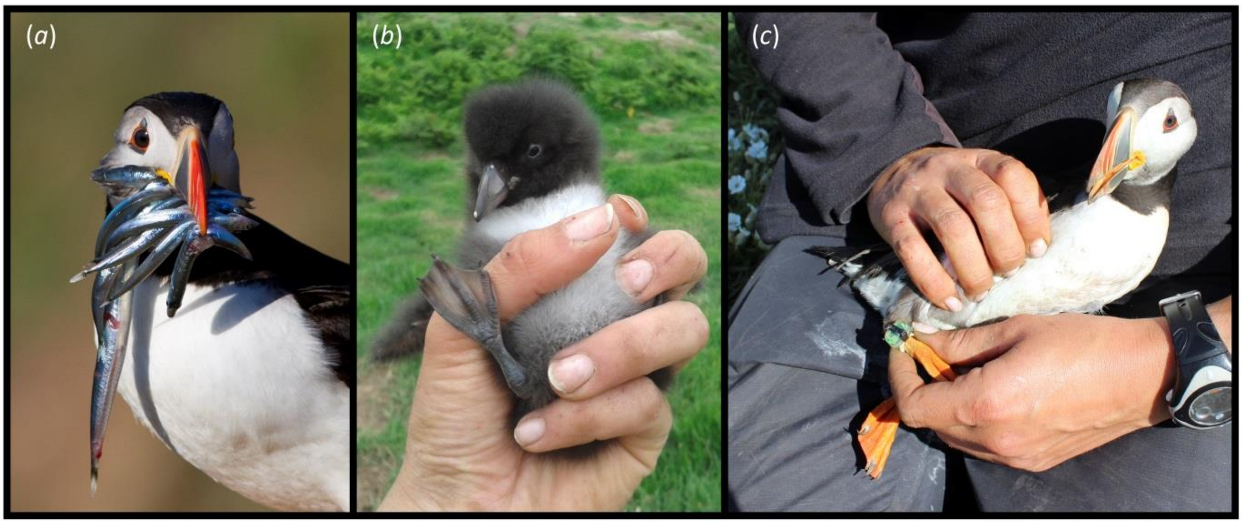

Figure 1. (*a*) An adult puffin carrying sandeels for its chick. (*b*) A puffin chick (~1 week old), with the egg-tooth still visible. (*c*) An adult puffin with a geolocator on its leg. Credits: B. Dean (*a*), A. Fayet (*b*), M. Kavelaars (*c*).

The Manx shearwater

The second study species in this thesis is the Manx shearwater *Puffinus puffinus*, a small (~400g) Procellariiform also breeding in the North Atlantic. Like with the puffin, this species is also described in detail in the book on the species by Brooke (1990), the main reference for most of this section. The main colonies of shearwaters are in the UK, in southern Scotland and southwest Wales, where our study colony, Skomer, hosts 300,000 breeding pairs (Perrins et al. 2012); over 50% of the world population. Smaller colonies can be found in Ireland, Iceland, France and in the Azores. As clumsy on land as they are majestic at sea (Figure 2a), shearwaters are vulnerable to rats and other terrestrial predators, and have been decimated on colonies where they used to thrive, the most notable example being the Calf of Man, which used to be a stronghold of the species and is at the origin of their name.

Manx shearwaters are long-distance trans-equatorial migrants. Ringing recoveries suggested they overwintered along the South American coast, and this was confirmed by recent tracking studies, which showed that all birds (from a range of UK colonies) migrate to the Patagonian shelf along the Argentinian coast (Guilford et al. 2009; Freeman et al. 2013). They are slightly longer lived than puffins (~30 years, although a 53 year-old bird currently holds the UK bird longevity record) and slower at breeding. The immature stage lasts for seven years on average, and the breeding season lasts for over five months. Like puffins, shearwaters form long-term monogamous bonds and show natal and breeding philopatry, and nest in burrows. They are nocturnal and all colony activity, at least above ground, occurs in the dark. After the arrival at the colony after their spring migration, shearwaters have a pre-laying period during which the female leaves on a ~2-week pre-laying exodus journey far at sea to build an egg, while males attend the colony on most nights to defend the burrow (Dean 2013). Incubation lasts ~51 days, during which partners alternate long incubation shifts (~5-8 days on average). The chick is provisioned with regurgitated, partly digested fish every 1-2 night(s) for ~60 days, and can sometimes grow enough to reach the weight of its two parents combined (Figure 2d). Fledging usually occurs within 10 days of the last feed, days during which the chick loses weight and takes excursions out of the burrow at night to exercise its wings. Parents leave the colony after ceasing to feed their chick and embark on their fall migration. Like in puffins (and most seabirds), it is not known where juvenile and immature shearwaters spend their first few years at sea, although ringing recoveries of juveniles in South America a few weeks after fledging suggest that fledgings follow the same migration route as adults when they leave their natal colony. Return to the colony is rare before 3 years old (Perrins et al. 1973, Figure 2b).

Manx shearwaters, like other members of their genus, are more robust and less sensitive to handling than auks. This higher tolerance combined with their slightly larger weight, makes them an easier species to study than puffins. Access hatches can be built above nest chambers to observe or catch adults and chicks without causing desertion and birds can be tracked for short-term periods with high-precision GPS loggers on their backs (Figure 2c, Guilford et al. 2008; Dean et al. 2012; Shoji, Aris-Brosou, et al. 2015).

I used shearwaters to answer questions which we could not realistically ask in puffins due to their high sensitivity. However, precautions were always taken to minimise disturbance and handling in shearwaters, and breeding success was compared to controls whenever possible.

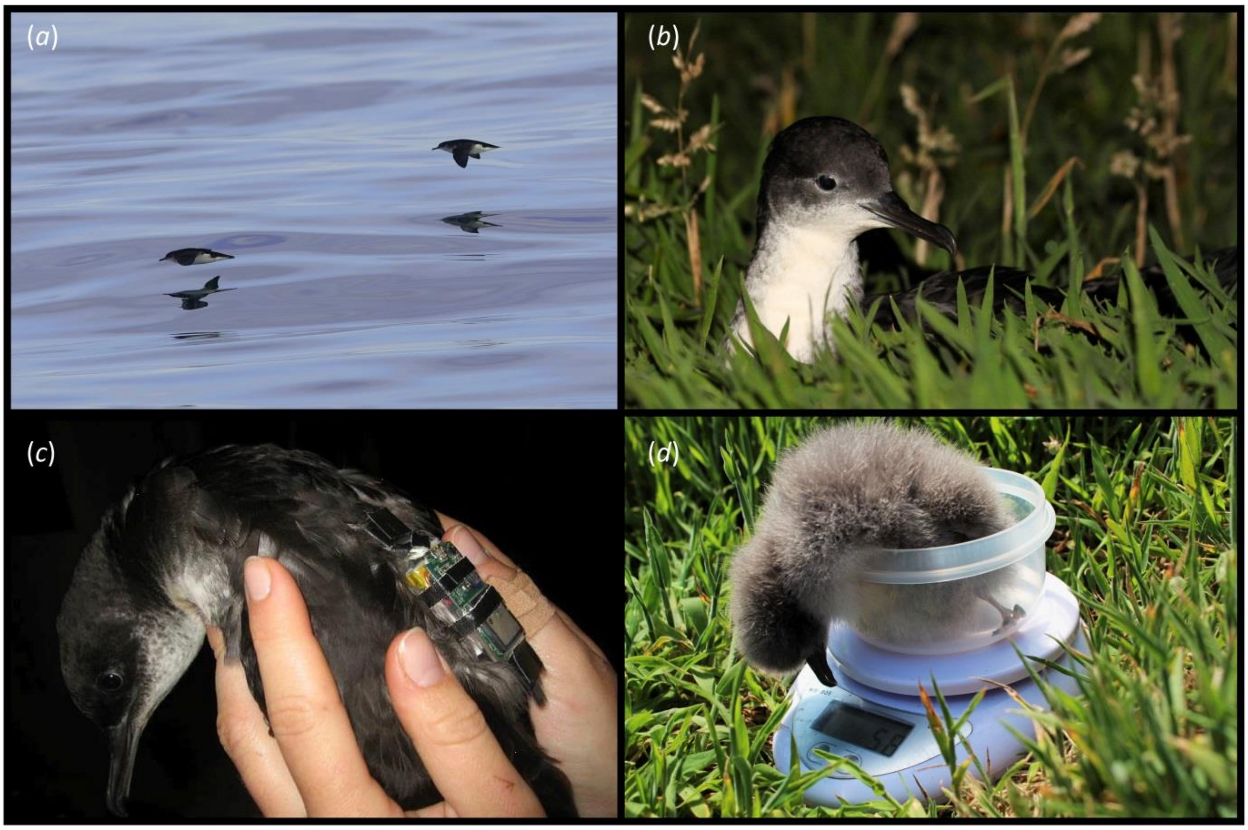

Figure 2. (*a*) Manx shearwaters at sea. (*b*) A juvenile Manx shearwater on the colony at night. (*c*) An adult Manx shearwater with a GPS logger attached to its back. (*d*) A Manx shearwater chick (~ 1 week old) concerned with its diet. Credits: B. Dean (*a*), A. Fayet (*b* and *d*), H. Kirk (*c*).

Objectives and structure of the thesis

This thesis explores the drivers of individual strategies during breeding and non-breeding movements of pelagic seabirds at sea, and investigates the potential fitness consequences of such individual variation. It is constituted of 5 research chapters, all of which are written in a manuscript format and can be read independently, although Chapters 3 and 4 rely on methods described in Chapter 2. Each chapter contains an introduction relevant to the set of questions it tests; therefore the current General Introduction was kept to a minimum to avoid repetitions.

Chapter 2 investigates the mechanisms promoting the development of flexible intraspecific migratory strategies, and their potential fitness consequences. I test the role of random dispersion, sex-segregation and intra-specific competition in driving the highly dispersive migration of Atlantic puffins, using a dataset of over 100 migration tracks collected with geolocators over seven years. In addition, in order to evaluate the potential life-history consequences of following strikingly different migratory routes, I estimate the energetic cost of migration (activity budgets and energy expenditure) for each route and test whether they result in differences in reproductive success.

Migrants engaged in long-term pair-bonds often maximise their breeding success by synchronising their return to the breeding site (Gonzales-Solis et al. 1999; Naves et al. 2007). How they achieve synchrony is poorly understood, especially in species with diverse migratory routes. **Chapter 3** addresses this question by investigating the within-pair strategies of puffins using migration tracks collected from pairs of puffins. In this chapter, I measure within-pair differences in migratory route, at a spatial but also behavioural level (activity budgets), and I test the potential consequences of such differences on the pair's breeding success.

In **Chapter 4**, I take up some of the general questions addressed in the previous chapters on individual differences in migratory strategies to investigate how these flexible migratory strategies vary on an ocean-wide scale. Combining a dataset of just under 300 tracks collected on 9 colonies across the whole breeding range of puffins, I investigate differences in migratory strategies among colonies on a spatial and behavioural level, and whether such differences can be explained by differences in environmental conditions.

Chapter 5 continues to explore the links between the two main events in the annual cycle of seabirds, reproduction and migration, and the influence of migration on life-history decisions. One way to address such questions is to test for so-called "carry-over effects" using experimental studies where parameters such as reproductive effort can be manipulated. Studies examining the relationship between non-breeding behavioural patterns and reproductive success in long distance migrants are scarce (Shoji et al. 2015). In this study I investigate the carry-over effects of reproduction on migratory and subsequent breeding behaviour by cross-fostering chicks of different age between nests to manipulate the reproductive effort of breeding birds, and tracking the adults with geolocators during the following migration and breeding season. I use Manx shearwaters as a study species instead of puffins because they are long-distance migrants and therefore carry-over effects may be easier to detect, and because the sensitivity of puffins to handling (let alone manipulation) makes them less suitable for such experiments (Erikstad et al. 2009).

Chapter 6 focusses on another life-history trait, juvenile development and skill acquisition. Intraspecific spatial segregation in monomorphic species can be observed between immatures and breeders (Jarman 1974; Field et al. 2005; Weimerskirch et al. 2006; Webb et al. 2012; Weimerskirch et al. 2013) and has often been predicted to result from inexperience, but this has not been properly tested, perhaps due to the challenge of tracking immature individuals. In this chapter I test the relationship between age, foraging efficiency and spatial segregation by tracking immature and adult Manx shearwaters with GPS loggers during central foraging trips from the colony. I estimate foraging efficiency by combining estimations of foraging effort obtained from behavioural classification of GPS data, and at-colony measurements of trip success (mass gain). I use environmental data to compare the productivity of areas visited by both groups.

Finally, in **Chapter 7** I summarise and discuss my main findings together and their potential applications for other fields such as conservation, and I conclude with future directions for this work.

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Chapter 2

Drivers and fitness consequences of dispersive migration in a pelagic seabird

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Abstract

Animals can be flexible in their migration strategies, using several wintering sites or a variety of routes. The mechanisms promoting the development of these migratory patterns and their potential fitness consequences are poorly understood. Here we address these questions by tracking the dispersive migration of a small pelagic seabird, the Atlantic puffin *Fratercula arctica*, using over 100 complete migration tracks collected over 7 years, including repeated tracks of individuals for up to 6 consecutive years. Because puffins have high flight costs, dispersion may generate important variation in costs of migration. We investigate differences in activity budgets and energy expenditure between different strategies. We find that puffin migrations are strikingly dispersive with different energy expenditures, but with strong inter-individual similarity in the *timings* of major movements. We consider three hypothetical mechanisms which could generate this pattern: i) random dispersion; ii) sex segregation; iii) intraspecific competition or differences in individual quality. First, we dismiss random dispersion because individuals show strong route fidelity between years. Second, we find that sex differences contribute to, but do not account fully for the migratory variation observed. Third, we find significant differences in breeding success between different overwintering destinations, which, together with differences in foraging levels between routes, support the idea that birds of different quality may visit different destinations. Taken together, our results show that dispersive migration is a complex phenomenon which can be driven by multiple factors simultaneously and can shape a population’s fitness landscape.

Introduction

A typical long-distance migrant species has an annual movement cycle between a breeding ground and a single broad area where all individuals spend the winter before returning for the next breeding season (Dingle 1980; Newton 2008). However, migratory patterns can be more complex, with animals following different routes to the same wintering ground (Brower 1996; Papi et al. 2000; Hake et al. 2003), or wintering in different areas (McConnell and Fedak 1996; Boustany et al. 2002; Dias et al. 2011; Tranquilla et al. 2014). This variation in individual migratory destinations and routes is exemplified in dispersive migrants, whose migration can occur in any direction from the breeding site but still involves a return journey (Newton 2008). Dispersive migration raises fundamental questions about how long distance movements are controlled, and how they affect fitness and breeding ecology. Some routes may be more dangerous to follow, more energetically demanding, or take more time to cover and lead to later breeding (Alerstam and Lindström 1990), while some wintering grounds may be more productive than others. Such consequences have been scarcely studied (Sergio et al. 2014; Weimerskirch et al. 2015) and remain poorly understood.

Migrants with a population-wide single wintering destination are thought to inherit at least the direction and duration of their migration route genetically (Berthold et al. 1992; Berthold 1996; Perdeck 1958; Helbig 1991), or to learn it by following family members or other conspecifics (Chernetsov et al. 2004; Harrison et al. 2010; Palacin et al. 2011). Dispersive migration does not lend itself to control by either of these mechanisms, mainly because of the complexity and diversity of routes (e.g. several stopovers linked by bouts of long flights in various directions) but also because of potential differences in timing of departure from the colony between family members (Guilford et al. 2011). Thus, it is unknown what controls the directional decisions of migrants when these are highly variable within a single population.

Several (not necessarily mutually exclusive) mechanisms could lead to dispersive migration. First, perhaps the most obvious mechanism that could generate individual variability in migratory directions is random dispersion from the breeding site. To our knowledge there is no strong evidence of this to date documented in any species. Random dispersion may be a risky and less profitable strategy unless the area covered during the non-breeding season has plentiful and homogenous resources and lacks major barriers or dangers (e.g. deserts). Comparing an individual's migratory routes over multiple years can help determine whether they follow random directions each year. Studies so far have provided mixed results, with some species showing a degree of fidelity to their route in a number of taxa (Hunter et al. 2003; Sakuragi et al. 2004; Shiu et al. 2006; Broderick et al. 2007; Yamamoto et al. 2010), but others showing high between-year variability (Berthold et al. 2004; Alerstam et al. 2006; Dias et al. 2013). Second, migratory segregation by sex might occur if males and females differ in foraging niche or energy requirements (Selander 1966; Cristol et al. 1999), or as a result of intraspecific competition (Marra and Holmes 2001). Spatial sex-segregation during the non-breeding season has mostly been observed in sexually dimorphic species (Brown et al. 1995; Stewart 1997; Akesson and Weimerskirch 2014 but see

Guilford et al. 2012; Müller et al. 2014). Third, dispersion could result from intra-specific competition (regardless of sex) in which individuals of lesser quality would migrate further if local resources were not sufficient to sustain the whole population during the winter (Gauthreaux 1982; Gunnarsson et al. 2005). Conversely, resources may be better further from the colony but only high quality individuals could afford the journey (Blake et al. 2013). This is not intra-specific competition *per se* but would result in a similar pattern. In either case we expect there to be fitness consequences of variation in migration routes and distances (Klaassen 2003; Alves et al. 2013). Other potential mechanisms driving dispersive migration, not specifically addressed here, include age-related differences, if younger individuals have different time or energy constraints or are physically less able to migrate than adults (Jonsson et al. 1990; Cristol et al. 1999; Thiebot et al. 2011; Riotte-Lambert and Weimerskirch 2013); or exploration in the early months or years of life followed by gradual refinement of the migratory journey (Guilford et al. 2011).

The aim of the current study is to test the role of random dispersion, sex-segregation and intra-specific competition as potential drivers of dispersive migration in a pelagic seabird, the Atlantic puffin *Fratercula arctica*. Puffins are small pelagic seabirds breeding in the North Atlantic that seem to exhibit dispersive migration (Guilford et al. 2011; Jessopp et al. 2013), although the degree of dispersion may vary between colonies (Harris et al. 2010). The migration strategies of pelagic seabirds, although much less well understood than those of terrestrial species, seem highly variable, making them good models to study flexibility in migratory strategies (along with breeding philopatry which makes it possible to track individuals over multiple years). Current understanding supports a variety of migratory strategies, ranging from a single flyway to a broad area (Guilford et al. 2009; Egevang et al. 2010; Hedd et al. 2012; Stenhouse et al. 2012) to multiple (2-3) wintering destinations (Phillips et al. 2006; Shaffer et al. 2006; Gonzales-Solis et al. 2007; Yamamoto et al. 2010; Bogdanova et al. 2011; Kopp et al. 2011; Fort et al. 2012) to even greater flexibility in non-breeding grounds (Weimerskirch et al. 2000; Croxall et al. 2005; Phillips et al. 2005). Here we track the migration of over 100 complete migrations of Atlantic puffins using miniature geolocators over 8 years. First, we investigate the role of random dispersal (or semi-random, as some directions of migration, e.g. in the direction of land, will be unviable) at the end of the breeding season by measuring between-year route fidelity over up to 6 years. Second, we compare the migration patterns of known male and female puffins to examine potential sex-driven segregation. Third, because different migratory routes may have different energy requirements, especially in a species with high flight costs such as the puffin (Pennycuick 1987), we test whether dispersive migration results from intraspecific competition (or other differences in individual quality). We use salt-water immersion data simultaneously recorded by the devices to identify flight, foraging and sitting on the water; estimate activity budgets during the winter and use a model developed in a closely related species to produce an estimation of the daily energy expenditure of wintering puffins. We examine potential relationships between activity budgets, energy expenditure, laying date and breeding success between different routes.

Methods

Ethical Note

All work adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, and was conducted after ethical approval by the British Trust for Ornithology Unconventional Methods Technical Panel (permit C/5311), Natural Resources Wales, Skomer Island Advisory Committee and the University of Oxford's Local Ethical Review Process. To avoid disturbance, handling was kept to a minimum, and indirect measures of variables such as laying date were preferred, where possible. Survival and breeding success of manipulated birds were monitored and compared to control birds.

Logger Deployment

Atlantic puffins are small auks (c. 370g) breeding in dense colonies across the North Atlantic. They spend most of the year at sea, only returning to land during the summer to breed. A long-lived monogamous species, they have a single egg clutch, usually in the same burrow (Harris and Wanless 2011). This study was carried out on Skomer Island, Wales, UK (51 degrees 44' N; 5 degrees 19' W), where over 9,000 pairs breed each year (Skomer seabird monitoring reports 2008-2014).

Between 2007 and 2014, 54 adult puffins were caught at their burrow nests on a small section of the colony using leg hooks and purse-nets. Birds were ringed using a BTO metal ring and a geolocator was attached to a plastic ring (models Mk13, Mk14, Mk18L or Mk18H - British Antarctic Survey, or Mk4083

– Biotrack; see Guilford et al. 2011 for detailed methods). All birds were also colour-ringed to allow visual identification. Handling took less than 10 minutes. Birds were recaptured in subsequent years to replace their geolocator. In total, 124 geolocators were deployed, and 105 complete (plus 6 partial) migration routes were collected from 39 individuals, including tracks from multiple (2-6) years from 30 birds (Table S1). In some instances both members of a pair were tracked simultaneously, these represented 30 out of the 111 tracks.

Route similarity

Light data were decompressed and processed using the BASTrack software suite (British Antarctic Survey) and MatLab R2010b (MathWorks Inc.). We applied a speed filter of 500km per day (8 h of sustained flight at mean speed of 64 km/h, (Pennycuick 1997), removed the data 15 days either side of the fall and spring equinox (due to equivalent day length everywhere on Earth, latitude is highly inaccurate around the equinox) and the breeding season (April - July), where the resolution is too low (normal resolution is ± 185km, Phillips et al. 2004). We used a conservative 15-day window around the equinox because (i) in our analysis we measure the total length of each route and errors may lead to large overestimations and (ii) unlike many seabirds which migrate during the equinox puffins have already reached their destinations, therefore excluding a few data points is likely to have a negligible effect on their general distributions. We calculated 2-day median positions for all tracks and filtered out those with high standard error ($SE_{longitude} > 40$ km, $SE_{latitude} > 30$ km). For analyses of route similarity we calculated the average nearest neighbour distance (NND, in km) of each migration track to all other tracks over a 20-day window (detailed methods in Guilford et al. 2011), to quantify the fidelity of each bird to its own migration route between years, and the similarity of its route to other birds' routes (within the same year only, to avoid potential differences due to environmental conditions). NND increases with the difference between two tracks. The use of a temporal window allowed us to account for temporal as well as spatial route similarity – 2 birds visiting the same place at different times have a larger NND than 2 birds visiting the same area within 20 days of each other.

We estimated the total distance covered by each bird migration by summing the great-circle distances between each daily median between August and March. Distance from the colony was calculated as the great-circle distance between the colony and each position. For positions in the Mediterranean Sea, to account for the flight around the Iberian Peninsula (puffins do not fly far over land), the distance was calculated between the position of interest and the Strait of Gibraltar, and added to the shortest at-sea distance from the colony to the Strait of Gibraltar (1752 km).

Activity budgets and energy expenditure

We used salt-water immersion data collected by geolocators (i.e. the proportion of time a logger spent immersed in salt-water for each 10-minute interval) to estimate daily activity and energy budgets. We allocated each 10-minute interval during daylight between August and March to one of three categories: sustained flight (≥ 98% dry), sitting on the water (≥ 98% wet), foraging (>2% dry and >2% wet, representing a succession of short flights while searching for prey and short wet bouts of sitting on the water and diving, as in Lecomte et al. 2010). At night our data were mainly constituted of long (several hours) dry or wet bouts. Studies of other auks have shown that flight is rare at night and that the dry periods observed are due to the birds tucking one leg under their wing while resting (Robertson et al. 2012; Elliott and Gaston 2014; Linnebjerg et al. 2014). Using data from four birds carrying two devices for a single winter we found that each bird tucked one leg preferentially (Fig. S1). Therefore, instead of estimating leg-tucking time (a proxy for resting or sleeping) by doubling the value measured from the leg carrying the geolocator (Elliott and Gaston 2014), we calculated the average leg-tucking time for these four birds (42% of the night) and applied this to our dataset to calculate time sleeping and sitting on the surface at night. Therefore, we obtained a daily proportion of each behaviour during day time (which therefore controls for latitudinal change in day length) and during night time. We used a model developed for guillemots *Uria aalge* (Elliott et al. 2013) to estimate energy costs, using at-colony metabolic rate as a proxy for at-sea rest, as in (Elliott and Gaston 2014). We then converted our results for an average-sized puffin weighing 370 g using the allometric equation developed for auks by Shaffer (2011) (see SI for details).

Phenology and Breeding Success

Incubation generally lasts around 44 days (Harris and Wanless 2011) and is shared by parents alternating shifts while the other forages. Because of the difficulty of intensive direct observation in this subterranean nesting, easily disturbed species, we estimated laying date indirectly using salt-water immersion data to detect the start of incubation (see SI for details). The accuracy of this method was verified using a subset of 5 nests which were checked daily with a burrowscope (Sextant Technology Ltd.) in 2012-2013 to determine precise laying date; its accuracy was ± 1.8 days. We calculated the birds' post-migration laying date for 89 of the 111 tracks in our dataset.

To avoid disturbance most nests were not checked directly during the 6-week chick-rearing period following incubation, except after 2012 when a burrowscope was available. Therefore we used a proxy for breeding success: the ability to hatch a chick and rear it for at least 15 days (mortality is highest during the first few weeks; Harris and Wanless 2011), estimated by direct observations of the parents breeding food to their chick (see SI for details). We observed burrows at dawn or dusk when adults can frequently be seen carrying fish to their burrows for their chick. Burrows were deemed successful if parents were seen provisioning on at least 2 occasions and at least 15 days apart (this is the lower threshold used in the standard method for this colony: Skomer Island seabird monitoring reports 2008-2014). In the majority of cases birds could be observed bringing food to their chick for longer periods. Combining the use of a burrowscope in 2013 and 2014 and this method for previous years, we measured pre- and post-migration breeding success for 84 and 94 tracks in our dataset, respectively.

Sexing

For licensing reasons we were only able to use DNA sexing in 2014, which we used to sex 20 birds using DNA extracted from feathers (Avian Biotech, UK). Birds which could not be recaptured in 2014 were sexed behaviourally, using a conservative combination of at least 2 of 3 different measures based on morphometrics, behavioural observations at the colony and identification of the bird taking the first incubation shift, using light and immersion data from geolocators (see SI for details). We used the DNA-sexed birds to validate these 3 methods and obtained a 100% match with each; to be conservative we only included the 7 birds for which we had results from 2 or 3 methods in our analysis of sex-differences. In total we sexed 27 birds (13 males and 14 females), including 20 with DNA methods, which represented a total of 82 migration tracks.

Statistics

We used Linear and Generalised Linear Mixed-Effects Models (LMMs for normally distributed data and GLMMs for Poisson and binomial distributions), including individual and year as random effects (lmer and glmer functions, {*lme4*} package, R 3.0.2 (R Core Development Team 2014). Statistical significance was obtained from comparing models to the null model (intercept + random effects). For descriptive convenience we classified routes into 4 groups using a set of quantitative criteria based on latitude and longitude thresholds, classifying separately routes going to the Mediterranean Sea, to the mid- or west Atlantic (longitude < -20°), or to both or neither destinations (Figure 1). In all analyses of between-route differences we excluded one of the four types of routes because of its small sample size (*n* = 3 vs 16, 45 and 47 for the other types). First, differences in total distance covered, behavioural activity and daily energy expenditure between route types were tested with LMMs and pairwise t-tests. Similarity in migration phenology was tested with randomization tests (10,000 iterations), for dates of arrival to and departure from the Atlantic, and departure to the Mediterranean Sea. We then considered three potential drivers of dispersion. LMMs were used to investigate random dispersion (testing differences within- and among- individual route similarity). We used GLMMs to test the effect of sex on migration type and distance from the colony. Spatial occupancy kernels were calculated with ArcGIS 10.0 (ESRI) and Geospatial Modelling Environment 0.7.2 (Spatial Ecology LLC) (parameters: bandwidth ~275km, resolution ~20km) and the overlap between sexes was calculated with the {*adehabitat*} package in R. To avoid multiple tracks from some individuals biasing the distributions, we calculated the monthly male-female overlap for each year separately, and then took the average across years. Months containing data for less than 2 males and 2 females were excluded. LMMs were used to test the effect of route type on laying date and GLMMS for breeding success (binomial distribution), and burrow was added as an supplementary random effect (because a few of the tracked birds formed breeding pairs). All means expressed in the text are ± SE. Data were log- or sqrt-transformed to meet parametric assumptions when necessary.

Results

Impact

No immediate nest desertion was witnessed post-handling. 45 out of 54 tracked birds were recaptured in following seasons. Of the nine birds not recaptured, all but one were present at the colony in at least one subsequent year, giving a minimum post-deployment overwinter survival rate of 98%. The average annual survival rate of manipulated birds was 89% and their average breeding success 83%, which is similar to numbers obtained from control birds on the colony (see Table S1 for details, Skomer seabird monitoring reports 2008-2014).

Route Diversity between Birds

We found a large diversity of routes taken by different individuals in all years (Figure 1), which covered from 1,500 to 7,000km over 8 months. While some birds spent most of the winter around Great Britain or Ireland, others travelled to the Northwest Atlantic near Iceland and Greenland, or south in the Bay of Biscay and along the coast of Portugal and to the Mediterranean Sea. The areas visited spread over 65° in longitude (from the Davis Strait near Canada to the east coast of Italy) and 36° in latitude (from the Moroccan coast to the Norwegian Sea). Because of the lack of a clear migration return journey to and from a single wintering destination (existence of multiple destinations or lack of large-scale movement movement), for simplification we call "migration period" the entire non-breeding season (August-March) when the birds are away from the colony, which for similar reasons can also be called "wintering period".

15 birds took a "local" route (47 tracks), while 17 birds followed an "Atlantic" route (45 tracks); 5 birds migrated to the Atlantic and then to the Med (16 tracks). Only 2 birds took a "local + Mediterranean" route (3 tracks), and these were excluded from route comparison analyses to avoid likely issues with statistical power.

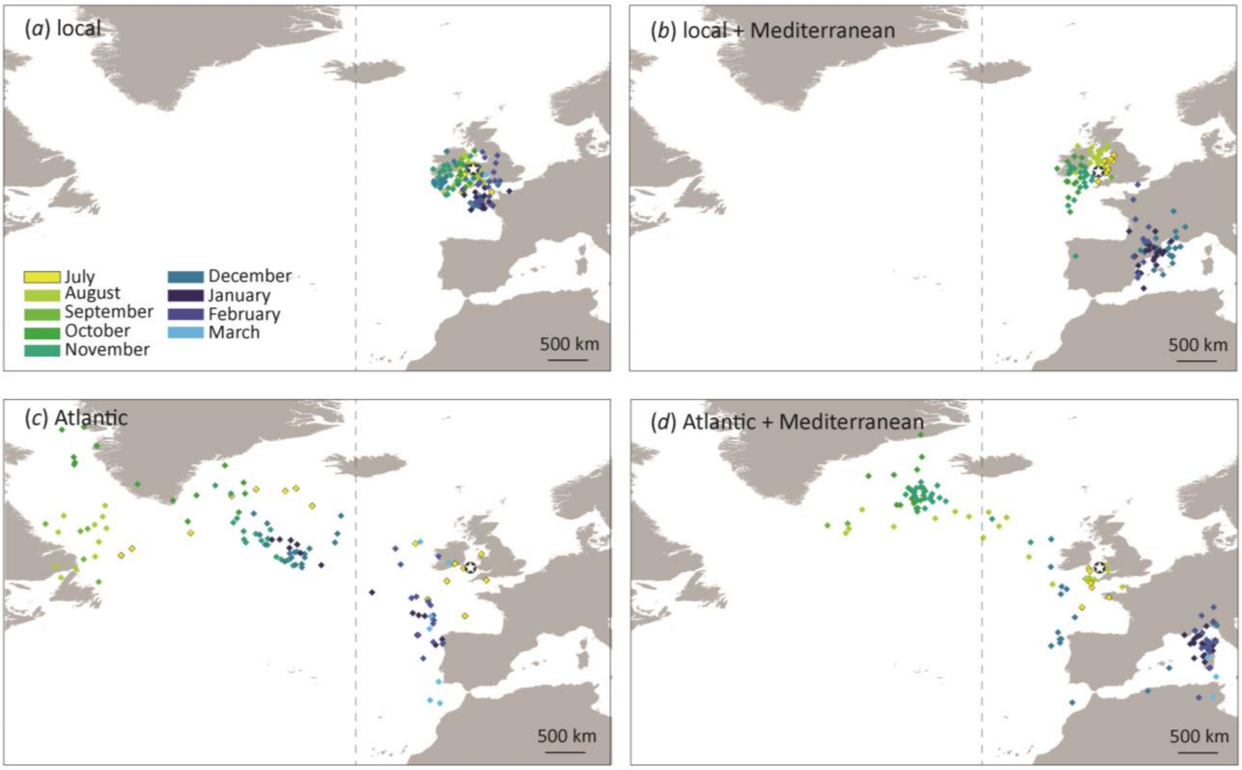

Figure 1 – Example of each type of migration routes. Each point is a daily position. Each colour represents a different month. The colony is represented with a star, the -20° meridian used as a threshold between "local" and "Atlantic" routes is represented with a dashed line. The breeding season (April to mid-July) is not represented. The points on land are due to low resolution of the data (~185km) rather than actual positions on land. (*a*) local (n = 47), (*b*) local + Mediterranean (n = 3), (*c*) Atlantic (n = 45), (*d*) Atlantic + Mediterranean (n = 16).

Within-Individual Route Fidelity

Puffins showed strong individual route fidelity, with consistent migratory routes between years both spatially and temporally (Figure 2). Of 30 birds tracked for multiple (2-6) years, only one switched route type ("local" to "Atlantic" and back to "local", Figure S2).

To quantify route fidelity we calculated the NND between each pair of tracks and compared between year, within-individual NND (the variability of an individual's route between years) to within-year, among-individual NND (the difference between individuals' routes within a year), controlling for individual and year differences. The average NND between repeat routes of birds (358 ± 15 km) was significantly lower than between different birds (706 ± 12 km; LMM: n = 1159, ΔlogLik = 30.87, ΔAIC

= -59.7, $\chi^2_1 = 61.7$, $P < 0.001$). In other words, in any given year, a puffin route is more similar to its own route in a different year, than to another route from any other bird that year.

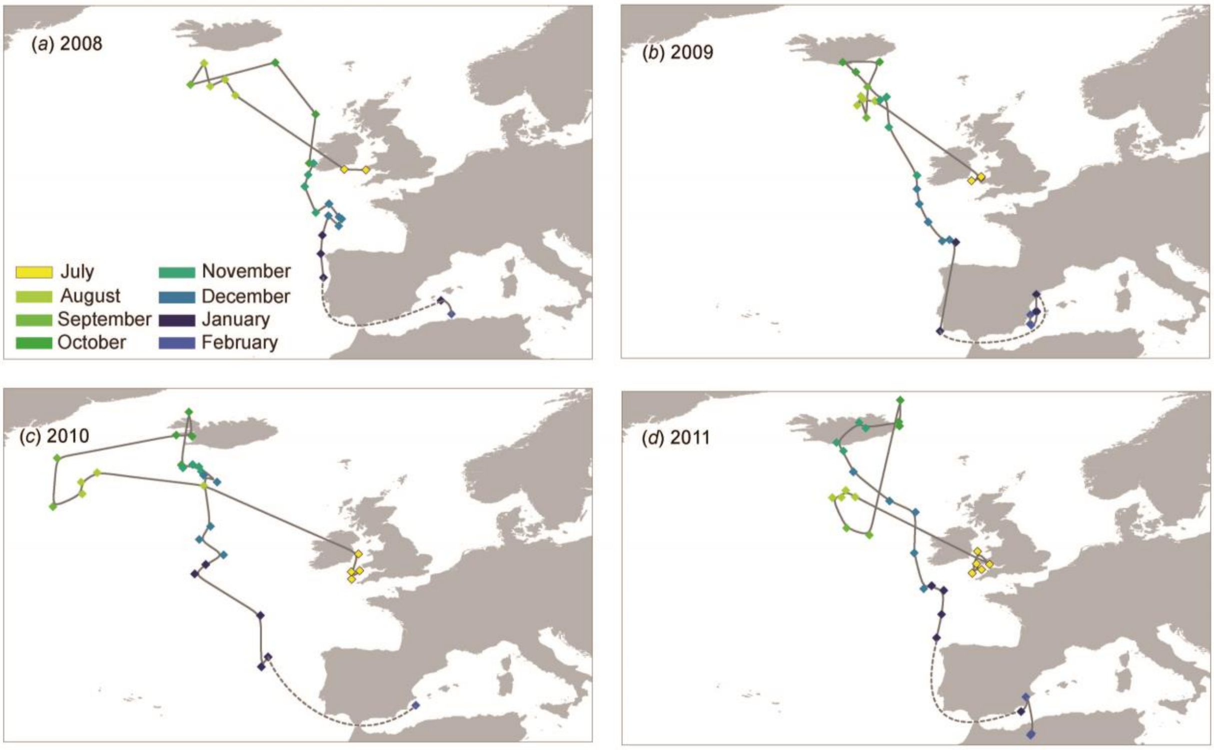

Figure 2 – An example of spatial and temporal route fidelity during migration over 4 years. Routes from a puffin tracked in 2007-2011. Each position represents a weekly median, each colour represents a month. The continuous lines link the positions, the dashed lines are the probable trajectories of the bird through the Strait of Gibraltar. The points on land are due to low resolution of the data (~185km) rather than actual positions on land.

Similarity in Timings within Route Types

We found similarities in the phenology of migration within route types (Figure 3). All birds migrating to the mid- or West Atlantic crossed the -20° meridian between late July and late August (median 1st August ± 1.2 days), which was significantly more constrained than expected by chance (randomisation test, 10,000 repetitions, $P < 0.001$). Similarly, birds migrating to the Mediterranean Sea all passed the Strait of Gibraltar between late December and early February (median 13th January ± 7.3 days), significantly different from a random distribution (randomisation test, 10,000 repetitions, $P < 0.001$). The duration of stay in the western Atlantic was slightly more variable: on average birds remained there 111.3 ± 5.0 days (range: 59-200 days, median return date east: 19th November), not significantly more constrained than expected by chance (randomisation test, 10,000 repetitions, *P* = 0.062). We did not calculate the duration of stay in the Mediterranean Sea because of the low resolution of the data in March due to the equinox. However it seemed that all birds stayed in the Mediterranean Sea until at least the end of February.

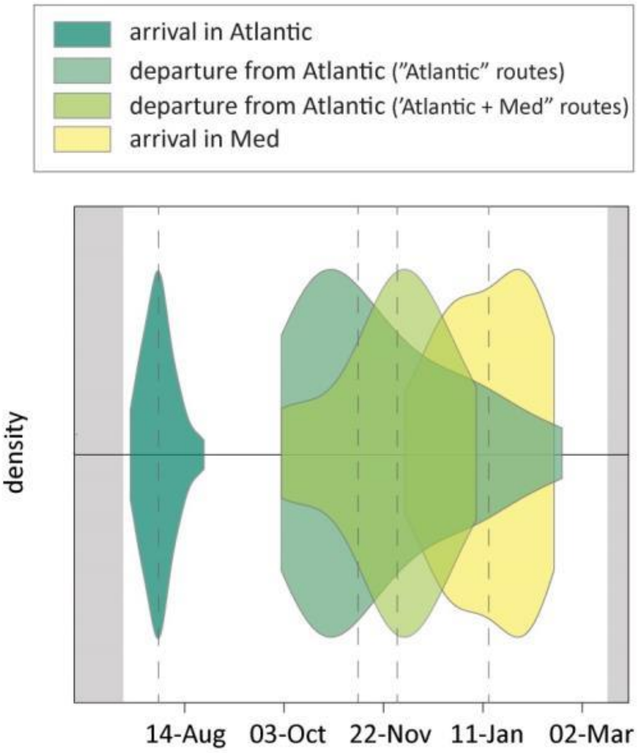

Figure 3 – Violin plot representing the timings of migration for puffins with "Atlantic", "Atlantic + Mediterranean" or "local + Mediterranean" types of routes (all years pooled). The "local" routes (*n* = 47) are not represented for lack of major spatial change to describe. Each violin represents the kernel density estimation of birds (normalised) entering or leaving a specific area: entering the Atlantic (crossing the 20° meridian east to west, dark green, *n*=61), leaving the Atlantic (crossing the 20° meridian west to east, medium green ('Atlantic' birds, *n*=45) and light green ('Atlantic + Mediterranean' birds, *n*=16)) or entering the Mediterranean Sea (crossing the Strait of Gibraltar west to east, yellow, *n*=16). A narrow violin indicates that all birds depart from or arrive in an area at a similar date. The median date for each movement indicated with a dashed grey line. The end and start of the breeding season (15th March and 15th July) are in grey.

Sex-Differences in Migration Routes

Sex had no effect on the type of migration route: both males and females used all types of routes almost equally ("Atlantic": 53.8% female, "local": 64.3% female, Atlantic_Mediterranean: 50% female; LMM: $n = 82$, ΔlogLik = 1.295, ΔAIC = 0.59, $\chi^2_1 = 2.59$, $P = 0.940$). However, after calculating distance from the colony for all birds of known sex (range: ~ 0 - 7500km), we found a complex interaction effect between sex and month on distance from the colony (LMM: $n = 2760$, ΔlogLik = 21.2, ΔAIC = -28.5, $\chi^2_7 = 42.51$, $P < 0.001$). To investigate this interaction further, we compared the distance from the colony between the sexes for each month. Although there were no significant differences between sexes at the start and the end of migration, females were significantly closer to the colony from November until January (Figure 4a, Figure S3). We calculated the average overlap between occupancy kernels for males and females for each month (Fig 4b). Overlap was highest during the breeding season, but varied substantially throughout the winter. It was high during the first 2 months of the non-breeding season then decreased sharply to remain low until February, and increased again to breeding season-levels in March. Looking at the distributions (Figure 4c-4h) revealed some patterns responsible for these results. From the start of migration until October the distributions were similar (Figure 4c-4d). From October onwards most females returned close to Europe while many males stayed in the Atlantic, and by December only 21% of females remained in the mid-Atlantic, vs. 50% of males (Figure 4e-4f). From January onwards 14% of females and 25% of males visited the Mediterranean Sea, and many individual of both sexes stayed closer to the colony (Figure 4g-4h). While many (>60%) females went near the west coast of Portugal, males avoided this area and remained further from the coast in the Atlantic (33%) or elsewhere.

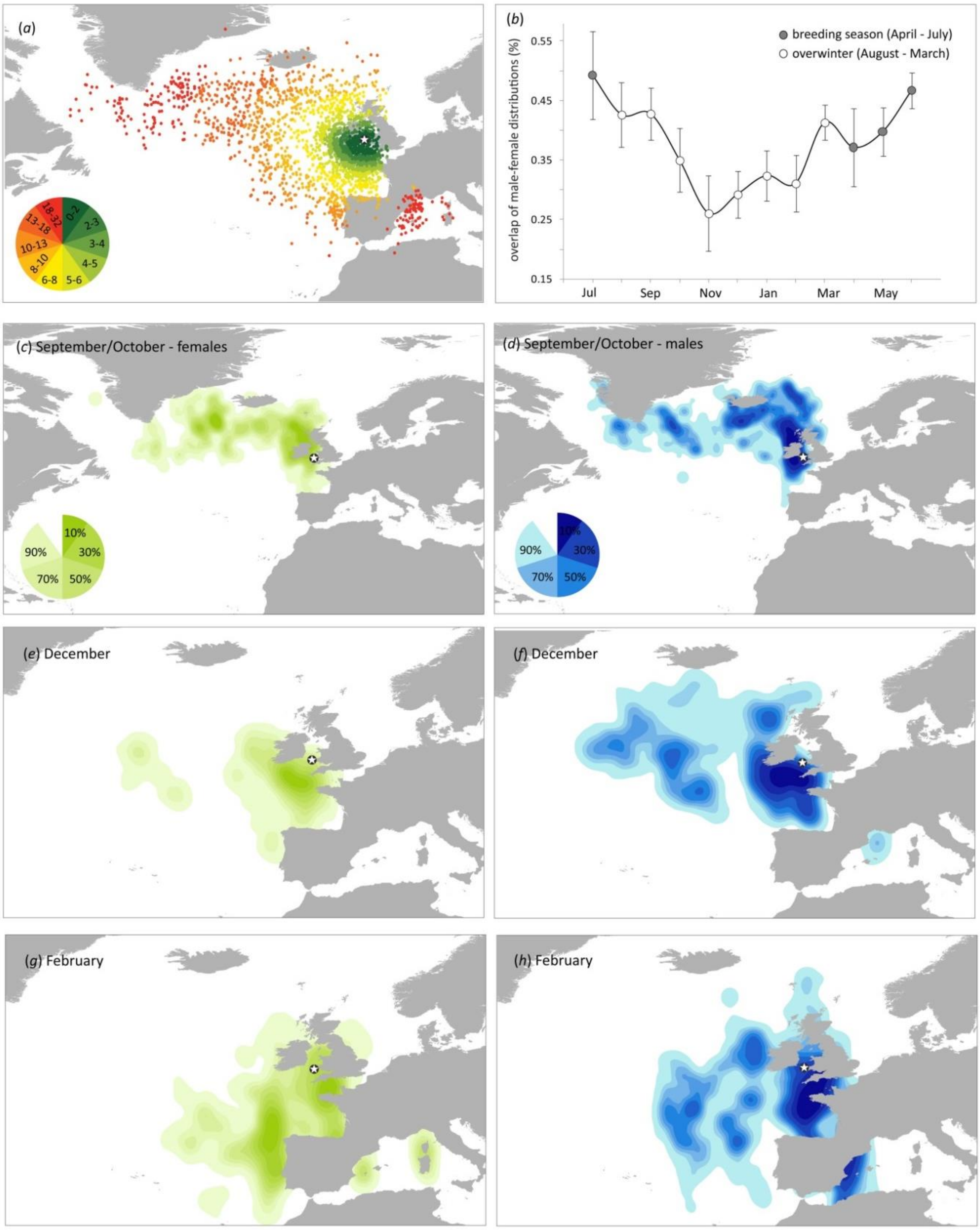

Figure 4 – Sex-differences throughout the non-breeding season. (*a*) Distance from the colony for all birds, by 10% quantiles (unit: 10^2 km). (*b*) Monthly overlap (%) of male and female 70% occupancy kernels (mean ± SE). The overwintering months are represented with open circles and the breeding months with grey circles. (*c*–*h*) Occupancy kernels during migration for females (green, left) and males (blue, right) in September/October (*c*-*d*), December *(e-f)* and February (*g*-*h*). Different shades represent different levels of occupancy, from 10% (darkest) to 70% (lightest). The colony is indicated with a star.

Energy expenditure and activity budgets

Activity and energy budgets differed significantly amongst route types (Table 1a). First, the total distance covered differed significantly between the 3 main route types (LMM: n = 107, ΔlogLik = 15.47, ΔAIC = -26.9, χ^2_2 = 30.95, P <0.001, see Table 1 for pairwise comparisons). Unsurprisingly, birds staying locally covered significantly less distance than birds going to the Atlantic, which themselves covered significantly less distance than those going to the Atlantic and then to the Mediterranean Sea. Second, the proportion of time spent foraging, sitting on the water and flying differed between route types (Figure 5a, see Table 1b for statistical tests). Birds migrating locally spent significantly less time foraging and more time sitting on the surface than all other categories, and less time in sustained flight than birds following the “Atlantic + Mediterranean” route. On “Atlantic + Mediterranean” migrations birds spent significantly more time flying and foraging, and less time sitting on the water, than all others. Birds on “Atlantic” routes had intermediate levels of foraging and sitting on the surface (significantly different from the 2 other route types), but spent a similar proportion of time in sustained flight to “local” birds.

When looking at the temporal patterns of each behaviour, we found that all birds in the Atlantic spent more time foraging than “local” birds during the first part of migration (August-November), while “local” birds spent more time sitting on the surface. However, during the second half of migration, “Atlantic” birds reduced their foraging dramatically to reach similar levels to “local” birds, while the “Atlantic + Mediterranean” birds continued to forage at a consistent level throughout the winter. The latter also spent consistently more time in sustained flight. It is important to note that the difference in flying and foraging between birds in the Mediterranean Sea and higher latitudes was not due to the former experiencing longer days because behaviours were expressed as a proportion of the total daylight duration; in fact birds in the Mediterranean Sea spent a higher proportion of a longer day foraging and flying than birds further north.

Table 1 – (*a*) Total distance covered and daily energy expenditure for each type of migration (mean ± SE and adjusted p-values for pairwise comparison). (*b*) Proportions of daytime spent foraging, flying and sitting on the surface for each type of migration route (mean ± SE and p-values from linear mixed models with binomial family). In all analyses the "local + Mediterranean" route type is excluded because of its small sample size (*n*=3). Significant values ($P < 0.05$) are in bold.

(*a*)		**distance covered (km)**			**daily energy expenditure (kJ/day)**		
route type	*n*	Mean ±SE	Atlantic	Atl.+ Med	Mean ±SE	Atlantic	Atl.+ Med
local	47	4434 ±248	**<0.001**	**<0.001**	1049 ±4	0.462	**<0.001**
Atlantic	44	5904 ±214	-	**<0.001**	1059 ±4	-	**<0.001**
Atl + Med	16	7902 ±244	-	-	1108 ±9	-	-

(*b*)	**foraging (% of time)**			**flying (% of time)**			**sitting on the water (%)**		
	Mean ±SE	Atlantic	Atl.+ Med	Mean ±SE	Atlantic	Atl.+ Med	Mean ±SE	Atlantic	Atl.+ Med
local	16.2 ± 1.1	**0.001**	**<0.001**	1.9 ± 0.4	0.231	**<0.001**	81.9 ± 1.3	**<0.001**	**<0.001**
Atlantic	19.2 ± 0.9	-	**<0.001**	2.5 ± 0.4	-	**<0.001**	78.3 ± 1.1	-	**<0.001**
Atl + Med	20.5 ± 0.9	-	-	4.2 ± 0.4	-	-	75.3 ± 1.1	-	-

As a consequence of these differences in activity, we found significant differences in the average daily energy expenditure during the non-breeding season (August-March) (GLMM: $n = 94$, ΔlogLik = 12.7, ΔAIC = -31.5, $\chi^2_2 = 25.3$, $P < 0.001$) (Table 1a, Figure 5b). The "Atlantic + Mediterranean" route is significantly more energy-demanding than the two other routes because birds on this route spend more time flying than other birds. The "Atlantic" and "local" routes did not differ significantly, although the average daily energy expenditure of birds on "Atlantic" routes was higher than that of birds on "local" routes.

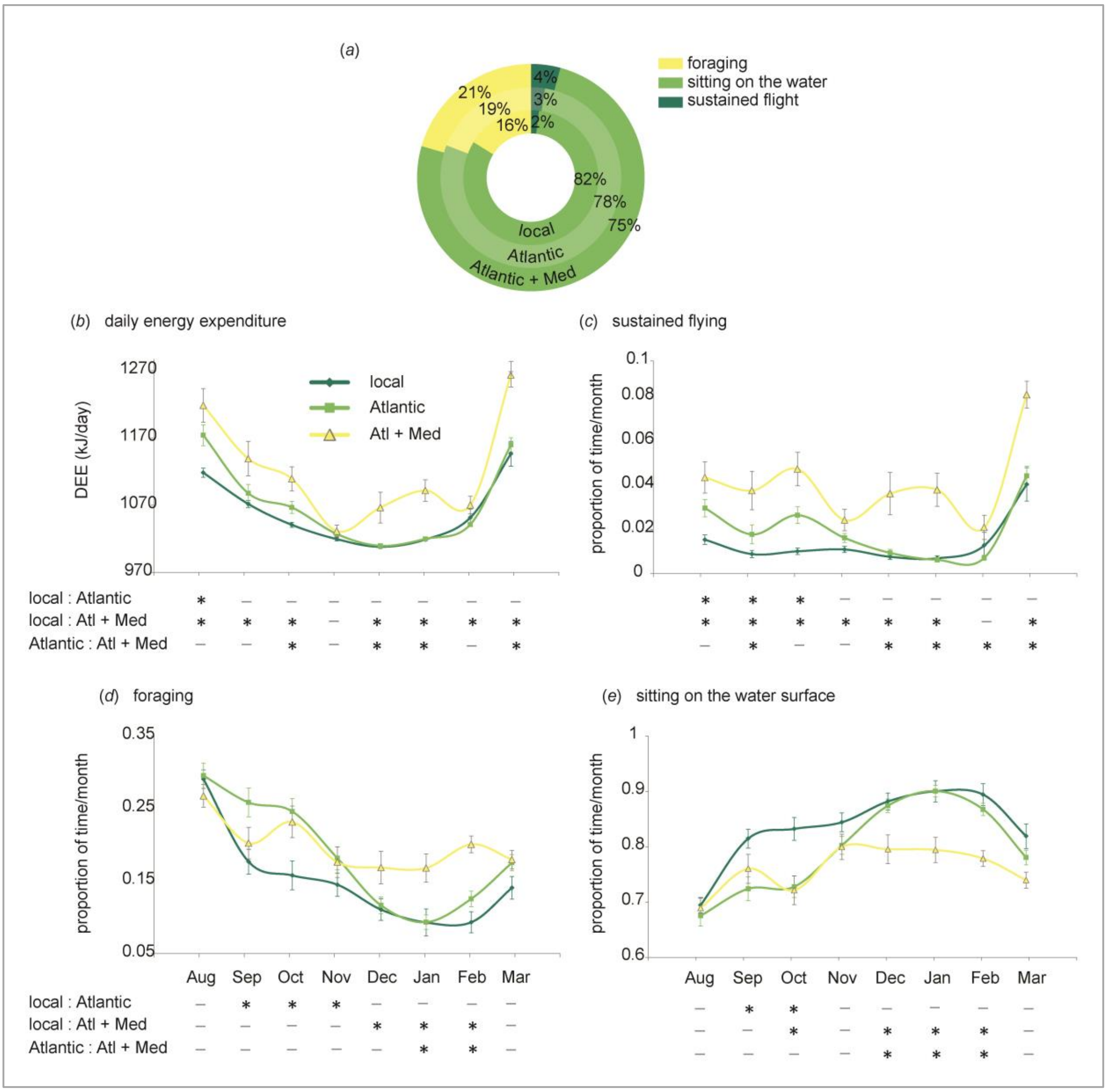

Figure 5. Activity budgets and average daily energy expenditure for different types of routes, for the "local" (dark green), "Atlantic" (light green) and "Atlantic + Mediterranean" routes (yellow). The "local + Mediterranean" route is not included because of small sample size (*n*=3). (*a*) Average winter activity budget for the 3 main routes. (*b* - *e*) Monthly average of (*b*) daily energy expenditure and time budget of (*c*) sustained flight, (*d*) foraging and (*e*) sitting on the surface for the 3 main types of routes. Means ± SE. The asterisks under the x-axis represent significant differences ($P < 0.05$) between two routes (exact *P*-values in Table S2).

Differences in Breeding Phenology and Success between Routes

To test whether different birds of different quality followed different routes, we compared breeding success between different types of migration route (controlling for individual differences and year). We found no significant effect of a bird's breeding success on its subsequent migration type (GLMM: family = binomial, n = 80, ΔlogLik = 0.124, ΔAIC = 3.75, χ^2_2 = 0.25, P = 0.89). However, we found a significant effect of the type of migration on the breeding success the following season (GLMM: family = binomial, n = 86, ΔlogLik = 3.35, ΔAIC = -2.71, χ^2_2 = 6.71, P =0.035). The "Atlantic + Mediterranean" route was the most successful with 100 ± 0 % post-breeding success (n = 13), followed by the "local" route with 82.0 ± 6.0 % (n = 40); the "Atlantic" route was the least successful with 72.7 ± 7.8 % (n = 33). These differences in breeding success could not be explained by different laying dates, as migration type did not affect subsequent laying date (LMM: n = 86, ΔlogLik = 0.18, ΔAIC = 3.63, χ^2_2 = 0.36, P =0.83). Furthermore, individual daily energy expenditure, total distance covered, or the proportion of time spent foraging or flying did not explain individual differences in breeding success (GLMM: family = binomial, n = 76, flight: Z = 0.45, P =0.650, foraging: Z = 1.10, P =0.270, DEE: Z = -0.75, P =0.45, distance covered: Z = -1.3, P =0.19).

Discussion

Atlantic puffins breeding at a major colony in the eastern north Atlantic had a strikingly dispersive migration. They visited areas near their colony and the UK but also across the North Atlantic, the Bay of Biscay and the Mediterranean Sea. Many birds visited several of these areas during the winter. In concert with these widely dispersed migratory destinations, there were large variations between routes and the distances birds travelled between them. To try to determine the life-history significance of this variation we used each bird's salt-water immersion log to calculate approximate daily activity schedules; from these we then estimated daily energy expenditure using calculations derived from a related auk (Common guillemot *Uria aalge,* Elliott et al. 2013) and the known allometric relationship amongst auks (Shaffer 2011). Our estimations of daily energy expenditure are in line but slightly higher than findings from studies conducted on puffins and other auks during the breeding season (Ellis and Gabrielsen 2001; Hansen 2003; Elliott et al. 2013), possibly due to migratory flights, and to our classification of foraging which is coarser than in (Elliott et al. 2013) due to the lack of diving data and directly measured metabolic rates.

We found that the “Atlantic+Mediterranean” routes were not only the longest but also the most energy consuming (with as much as a 15% increase in daily energy expenditure compared to some local routes). Furthermore, this was reflected in a greater proportion of the day spent foraging (an estimated 21% vs 16% on average) and less time resting on the water during the day (75% vs 82% on average). Birds migrating only into the Atlantic showed behaviour consistent with these relationships, having intermediate distances, activity schedules, and energy expenditure. These different migratory strategies were reflected in differential breeding success in the following season. This is unlikely to be a simple year effect as all routes were evenly spread across years, year differences were controlled for in our analysis, and the average breeding success of our study birds was consistent throughout the study period (Table S1). Despite the longer distances travelled, greater flight and foraging activity, and higher energetic costs, birds choosing to migrate first to the Atlantic and then into the Mediterranean Sea had significantly elevated chances of raising a chick (for at least a substantial part of the provisioning period) than birds overwintering locally or just visiting the Atlantic. If such differences were sustained in the long-term, it is doubtful that dispersive migration could persist in the population, so it is likely that they are either balanced by competing fitness costs and risks which we have yet to identify, reflect only a short window on a fitness landscape fluctuating over a longer timescale (in our study survival and breeding success were consistently high in all but the last year), or are a response to differential quality or competitiveness amongst individuals.

Further research will be needed to understand the environmental drivers behind the choice of migratory routes and destinations: even if the area west of the mid-Atlantic ridge near the Labrador Sea is a known hotspot for migratory seabirds (Boertmann 2011; Frederiksen et al. 2011; Montevecchi et al. 2012), we still know very little about the winter diet of adult puffins, although some evidence suggests that they are generalists (Harris et al. 2015) and that zooplankton are important (Hedd et al. 2010).

The differences in foraging effort observed between different areas (e.g. higher in the Mediterranean Sea than anywhere else during the second part of the winter) are complex and cannot be easily interpreted without data on the nature and quantity of prey caught. More foraging could equally reflect productive waters (an abundance of prey allowing for more foraging), the opposite (birds having to forage longer to catch enough prey), or birds attempting to build more reserves. The lack of correlation between the time spent foraging and individual breeding success suggests that it is not how much birds forage, but where they forage, which affects how successful they are during the following breeding season.

Potential Mechanisms Underlying Dispersive Migration

Our results shed light on three potential mechanisms underlying dispersive migration. Tracking individuals over multiple years (and up to a third of a puffin's 19-year average breeding lifespan, Harris and Wanless 2011) revealed that birds follow the same routes to the same approximate destinations consistently year after year. Thus the movements of wintering puffins are not simply the result of random dispersion each year. This is also supported by the fact that some areas attracted many birds but others were not visited at all. The individual route fidelity we observed suggests that individuals are not adapting their migrations over time – why this is the case remains to be understood. Studies of migration route fidelity in birds have found that most species show at least some flexibility during their migration: some show fidelity only for part of the migratory journey (Dias et al. 2013; Müller et al. 2014), others show fidelity in timings but not in routes (Vardanis et al. 2011; Stanley et al. 2012; Lopez-Lopez et al. 2014) . However species showing high consistency in routes and schedules during the whole winter also exist but seem scarcer and, so far, almost exclusively pelagic (Hunter et al. 2003; Shiu et al. 2006; Broderick et al. 2007; Yamamoto et al. 2010; Fifield et al. 2014). Resources in the marine environment may be spatially either predictable (e.g. near a shelf break) or unpredictable (in the open ocean); their predictability also depends on the temporal and spatial scales involved (Weimerskirch 2007). Some of the areas visited by our study birds are known seabird hotspots (Boertmann 2011; Frederiksen et al. 2011; Montevecchi et al. 2012). This may lead to fidelity in stopover sites or migratory routes. However some degree of flexibility could be an adaptive advantage in the current context of rapid changes in the marine environment (Grémillet and Boulinier 2009), and the apparent extremely high fidelity to their migration routes over long time scales may have important implication for the species' persistence in the future. The apparently less frequent migration route fidelity in non-marine species may reflect a more changeable environment where migrants need to respond to year-to-year changes in timings of resource availability or changing environmental conditions (e.g. Charmantier et al. 2008). However, it may also simply be a bias of long-term studies of individual migratory behaviour towards marine species, which tend to be long-lived and to show high breeding philopatry, enabling the tracking of the same individuals over multiple years.

The second mechanism we explore is spatial sex-segregation, which could result from competition between sexes, or from differences in nutritional needs or foraging niche (Selander 1966; Ruckstuhl 2007). Although sex-segregation alone is unlikely to explain the patterns we observe (divergence between the sexes could only lead to 2 different types of routes), it may be a contributing factor. Sex-segregation has been observed in many sexually size-dimorphic species (Brown et al. 1995; Carbone and Owen 1995; Stewart 1997; Catry et al. 2004; Duijns et al. 2014) including seabirds (Croxall et al. 2005; Phillips et al. 2009; Phillips et al. 2011; Akesson and Weimerskirch 2014), but examples in monomorphic species are rare (Bogdanova et al. 2011; Guilford et al. 2012; Müller et al. 2014) and the causes behind the segregation are unclear. We did not find any sex differences between sexually monomorphic puffins following different types of routes. However, we found some spatial sex-segregation in wintering grounds and sex-differences in the birds' distance from the colony. On average, the overlap between males and females was considerable during the first 2-3 months of migration but then sharply decreased, and substantial (but not total) spatial sex-segregation arose from November onwards. With the exception of the pre-laying exodus in procellariiformes (Warham 1990), sex-segregation in seabirds, and in migratory species in general, usually occurs either throughout the entire non-breeding period (Brown et al. 1995; Stewart 1997; Marra and Holmes 2001; Phillips et al. 2011; Akesson and Weimerskirch 2014), or not at all (Guilford et al. 2009; Egevang et al. 2010; Hedd et al. 2012; Stenhouse et al. 2012), although some UK-breeding male black-legged kittiwakes *Rissa tridactyla* have been shown to take a long pre-breeding trip to the mid-Atlantic (Bogdanova et al. 2011). The winter diet of adult puffins is poorly known but there seems to be no clear partitioning between sexes (Harris et al. 2015), while sexual monomorphism makes size-related segregation by dominance unlikely (Harris and Wanless 2011). To our knowledge this is the first time that winter sex-segregation of such extent is reported in auks, but the mechanisms behind such differences remain unclear and need further investigation.

The third and last potential driver of dispersion we explore is intra-specific competition. Intra-specific competition could drive lower quality individuals to migrate further (more energetically demanding routes) if local resources are not sufficient to sustain the whole population during the winter. This has been suggested as a cause of differential migration in several bird species (Owen and Dix 1986; Carbone and Owen 1995; Gunnarsson et al. 2005; Bogdanova et al. 2011). Alternatively, higher resource availability in distant areas could justify a cross-Atlantic trip, but only for birds which can afford the long flight. Both alternatives should lead to fitness differences between routes (Alves et al. 2013). The higher breeding success of "local" birds compared to birds which travel to the Atlantic suggests a role of intraspecific competition in the dispersion we observe. However, this is contradicted by those birds that travel the furthest ("Atlantic + Mediterranean") and have the highest breeding success. Perhaps only high-quality individuals are able to undertake the longer flights required, and the higher levels of foraging in the Mediterranean Sea may indicate a productive area which allows birds to reach a better body condition in time for the breeding season. If so, why only a minority of birds reach it is puzzling, although perhaps the only access through the narrow Strait of Gibraltar makes it difficult to locate, or is dissuasive if puffins are adverse to land (they are not seen inshore in winter). However, understanding the environmental conditions of these migrations and their relationship to the behavioural states is beyond the scope of this study and are unlikely to alter our findings about migratory dispersion – the key finding here is that there are different fitness consequences of different migratory routes within a single population, which has to our knowledge not been reported before in a free-ranging animal.

There are other potential mechanisms of dispersive migration which we were not able to explore in this study. Age-related segregation is commonly observed between wintering adult and immature animals (Cristol et al. 1999; Riotte-Lambert and Weimerskirch 2013). All our study birds were breeding adults therefore it is unlikely to be an important mechanism behind the dispersive patterns we observe. Exploration-refinement (i.e. the exploratory behaviour during the first few years of life followed by gradual refinement of the route) has also been suggested as a potential driver of the migratory patterns observed in puffins (Guilford et al. 2011) but can only be investigated by tracking juvenile individuals over long periods, which currently remains technically challenging.

In summary, we found that puffin migration is strikingly dispersive but with remarkable within-individual consistency between years, and that different types of route require different energy budgets and lead to fitness differences. The remarkable within-individual route fidelity demonstrates that dispersive migration in puffins is not a result of random dispersion, while sex-differences in winter distributions contribute to, but do not explain, dispersion. A key finding of our study is that birds following the longest route with the highest energy expenditure, but which spent more time foraging, have a higher breeding success than birds remaining local and spending less time flying and foraging, while birds on an intermediate route do the worst. Overall, our study provides the first in-depth insight into potential drivers and fitness consequences of dispersive migration, an unusual (but perhaps underreported) migratory pattern in animals.

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Supplementary material

Supplementary Methods

Estimating leg-tucking at night

We estimated leg-tucking by using activity and light data for each 10min interval. We assumed that there was no flight at night and that the dry periods observed were due to the birds tucking one leg under their wing while sleeping (Robertson et al., 2012; Linnebjerg et al., 2014). However, using data from 8 geolocators deployed simultaneously on the 2 legs of 4 birds during the 2010-2011 winter, we found that each bird was tucking one leg preferentially to the other (Fig S01). Therefore, instead of multiplying the proportion of nightly dry time by two we calculated the average leg-tucking (i.e. sleeping) time for these four birds (42% of the night) and applied this to our dataset to calculate time sleeping and resting at night. All four birds spent very little time with both legs up (~0.15% of the night).

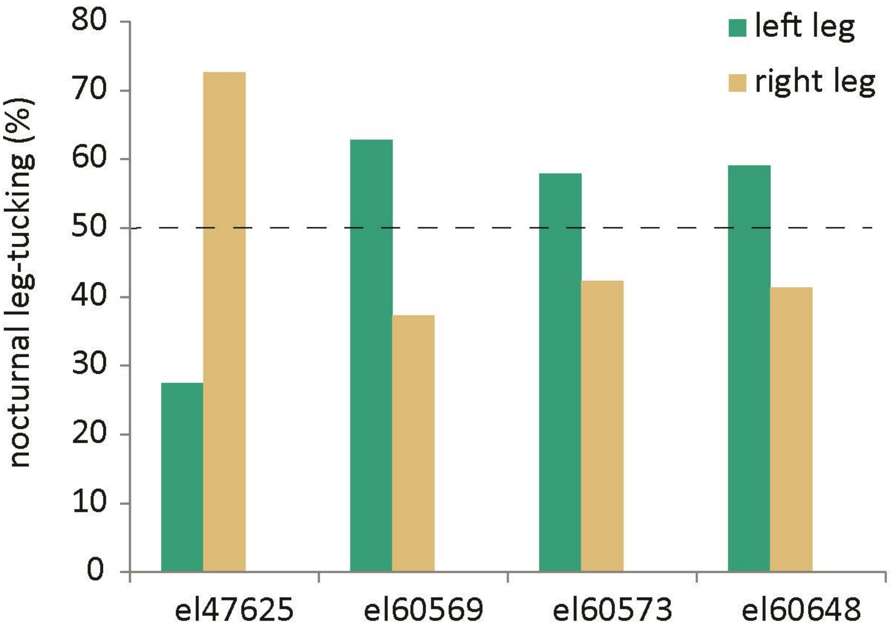

Figure S01. Proportions of left and right leg tucking at night by 4 puffins during the 2010-2011 winter.

Energy costs

We used a model developed on murres from (Elliott et al., 2013) to calculate energy costs:

$$DEE\ (Watts) = 8.9 * T_R + 148 * T_F + 28 * T_{WS} + 27 * T_D$$

where in the original equation T_R is the resting time at the colony, T_F time in flight, T_{WS} time sitting on the water surface and T_D diving time. Here we use time foraging as a proxy for diving time and time sleeping (tucked leg) as a proxy for resting time (there is evidence that resting time at the colony is similar to resting on the surface, Elliott & Gaston, 2014). We then converted our results to kJ/day and use the allometric equation developed for auks by Shaffer (2011) to adjust the results to a 370g puffin.

$$Field\ Metabolic\ Rate\ (kJ.day^{-1}) = 15.537 * Mass^{0.689}$$

Laying date

Incubation generally lasts around 44 days (Harris and Wanless 2011) and is shared by parents alternating shifts while the other forages. Because of the difficulty of intensive direct observation in this subterranean nesting, easily disturbed species, we estimated laying date indirectly using salt-water immersion data to detect the start of incubation. For those pairs in which we tracked both birds, lay date was identified as the start of the first continuous 6 h daytime period in which one or other bird’s immersion logger was dry (i.e. combined activity showed consistently that at least one parent was not on the water). This method also allowed us to detect failure of the first egg followed by relaying (Figure S1). When only one bird of a pair was tracked, we estimated lay date as the start of the bird’s first incubation shift. The accuracy of this method was verified using a subset of 5 nests which were checked daily with a burrowscope (Sextant Technology Ltd.) in 2012-2013 to determine precise laying date; its accuracy was ± 1.8 days. We calculated the birds’ post-migration laying date for 89 of the 111 tracks in our dataset.

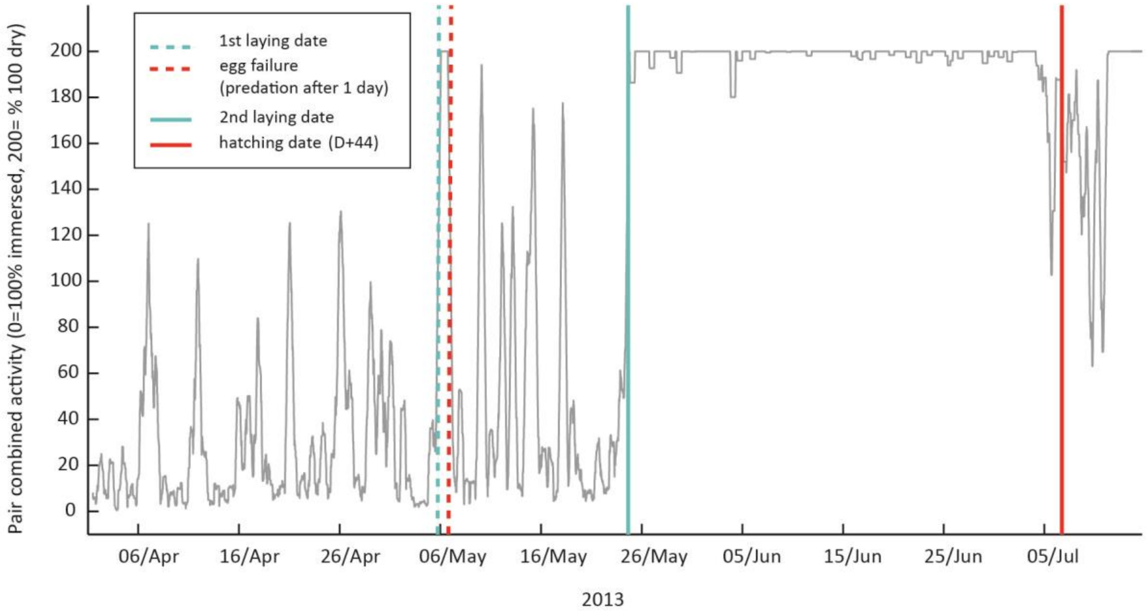

Figure S1 – Combined immersion activity for an example pair during the pre-laying and incubation period of 2013. Lay dates (defined as the start of a long (>6h) dry period) are in blue. The first egg was lost to predation the day after it was laid (pers. observation), the 2nd egg successfully hatched. The end of incubation is indicated with a red line: in the first case after predation of the first egg, the second (hatching) 44 days after relaying (in this case presence of the chick was verified with a burrowscope). During these 44 days there was always an adult present on the colony, except for short bouts of maximum 1min.

Breeding success

We did not check nests directly during the 6-week chick-rearing period following incubation to minimise disturbance, except after 2012 when a burrowscope was available. Nests which failed during incubation (unsuccessful incubation, egg damaged or infertile) were identified using the same immersion data technique used to identify laying date: nests with an incubation period unusually short or long, i.e. outside of a 14-day window around the average 47 days estimated from our dataset, were deemed unsuccessful.

For the nests which manage to hatch a chick, we used a proxy for breeding success: the ability to hatch and rear a chick for at least 15 days (mortality is highest during the first few weeks; Harris and Wanless 2011). This was estimated by direct observations of the parents breeding beakfuls of sandeels to their burrow. During the chick-rearing season (late May to early July) we regularly observed burrows at dawn or dusk when feeding is most likely to occur (observation took place for a few hours several times a week during this whole period, each year). The birds were deemed to have a successful season if they were seen provisioning their chick at least 15 days apart (i.e. their chick reached at least 15 days, this is the lower threshold used in the standard method for this colony: Skomer Island seabird monitoring reports 2008-2014). Although 15 days was our cut-off value, in the most cases birds could be observed bring food to their chick for longer periods.

Sexing

We sexed 20 birds using DNA extracted from 5 breast feathers plucked during device retrieval (Avian Biotech, UK). 7 additional birds which could not be recaptured in 2014 were sexed behaviourally, using a conservative combination of at least 2 of 3 different measures. First, we compared bill size between partners, the main method used to sex puffins before DNA methods; females usually have a smaller beak than their partner (Corkhill 1972; Friars and Diamond 2011). Second we used repeated observations (conducted for 1-2h at least 1-2 times a week during the 2007-2013 breeding seasons) of typical male-behaviour at the colony (e.g. head-flicking display, Taylor 2011) and propensity to fight (Creelman and Storey 1991) or copulation. Finally, when both members of a pair were tracked with a geolocator, we used the technique used to measure laying date to identify the bird which took the first incubation, which tends to be male in many other burrow-nesting seabirds (Warham 1990; Pinet et al. 2012). We used the DNA-sexed birds to validate these 3 methods. The accuracy obtained were 100% for the bill-size method (validated on 7 pairs), 100% for behavioural observations (validated on 10 pairs), and 100% for the first incubation shift method (validated in 6 pairs). However, to be conservative we only included the 7 birds for which we had results from 2 or 3 methods in our analysis of sex-differences (7 other birds for which we only had one of the 3 measurements were excluded). In one pair (which we did not include in our analysis), one of the three methods was in disagreement with the two others, which shows that none of these methods apart from DNA sexing are 100% reliable (despite our 100% validation), which is we only included birds for which we had 2 or 3 (agreeing) measures. In total we sexed 27 birds (13 males and 14 females), including 20 with DNA methods and 7 with behavioural methods.

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Supplementary Figures (S2-S3)

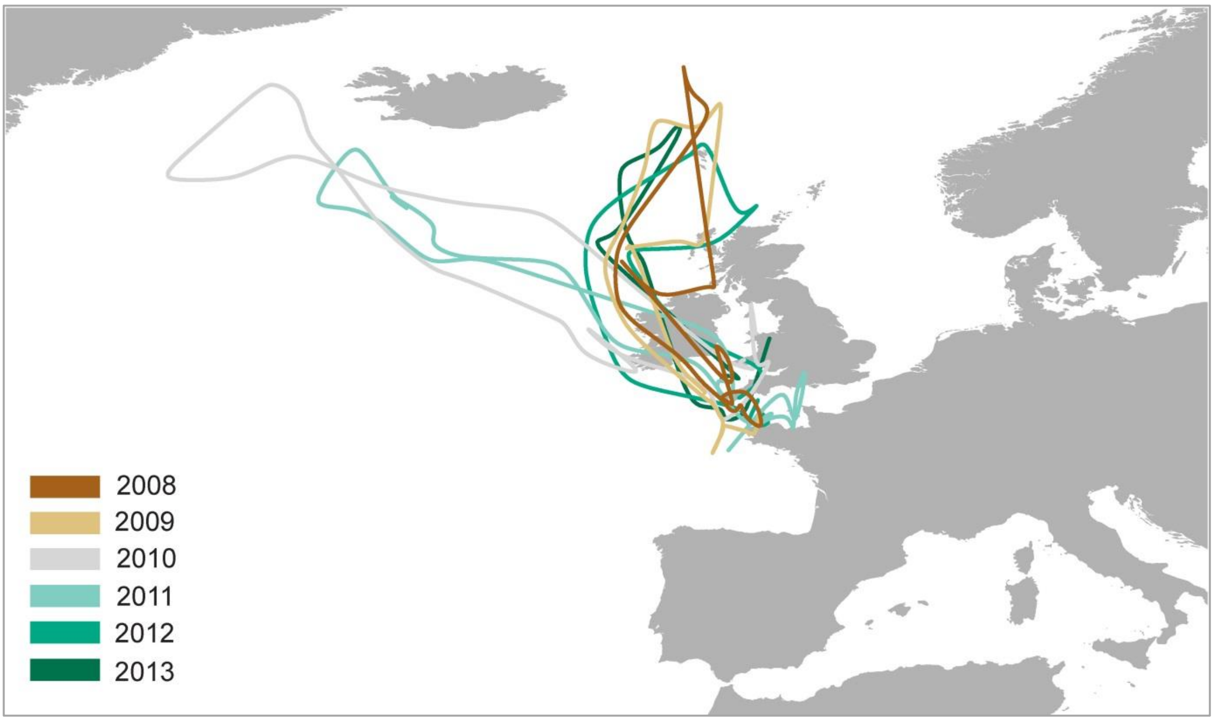


Figure S2. Switch of migratory route over 6 years in a puffin. Data obtained between 2008 and 2014 on puffin EJ47626. The trajectories are straight lines between weekly medians (July-March), smoothed over 3 decimal degrees. Each colour represents one year (see legend). This bird had a "local" migration route in 2008, and 2009, switches to an "Atlantic" route in 2010 and 2011, and reverses back to "local" in 2012 and 2013. It is the only bird in our dataset which shows such a clear switch in migration route.

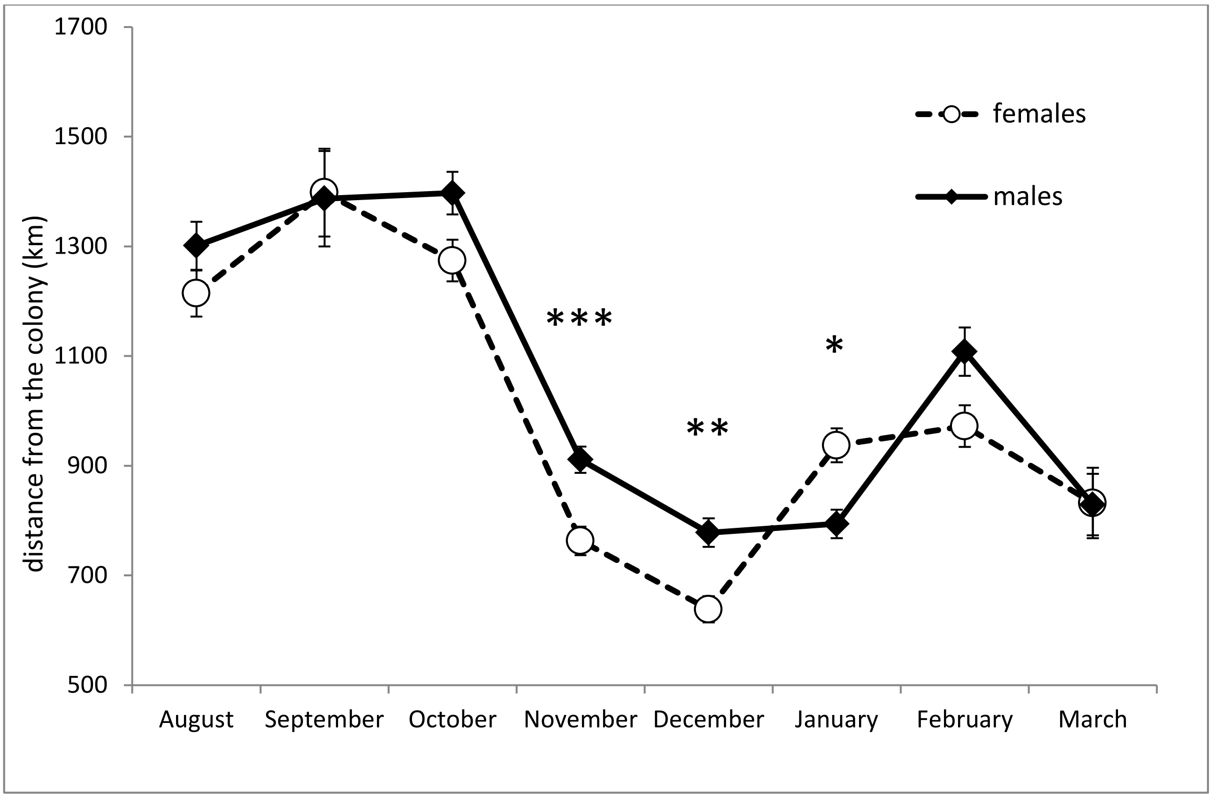
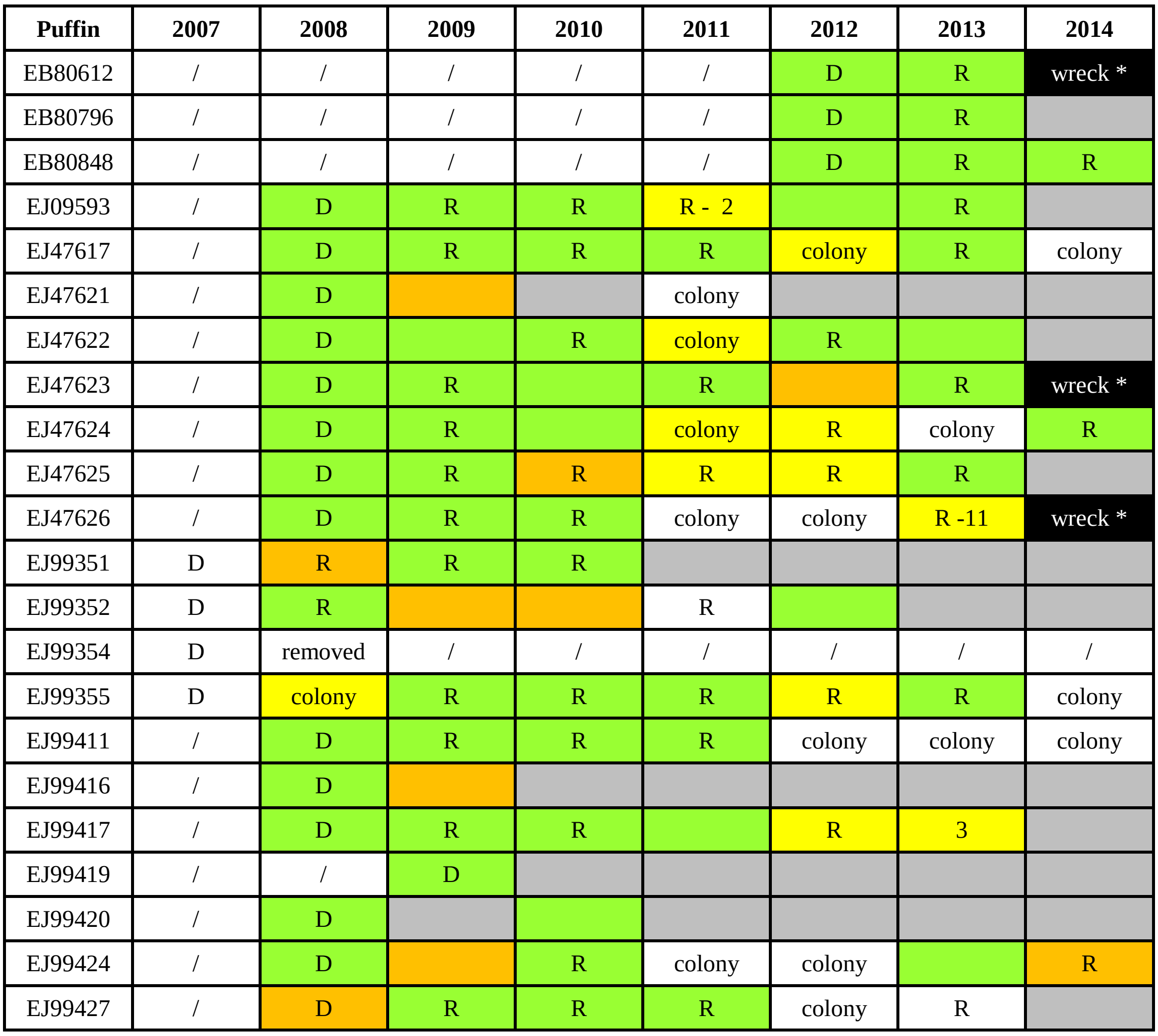


Figure S3. Average monthly distance from the colony for both sexes. The males are represented with black diamonds and a continuous line, the females with open circles and a dashed line. Data presented are mean ± SE. Asterisks indicate significant differences between males and females (Wilcoxon tests, *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$).

Supplementary Tables (S1 – S2)

Table S1. Details of geolocator deployments on puffins since 2007. The table indicates when the birds were captured for a first geolocator deployment (D), recaptured (R), if their device was removed and not replaced ("removed"), or if the birds were present at the colony but not recaptured ("colony"). The background colour indicates breeding success: green indicates that the birds successfully hatched a chick which survived over 2 weeks (i.e. the parents were seen bringing fish to their burrow at least two weeks after hatching date), yellow indicates that a chick hatched but it is unknown whether it survived for over two weeks. Orange indicates that the birds failed to lay or to hatch an egg. White indicates an unknown reproductive success (but the birds were seen at the colony). Grey indicates that the birds were not seen at all at the colony. The number next to some letters indicate the minimum age of the chick when the parents were last observed feeding it (above 14 is here considered as successful breeding success). The survival rate and breeding success of study birds can be found for each year at the bottom of the table, along with the annual general survival rate and breeding success of the colony as a whole (Skomer Island Seabird Reports 2008-2014).



Puffin	2007	2008	2009	2010	2011	2012	2013	2014
EB80612	/	/	/	/	/	D	R	wreck *
EB80796	/	/	/	/	/	D	R	
EB80848	/	/	/	/	/	D	R	R
EJ09593	/	D	R	R	R - 2		R	
EJ47617	/	D	R	R	R	colony	R	colony
EJ47621	/	D			colony			
EJ47622	/	D		R	colony	R		
EJ47623	/	D	R		R		R	wreck *
EJ47624	/	D	R		colony	R	colony	R
EJ47625	/	D	R	R	R	R	R	
EJ47626	/	D	R	R	colony	colony	R -11	wreck *
EJ99351	D	R	R	R				
EJ99352	D	R			R			
EJ99354	D	removed	/	/	/	/	/	/
EJ99355	D	colony	R	R	R	R	R	colony
EJ99411	/	D	R	R	R	colony	colony	colony
EJ99416	/	D						
EJ99417	/	D	R	R		R	3	
EJ99419	/	/	D					
EJ99420	/	D						
EJ99424	/	D		R	colony	colony		R
EJ99427	/	D	R	R	R	colony	R	

EK59012	/	/	/	/	/	D	R	▨
EL60569	/	/	D	R	R	🟧	R	colony
EL60571	/	/	D	R	🟩	R	▨	▨
EL60572	/	/	D	R	colony	▨	▨	▨
EL60573	/	/	D	R	R	R	R - 13	🟧
EL60575	/	/	D	R	▨	▨	▨	▨
EL60579	/	/	D	R	R	R	colony	▨
EL60647	/	/	/	/	/	D	▨	▨
EL60648	/	/	D	R	R	🟧	R -7	▨
EL60862	/	/	/	D	colony	R	🟩	R
EL60863	/	/	/	D	R	R	R	R
EL60866	/	/	/	D	colony	colony	▨	▨
ET43490	D	R	R	R	R	R	R	R
EX83106	/	/	/	/	D	colony	🟩	▨
EX83181	/	/	/	/	D - 2	🟩	R	R
EX93522	/	/	/	/	/	D	🟧	colony
EX93804	/	/	/	/	/	/	D	wreck *
EY07414	/	/	/	/	/	D	colony	▨
EY07420	/	/	/	/	/	D	🟧	▨
EY07421	/	/	/	/	/	D	R	R
EY07422	/	/	/	/	/	D	🟧	colony
EY07423	/	/	/	/	/	D	R	colony
EY07424	/	/	/	/	/	D	R	colony
EY07425	/	/	/	/	/	D	R	▨
EY07259	/	/	/	/	/	D	R	wreck *
EY07260	/	/	/	/	/	D	R	▨
EY07261	/	/	/	/	/	D	R	🟩
EY07262	/	/	/	/	/	D	R	R
EY07263	/	/	/	/	/	D	R	🟧
EY07264	/	/	/	/	/	D	R	R
EY07265	/	/	/	/	/	D	R	▨
EY07267	/	/	/	/	/	D	R	R
	2007	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**
GLS birds survival rate	n/a	100 % (5/5)	100% (18/18)	92.3% (24/26)	92.6% (25/27)	92.3% (24/26)	91.1 % (41/45)	52.4 % (22/42) *
colony survival rate	84.70%	93.90%	93.40%	83.80%	93.60%	97.80%	84.2 %	59.5 % *
GLS birds breeding success	/	87.5% (14/16)	80% (20/25)	84.6% (22/26)	100% (11/11)	74.1% (20/27)	83.9 % (26/31)	71.4 % (10/14)
colony breeding success	79%	63%	77%	80%	84%	80%	78%	53 %

* In February 2014, exceptionally violent storms left 28,000 puffins wrecked on the French Atlantic coast, 5 (~10%) of our study birds were found dead among them (marked “wreck” in the table). Approximately half of our study birds were missing from the colony in summer 2014 – a number much higher than usual but equivalent to the numbers obtained on a colour-ring study on a different part of the colony.

Table S2. Test results investigating differences between route types in proportions of time spent flying, foraging and sitting, and daily energy expenditure, for each month of the migration period, as presented on Figure 2. The *P* values are obtained from GLMMs and pairwise comparisons with adjustment for multiple comparisons. Significant p-values (<0.05) are in bold.

	Aug	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**
Flight								
local_Atlantic	**0.004**	**0.010**	**0.001**	0.103	0.406	0.693	0.063	0.946
local_Atlantic + Med	**0.000**	**0.000**	**0.000**	**0.023**	**0.000**	**0.000**	0.190	**0.018**
Atlantic_Atlantic + Med	0.166	**0.048**	0.054	0.287	**0.000**	**0.000**	**0.005**	**0.026**
Forage								
local_Atlantic	0.976	**0.005**	**0.003**	0.299	0.754	0.983	0.059	0.176
local_Atlantic + Med	0.976	0.461	0.076	0.607	0.079	**0.024**	**0.000**	0.239
Atlantic_Atlantic + Med	0.976	0.215	0.678	0.854	0.088	**0.024**	**0.003**	0.863
Sitting on water surface								
local_Atlantic	1.000	**0.004**	**0.001**	0.215	0.700	0.989	0.209	0.226
local_Atlantic + Med	1.000	0.289	**0.009**	0.321	**0.006**	**0.001**	**0.000**	0.054
Atlantic_Atlantic + Med	1.000	0.326	0.867	0.935	**0.009**	**0.001**	**0.005**	0.226
Daily Energy Expenditure								
local_Atlantic	**0.015**	0.280	0.154	0.287	0.866	0.814	0.113	0.338
local_Atlantic + Med	**0.002**	**0.008**	**0.001**	0.377	**0.001**	**0.000**	0.805	**0.009**
Atlantic_Atlantic + Med	0.164	0.058	**0.015**	0.910	**0.001**	**0.000**	0.162	**0.001**

Chapter 3

Within-pair migration strategies in a dispersive migrant and implications for fitness

Annette L. Fayet, Robin Freeman, Akiko Shoji, Dave Boyle, Holly L. Kirk, Chris M. Perrins, Tim Guilford

Abstract

Long-lived migratory animals engaged in long-term partnerships often synchronise their return to the breeding site to start breeding earlier and maximise breeding success. How they achieve synchronous returns is currently poorly understood, in particular in species with diverse migratory routes, where pair members may winter far apart. Although pair synchrony in such species has been documented, its prevalence, the mechanisms behind it, and how it affects breeding performance, are unknown. Here we investigate the within-pair migration strategies of a pelagic seabird with dispersive migration, the Atlantic puffin *Fratercula arctica,* by tracking the migration routes of 12 pairs over 1-3 years with miniature geolocators. We aim to (i) measure route similarity between pair members and test whether they benefit from following similar migratory routes; (ii) estimate within-pair differences in migratory behaviour and examine the potential relationship between behavioural differences and route divergence and (iii) investigate the potential fitness consequences of such behavioural differences. We find that although pairs were unlikely to be migrating together, they followed similar routes at the start of migration, but these later diverged. Pairs following more similar routes laid earlier the following season, which in this species is associated with higher fledging success. Using the saltwater-immersion data collected by geolocators to calculate day-to-day activity budgets and estimate daily energy expenditure, we show that females had a higher overwinter energy expenditure. This difference was especially pronounced in the second part of the winter, with females spending more time foraging and less time sitting on the water than males. This also coincided with route divergence from their partner. Females which spent more time foraging overwinter laid earlier and had a higher breeding success the following season. This suggests that females may bear a larger part of the cost of breeding by laying the egg and need to invest more effort in building reserves than males during the winter. Overall, our study shows that within-pair similarity in migration routes may benefit dispersive migrants but that adequate body condition at the start of the breeding season, especially of females, may be more critical than pair synchrony for maximising breeding success.

Introduction

Many long-lived animals form monogamous, long-term mating systems throughout the animal kingdom (Emlen and Oring 1977). These include invertebrates (Rahman et al. 2003), fish (Whiteman and Côté 2004), mammals (Clutton-Brock 1989; Lukas and Clutton-Brock 2013) and reptiles (Bull 2000), but primarily birds (Black 1996). Reproductive success often increases with pair duration and mate retention (Dubois and Cézilly 2002; Sanchez-Macouzet et al. 2014), and changing mate (by divorce or after death of a mate) is costly (Choudhury 1995).

In migratory birds, phenology of migration and reproduction, the two main events in the annual cycle of migrants, are crucial, because animals need to match their behaviour to environmental conditions which may be temporally restricted, such as food availability to feed their offspring (Gunnarsson et al. 2005) or weather conditions (e.g. to avoid adverse weather during migration, Newton 2007). Birds tend to have well-orchestrated timings of return to the breeding ground, with males usually returning first to defend a nest site (Newton 2008). Pairs which return from migration at similar times tend to do better and experience fewer divorces (Gonzales-Solis et al. 1999; Naves et al. 2007). Pair synchrony may be more difficult to achieve in species migrating to distant wintering grounds, and such species may have a lower chance of reuniting after migration (Rowley 1983). There is also evidence that at least in some long-distant migrants, pairs do not stay together during the non-breeding season (Müller et al. 2015; Thiebot et al. 2015).

Pair synchrony may be particularly challenging in dispersive long-distance migrants – which by definition may follow migratory routes in any direction from the breeding site (Newton 2008). In these species, the diversity of migration routes is likely to influence individual timings of return to the colony and potentially timing of breeding (Alves et al. 2013), and to make it harder for pairs to synchronise their returns. Indeed, while pairs of migrants with a single overwintering ground could synchronise their return by migrating together or simply by being exposed to the same conditions overwinter, pairs of dispersive migrants may disperse to different areas and experience different conditions. In these species, the prevalence and the importance pair synchrony are poorly known, although it has been documented in a least one species of waders (Gunnarsson et al. 2004). Furthermore, how synchrony may develop within pairs, and more generally the within-pair dynamics of migration, remain to be understood.

Here we investigate the within-pair dynamics of migration, and the existence, potential drivers and fitness consequences of winter within-pair coordination in a dispersive migrant, the Atlantic puffin. Puffins are small pelagic seabirds breeding and wintering in the Atlantic Ocean and along its coasts. Pelagic seabirds are ideal species to study these questions and investigate potential relationships between pairs' migratory routes, mate fidelity, and breeding success. They are typically long-lived, long-distance migrants with high mate fidelity (Schreiber and Burger 2002). They also show high fidelity to their nest site, and unlike many other (mostly passerine) migrants they tend to be large enough to carry tracking devices year round, although negative device effects can occur depending on the type of logger and the species (Igual et al. 2004; Paredes et al. 2005; Quillfeldt et al. 2012; Robinson and Jones 2014). While many seabirds migrate to a single wintering ground using a single route (Guilford et al. 2009; Egevang et al. 2010; Hedd et al. 2012), some species show more flexibility and use multiple wintering destinations (Weimerskirch et al. 2000; Croxall et al. 2005; Shaffer et al. 2006; Gonzales-Solis et al. 2007). Puffins belong to the latter category and show highly dispersive migration (Guilford et al. 2011, Chapter 2). In this study, using miniature geolocators, we track the migratory routes of 12 pairs of breeding Atlantic puffins for 1-3 years. We combine spatial data with estimations of individual daily at-sea activity budgets and energy expenditure obtained from saltwater-immersion data recorded by the geolocators, to investigate the spatial and behavioural differences in migratory strategies between pairs members, and their potential consequences on pair fitness.

Methods

Device Deployment

Atlantic puffins are small auks (~370g) breeding in dense colonies across the North Atlantic. They spend most of the year at sea, only returning to land during the summer to breed. A long-lived monogamous species with very low extra-pair paternity (Nilssen et al. 2008), they raise a single chick every year, usually in the same burrow (Harris and Wanless 2011). This study was carried out on Skomer Island, Wales, UK (51 degrees 44’ N; 5 degrees 19’ W), where over 10,000 pairs of puffins breed each year (Skomer Island seabird monitoring reports 2008-2015).

Between 2009 and 2015, 20 pairs of breeding puffins (40 birds) were caught at their burrows using leg hooks and purse-nets. Birds were ringed using a BTO metal ring and a geolocator was attached to a plastic ring (models Mk13, Mk14, Mk18L or Mk18H - British Antarctic Survey, or Mk4083 – Biotrack; see (Guilford et al. 2011 for detailed methods). Handling took less than 10min on average. 37 birds were recaptured in subsequent years to have their device replaced (for multiple-year tracking). After many devices failed, we collected a total of 20 pairs of tracks from 12 pairs (24 birds), with pairs being tracked simultaneously for 1-3 years. All tracks with the exception of those from 2014-2015 are also used in Chapter 2.

All work was conducted after approval by the British Trust for Ornithology’s Special Methods Technical Panel (permit C/5311), Natural Resources Wales, Skomer Island Advisory Committee and the University of Oxford’s Local Ethical Review Process. No immediate nest desertion was witnessed post-handling; 37 out of 40 tracked birds were recaptured in following seasons. Of the 3 which were not recaptured, 2 were present at the colony in at least one subsequent year. The annual survival rate and average breeding success of manipulated birds were similar to the colony as a whole (Table S1, Skomer Island seabird monitoring reports 2008-2015).

Data Processing and Analysis

Geolocator data were processed and analysed using the same methods and data filters (speed, equinox, breeding season) as in Chapter 2. We used the filtered spatial data (2 positions per day) to calculate 2-day median positions for all tracks, those with high standard error (longitude > 40 km, latitude > 30 km) or sample size < 2 positions were filtered out. For analyses of route similarity we calculated the average nearest neighbour distance (NND, in km) of each migration track to all other tracks over a 20-day window, as in Chapter 2 (detailed methods in Guilford et al. 2011). The only difference with Chapter 2 was the addition of a 3rd group, “within-pair”, to the previous “within-individual” and “between-individual” comparisons. Tracks were only compared within the same year to avoid potential differences due to environmental conditions, except in the “within-individual” category. We used the same methods described in Chapter 2 to calculate the total distance covered by each bird on migration and distance from the colony (spatial data) and estimates of activity and energy budgets (saltwater-immersion data).

Phenology of migration

Because of the low resolution of geolocation data, it is not possible to detect the departure or return of birds from the colony – unless it is immediately preceded or followed by a large longitudinal movement. Similarly, it is not possible to use the saltwater immersion data with precision to detect the first or last visit to the colony of the season, as at the start and the end of the breeding seasons puffins make short visits to the colony, which could also look like flight. Therefore we could only extract migration timings from pairs which migrated to the Atlantic Ocean – for these birds we measure the first and last date in the winter when they crossed the -20 degrees meridian. Although we mention briefly the results obtained, they only represent 5 pairs of migration tracks from 4 puffin pairs and therefore are not included into any statistical analysis.

Sex, Phenology and Breeding Success

The methods used to estimate laying date and breeding success are described in Chapter 2. Combining these methods with the use of a burrowscope in 2013-2015, we obtained pre-migration laying dates for 18 of the 20 pairs of tracks and post-migration laying dates for 19 of the 20 pairs (in the remaining cases the pair’s devices had both failed too early to determine the start of incubation), and measured pre- and post-migration breeding success for 19 out of 20 pairs.

We measured sex for 22 out of 24 birds (11 out of 12 pairs). After 2013, 7 out of 12 pairs were sexed using DNA techniques using 5 breast feathers we plucked from the birds during device retrieval (Avian Biotech, UK). 4 out of the remaining 5 pairs which could not be recaptured after 2013 were sexed behaviourally using the method described in Chapter 2 (which was validated by DNA results, see Chapter 2 for details). We did not have enough behavioural information to sex birds in the remaining pair, which was excluded from analyses of sex differences.

Statistics

We use Linear Mixed-Effects Models (LMMs) throughout our analysis ({*lme4*} package, R 3.0.2 (R Core Development Team 2014). Bird or pair identity and year were always included as a random effect in our models. Route type was controlled for when testing the effect of within-pair route similarity on laying date. Statistical significance was obtained from comparing models to the null model (intercept + other potential fixed effects + random effects). For descriptive convenience we classified routes into 4 groups using a set of quantitative criteria based on latitude and longitude thresholds (see Chapter 2 for details). All means expressed in the text are ± SE. Data were log- or sqrt-transformed to meet parametric assumptions when necessary. The occupancy kernels showed in Figure 1 were obtained with ArcGIS and GME (Geospatial Modelling Environment, Spatial Ecology Ltd), using the same parameters as in Chapter 2 (bandwidth ~275km, resolution ~20km).

Results

Route Similarity between partners

It is important to note that the resolution of geolocator data does not allow us to test whether pairs actually migrate together (Phillips et al. 2004), only whether they follow similar routes (although large differences would prove they do not). We found a diversity of routes taken by different individuals in all years. These routes are described in more detail in Chapter 2. An overview of males and females distributions are given in Figure 1. Briefly, migration routes could be classified in four broad categories: “local”, with birds staying relatively locally around Great Britain or Ireland, and sometimes venturing south later in the winter to the Iberian peninsula and the Bay of Biscay (12/24 birds, 22/40 tracks), “Atlantic”, with birds spending most of the winter in the Northwest Atlantic near Iceland and Greenland (7/24 birds, 12/40 tracks), “Atlantic + Mediterranean”, with birds following a similar route to the “Atlantic” category for the first part of the winter but then spending the second part in the Mediterranean Sea (3/24 birds, 5/40 tracks), and “local+Med”, a combination of the first half of the “local” category and a subsequent visit to the Mediterranean (1/24 birds, 1/40 tracks). As previously found in Chapter 2, individual route fidelity between years was high; all 14 birds which we tracked for 2-3 years kept the same type of migration throughout the tracking period.

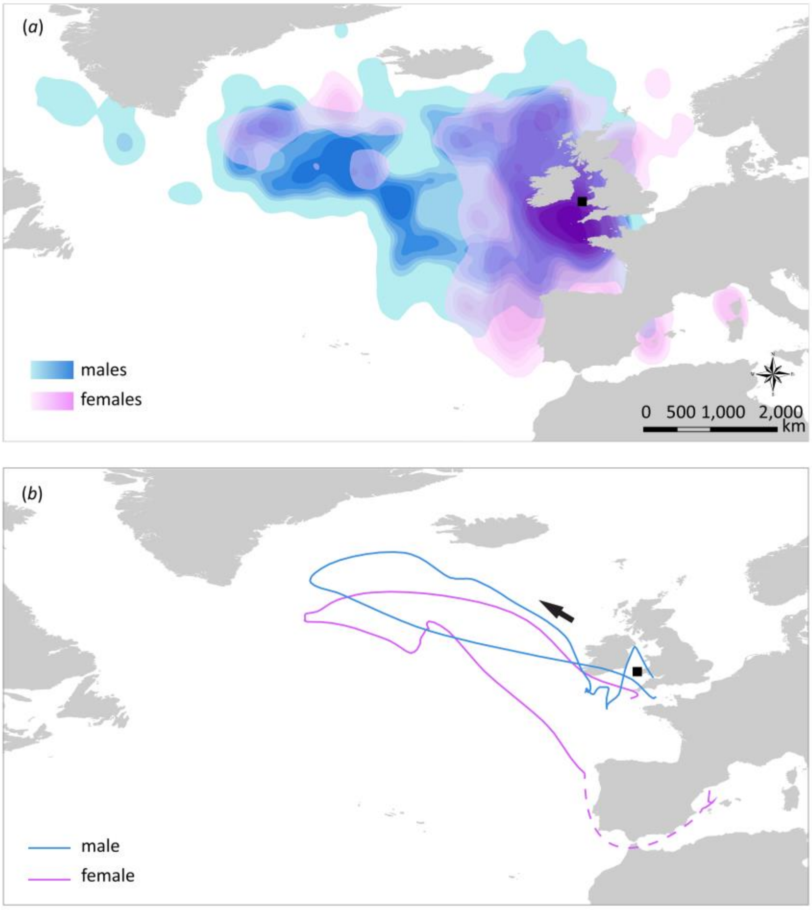


Figure 1. (*a*) Winter distribution of 12 pairs of puffins from Skomer Island, Wales, with males in blue and females in purple. 90% density kernels, with darker shades representing core areas. (*b*) An example of the migratory journey of a pair, with the male in blue and the females in purple. The arrow represents the direction of migration. On both panels the colony is indicated with a black square.

To quantify route similarity between partners we calculated the NND between each pair of tracks. On average over the whole winter, within-individual routes were most similar (NND = 280 ± 27 km, n = 18), followed by between-partners (NND = 646 ± 78 km, n = 20) and between non-partners (NND = 680 ± 25 km, n = 152). While the within-individual NND was significantly smaller than both NND between partners (LMM, $\chi_1^2 = 12.1$, $P < 0.001$) and between non-partners (LMM, $\chi_1^2 = 19.8$, $P < 0.001$), the difference between partners and non-partners was not significant (LMM, $\chi_1^2 = 0.7$, $P = 0.794$). These results held when removing two pairs with very large NNDs which were statistical outliers (Grubbs test, U=0.24, $P = 0.020$; we discuss the significance of these outliers in the Discussion). Within-individual route similarity was still highest (NND = 241 ± 23 km, $n = 16$) and significantly more than between partners (NND = 521 ± 56 km, $n = 16$, LMM, $\chi_1^2 = 19.8$, $P < 0.001$) and non-partners (NND = 601 ± 29 km, $n = 86$, LMM, $\chi_1^2 = 19.1$, $P < 0.001$), but the difference remained non-significant between partners and non-partners ($\chi_1^2 = 0.6$, $P = 0.458$).

However, a different pattern appeared when looking at NND averaged over each month instead of over the whole winter, with the route similarity between partners becoming significantly higher than that between non-partners (LMM, $\chi_1^2 = 3.6$, $P = 0.05$, Figure 2a). Comparing NND between all groups for each month of the winter showed that while within-individual route similarity is always significantly higher than between non-partners, route similarity between partners varies over the course of the winter (Figure 1b, Figure 2b). During the first part of the winter (July to October-November), there are no differences in route similarity within-individuals and between partners, while non-partners have significantly less similar routes. This patterns gradually changes in October – November, with between-partner similarity decreasing (as well as route similarity increasing between non-partners). From December onwards, route similarity between partners becomes similar to that of non-partners, and is significantly lower than within-individuals (see Table 1 for statistical details). In other words, pairs seem to follow similar migratory routes during the first part of the winter, but this similarity disappears during the second half of the winter. In 4 of the pairs, this occurred when one member went to the Mediterranean Sea from December/January onwards, while the other member remained in the Atlantic Ocean or near the Bay of Biscay or Iberian coast.

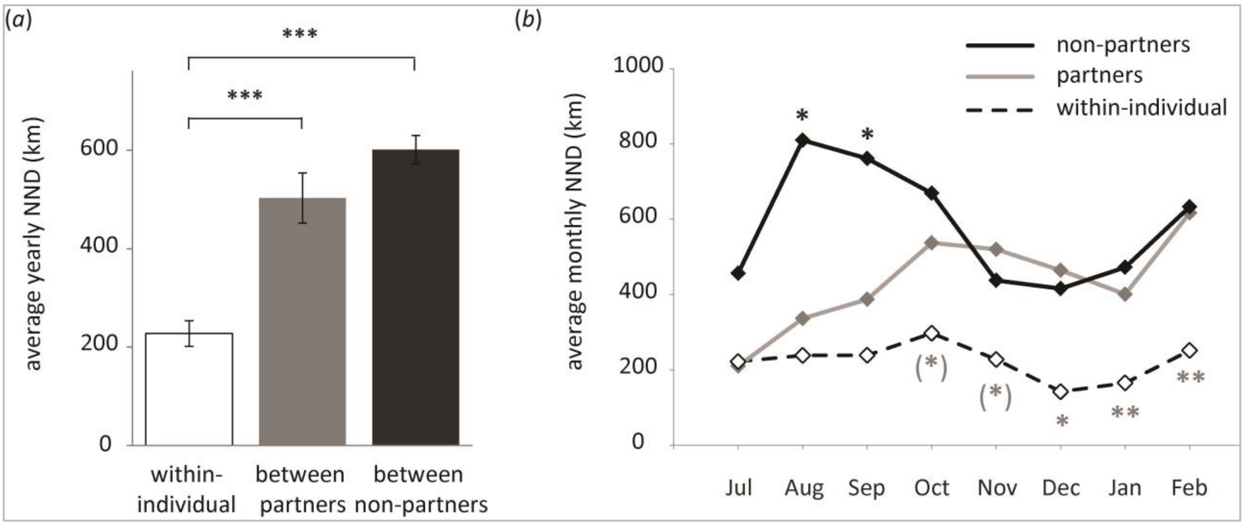


Figure 2. Comparison of route similarity within-individual (white bar or dashed black line), between partners (grey) and non-partners (black), averaged over the whole winter (*a*) or by month (*b*). Stars show significance between groups, on the right panel grey stars indicate significant differences between within-individual route similarity and between partners, while black stars indicate a significant difference between partners and non-partners (*: $P \leq 0.05$; **: $P < 0.01$; ***: $P < 0.001$). Within-individual route similarity is always higher than between non-partners, but this was not indicated on the graph for clarity. Means ± SE.

Table 1. Monthly averages of nearest neighbour distance within-individuals, between partners and non-partners, and the pairwise comparisons between each group. The statistics are obtained from LMMs, significant differences ($P \leq 0.05$) are in bold. WI = within-individual, P = between partners, NP = between non-partners. Means ± SE.

month	within-individual NND (km)	between partners NND (km)	between non-partners NND (km)	statistics
July	222 ± 24	210 ± 54	456 ± 25	WI – NP: $X^2_1 = 2.6$, *P* = 0.109 WI – P: $X^2_1 = 0.6$, *P* = 0.445 P – NP: $X^2_1 = 2.1$, *P* = 0.152
August	238 ± 23	337 ± 48	810 ± 22	WI –NP: $X^2_1 = 13.2$, *P* < 0.001 WI – P: $X^2_1 = 0.5$, *P* = 0.495 **P – NP: $X^2_1 = 4.5$, *P* = 0.034**
September	239 ± 70	387 ± 115	761 ± 40	WI – NP: $X^2_1 = 14.6$, *P* < 0.001 WI – P: $X^2_1 = 1.7$, *P* = 0.197 **P – NP: $X^2_1 = 5.2$, *P* = 0.022**
October	297 ± 26	537 ± 53	669 ± 19	WI – NP: $X^2_1 = 14.4$, *P* < 0.001 WI – P: $X^2_1 = 2.8$, *P* = 0.095 P – NP: $X^2_1 = 2.0$, *P* = 0.156
November	228 ± 15	520 ± 27	438 ± 13	WI – NP: $X^2_1 = 6.3$, *P* = 0.012 WI – P: $X^2_1 = 2.9$, *P* = 0.090 P – NP: $X^2_1 = 0.0$, *P* = 0.869
December	142 ± 13	464 ± 25	416 ± 11	WI – NP: $X^2_1 = 12.5$, *P* < 0.001 **WI – P: $X^2_1 = 5.2$, *P* = 0.022** P – NP: $X^2_1 = 0.4$, *P* = 0.552
January	165 ± 10	401 ± 24	472 ± 11	WI – NP: $X^2_1 = 17.7$, *P* < 0.001 **WI – P: $X^2_1 = 9.5$, *P* = 0.002** P – NP: $X^2_1 = 0.4$, *P* = 0.537
February	252 ± 20	617 ± 25	633 ± 16	WI – NP: $X^2_1 = 12.2$, *P* < 0.001 **WI – P: $X^2_1 = 8.1$, *P* = 0.004** P – NP: $X^2_1 = 0.2$, *P* = 0.620

Within-pair similarity in timings of migration

We could only measure the timings of large-scale migratory movements for 4 pairs (10 tracks) going to the Atlantic Ocean. Although we cannot do any statistical analysis, our measures show that partners do not migrate together at least some of the time – in 2 out of 5 pairs of migration routes partners crossed the -20 degrees meridian more than 12 days apart. In the other three the difference was 0-2 days, which suggests that the birds did their journey with similar timings, but due to the low resolution of geolocation data (±185km, Phillips et al. 2004), it is not enough to conclude whether the birds were together. Birds left the Atlantic ocean at very different times (range 21 to 79 days apart). In 4 instances out of 5, one bird (1 male, 3 females) left the Atlantic to go the Mediterranean Sea. These results show that partners migrate separately during most of the winter. Whether some birds did the first leg of the journey to the Atlantic together is unclear.

Implications for breeding phenology and success

We did not find any effect of a pair's previous breeding success on within-pair route similarity during the subsequent winter (LMM, $n_{fail} = 7$, $n_{success} = 12$, parameter estimate = 0.07 ± 0.13, $\chi^2_1 < 0.1$, $P > 0.05$). Neither did we detect an effect of within-pair route similarity on the pair's subsequent reproductive success: (LMM, $n_{fail} = 2$, $n_{success} = 17$, parameter estimate = -0.08 ± 0.15, $\chi^2_1 = 0.6$, $P = 0.451$). However, we found that pairs with more similar routes laid earlier the following breeding season (LMM, n = 19, parameter estimate = 1.02 ± 0.01, $\chi^2_1 = 5.5$, $P = 0.019$), which is strongly associated with breeding success in puffins (Nettleship 1972; Harris 1980; Davidson 1994). This result held when controlling for location (local/Atlantic/Atlantic+Mediterranean, LMM, n = 19, parameter estimate = 1.03 ± 0.01, $\chi^2_1 = 5.8$, $P = 0.016$). There was no effect of lay date prior to migration (i.e. presumably correlated with the timing of the end of breeding) on route similarity (LMM, $n = 17$, parameter estimate = 0.0003 ± 0.0006, $\chi^2_1 < 0.1$, $P > 0.05$).

Sex-differences in activity budgets and energy expenditure

We found no difference in the total distance covered overwinter between males and females (LMM, $n_{females} = 19$, $n_{males} = 19$, $\chi^2_1 = 1.4$, $P = 0.238$). However females had a higher total energy expenditure over the winter than males (females = 240747 ± 1442 kJ, males = 237536 ± 1043 kJ, LMM, $n_{females} = 16$, $n_{males} = 15$, $\chi^2_1 = 4.19$, $P = 0.041$). Although this difference originates from differences in activity budgets, we found no significant differences between sexes in the total time spent engaged in different behaviours across the whole non-breeding season (LMMs, sitting: $\chi^2_1 = 0.28$, $P = 0.594$; flying: $\chi^2_1 = 1.93$, $P = 0.164$; foraging: $\chi^2_1 = 0.06$, $P = 0.811$).

To determine the origin of the sex difference in energy expenditure, we compared males and females' daily energy expenditure throughout the winter (Figure 3a). For both sexes daily energy expenditure was higher at the start of the non-breeding season, presumably because of the coordination of the first migratory movement away from the colony. We found no sex-differences in daily energy expenditure during the first part of the non-breeding season (August to October), however females had a significantly higher daily energy expenditure than males during the second part of the wintering period (November to January). Both sexes returned to similar levels of daily energy expenditure in February. When we looked at individual behaviours separately (Figure 3b-d), which also varied during the winter, we found that sex-differences in the proportion of time spent in each behavioural state were only significant in November (flying) or January (sitting and foraging). These months, females spent significantly more time flying and foraging, and less time sitting on the water, than males (see Table 2 for details).

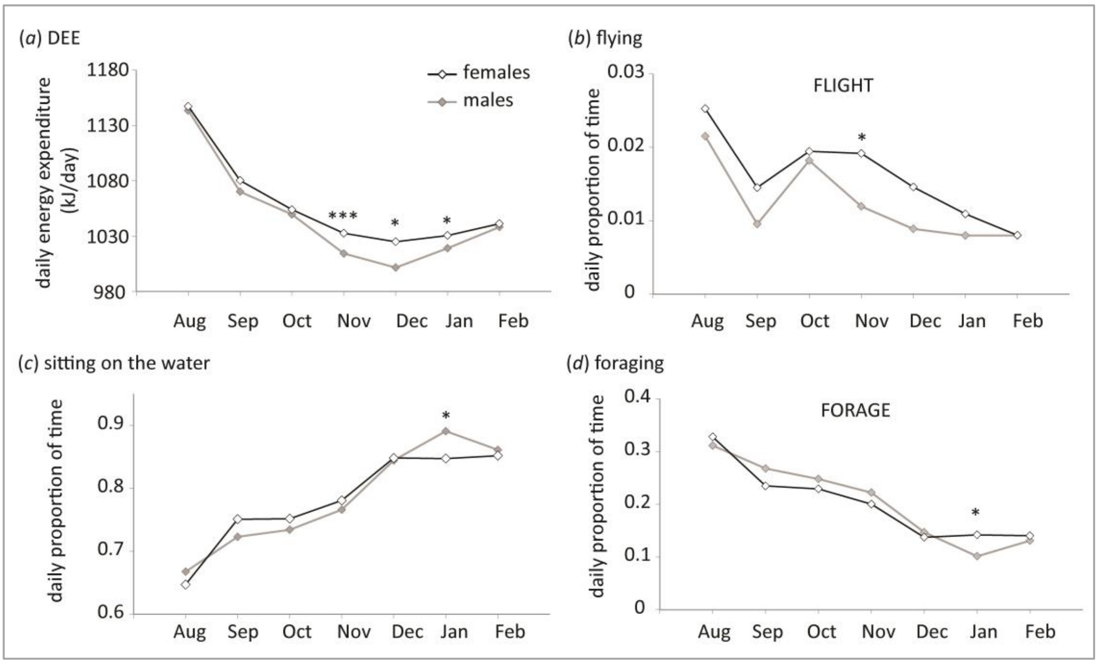


Figure 3. Monthly averages of (*a*) daily energy expenditure and proportion of time spent (*b*) flying, (*c*) sitting on the water and (*d*) foraging for males (grey) and females (black with white diamonds). Significant differences are indicated with stars (*: $P \leq 0.05$; ***: $P < 0.001$). Means ± SE.

Table 2. Monthly averages of different types of behaviour and daily energy expenditure for males and females. Means ± SE. The statistics are obtained from LMMs, significant differences ($P \leq 0.05$) are in bold.

	month	**males**	**females**	**statistics**
foraging (proportion of time %)	Aug	31.1 ± 1.5	32.6 ± 2.3	$\chi^2_1 = 0.1$, $P = 0.757$
	Sep	28.0 ± 2.8	23.3 ± 3.1	$\chi^2_1 = 0.8$, $P = 0.378$
	Oct	25.2 ± 2.4	22.9 ± 3.5	$\chi^2_1 = 0.1$, $P = 0.726$
	Nov	21.8 ± 2.5	19.7 ± 2.9	$\chi^2_1 = 0.0$, $P = 0.848$
	Dec	15.4 ± 1.7	13.7 ± 2.3	$\chi^2_1 = 0.5$, $P = 0.479$
	Jan	**9.7 ± 1.9**	**14.5 ± 2.9**	**$\chi^2_1 = 4.6$, $P = 0.032$**
	Feb	13.5 ± 1.9	14.0 ± 2.1	$\chi^2_1 = 0.4$, $P = 0.538$
flying (proportion of time %)	Aug	2.1 ± 0.4	2.5 ± 0.5	$\chi^2_1 = 2.8$, $P = 0.092$
	Sep	1.1 ± 0.2	1.4 ± 0.3	$\chi^2_1 = 1.8$, $P = 0.185$
	Oct	1.9 ± 0.4	2.0 ± 0.4	$\chi^2_1 = 0.4$, $P = 0.542$
	Nov	**1.1 ± 0.3**	**1.9 ± 0.3**	**$\chi^2_1 = 4.5$, $P = 0.033$**
	Dec	0.8 ± 0.2	1.4 ± 0.4	$\chi^2_1 = 2.6$, $P = 0.104$
	Jan	0.8 ± 0.2	1.1 ± 0.2	$\chi^2_1 = 3.4$, $P = 0.065$
	Feb	0.9 ± 0.3	0.8 ± 0.2	$\chi^2_1 = 0.0$, $P = 0.890$
sitting (proportion of time %)	Aug	66.8 ± 1.5	64.9 ± 2.5	$\chi^2_1 = 0.3$, $P = 0.576$
	Sep	70.9 ± 2.9	75.2 ± 3.4	$\chi^2_1 = 0.5$, $P = 0.467$
	Oct	72.9 ± 2.6	75.1 ± 3.7	$\chi^2_1 = 0.1$, $P = 0.807$
	Nov	77.1 ± 2.6	78.4 ± 3.0	$\chi^2_1 = 0.0$, $P = 0.967$
	Dec	84.1 ± 1.8	84.8 ± 2.5	$\chi^2_1 = 0.2$, $P = 0.652$
	Jan	**89.4 ± 2.0**	**84.4 ± 3.0**	**$\chi^2_1 = 4.4$, $P = 0.035$**
	Feb	85.6 ± 2.0	85.1 ± 2.2	$\chi^2_1 = 0.3$, $P = 0.564$
daily energy expenditure (kJ/day)	Aug	1144 ± 13	1146 ± 16	$\chi^2_1 = 1.2$, $P = 0.266$
	Sep	1071 ± 6	1080 ± 10	$\chi^2_1 = 1.0$, $P = 0.317$
	Oct	1052 ± 9	1054 ± 8	$\chi^2_1 = 0.3$, $P = 0.555$
	Nov	**1010 ± 4**	**1033 ± 4**	**$\chi^2_1 = 11.7$, $P = 0.001$**
	Dec	**999 ± 3**	**1024 ± 9**	**$\chi^2_1 = 6.2$, $P = 0.013$**
	Jan	**1018 ± 4**	**1031 ± 5**	**$\chi^2_1 = 4.7$, $P = 0.030$**
	Feb	1039 ± 7	1041 ± 5	$\chi^2_1 = 0.3$, $P = 0.612$

Effect on breeding success

To test whether these differences in winter activity influenced reproductive success the following season, we investigated potential relationships between the total time spent foraging, breeding success and lay date. We found a significant relationship between the amount of time spent foraging during the winter and the birds' breeding success the following year. The directions of the relationship for males and females were opposite; while there was a strong and very significant positive effect of total time foraging on post-migration breeding success (LMM, parameter estimate = 4.6 ± 4.1, $\chi^2_1 = 19.7$, $P < 0.001$) in females, there was a weaker and less significant negative relationship in males (parameter estimate = -1.8 ± 1.6, $\chi^2_1 = 4.3$, $P = 0.037$). In other words, successful females had spent more time foraging before the breeding season, while successful males had spent less time foraging. We found a significant negative relationship between the total time spent foraging in the winter in both males and females and subsequent lay date, which was more significant in females (LMMs, $n_{males} = n_{females} = 16$; females: parameter estimate = -0.25 + 0.9, $\chi^2_1 = 35.2$, $P < 0.001$; males: parameter estimate = -0.16 ± 0.04, $\chi^2_1 = 11.2$, $P = 0.001$). In other words, birds which spent less time foraging during the winter laid later the following season, and this was more pronounced in females.

Discussion

In this study we investigated within-pair migratory strategies in puffins, compared the migratory routes, at-sea behaviour, and energy expenditure of 12 pairs of adult puffins over 1-3 years, and examined potential effects on breeding phenology and breeding success. We found that individuals followed a large diversity of routes, and that within-individual route fidelity between years was high (as found in Chapter 2). Compared over the whole winter, pairs did not follow significantly more similar routes than other birds. However, when we looked at the variation of route similarity during the winter, we found that pair members followed significantly more similar routes than non-partners during the first part of the non-breeding season. Differences started to emerge in the second part of the non-breeding season, and route similarity gradually decreased until pairs' routes were no more similar than non-partners' routes.

Within-pair interactions during the non-breeding season have seldom been investigated in birds, often because all individuals of a population migrate to the same area, making individual differences difficult to detect. Cranes, swans, and geese, among others, are known to migrate in family groups (Harrison et al. 2010; Newton 2008), but we report here one of the rare evidences of within-pair migration route similarity in seabirds (with Müller et al. 2015, Thiebot et al. 2015). Although we could only obtain data on the timings of migration for a third of the pairs, these revealed that at least some pairs travelled several days apart, indicating that they were not migrating together despite following similar routes during the first part of the winter. In other pairs, timings were very similar but the resolution of the spatial data does not allow us to conclude whether the pair members were actually together. Migration in pairs seems unlikely in puffins as the majority of birds seen at sea during the winter are alone, especially in the Atlantic Ocean (Harris and Wanless 2011).

Even if they do not migrate together, partners could potentially benefit from following similar routes (in space and time). The strong temporal similarity in the movements of birds wintering in similar areas found in Chapter 2 suggests that partners with similar routes would be likely to return to the colony at similar times. How pairs would synchronise their return to the breeding grounds if they are in different areas is unknown, but synchronisation has been observed in at least one species (the black-tailed godwit *Limosa limosa*, Gunnarsson et al. 2004), and may involve some genetic or physiological control of timings of migration. The spatial resolution of our data did not allow us to measure precisely the departure and return of each bird to the colony, and therefore we could not directly examine whether pairs synchronised their return to the colony. However, observations of colour-ringed puffins (A.F., *personal observation*) suggest that they do not follow the pattern traditionally observed in migratory birds (including seabirds) of males returning slightly before females (Morbey and Ydenberg 2001; Phillips et al. 2005; Guilford et al. 2012). In fact, although this may not necessarily be a precise measure of return to the colony, most birds make landfall at the start of the breeding season on the same day. As a result, pair synchrony may simply be a by-product of colony-wide synchrony (Ashcroft 1976; Harris and Wanless 2011; A.F. *personal observation*). The mechanisms behind colony-wide synchrony are unclear.

Nonetheless, our results suggest that puffins benefit from following a similar route to their partner. Although we found no direct effect of within-pair route similarity on breeding success (the coarseness of this binary indicator may have masked subtle differences, e.g. in chick condition), we did find that pairs with more similar routes laid earlier the following season. This result held when we controlled for migratory destination, therefore it was not a simple effect of the birds' location. In puffins as in many other seabirds, breeding early tends to lead to higher reproductive success and fledgling survival (Davidson 1994; Harris 1980; Nettleship 1972), but lay date is not genetically determined (Davidson 1994). Having a similar migration route to one's partner may improve the chances of raising a chick by starting to breed earlier, an effect perhaps reinforced if successfully fledging a young also allows parents to leave on migration more synchronously themselves.

In order to investigate within-pair differences in migratory strategies not only in space but in behaviour, we estimated at-sea daily activity budgets and energy expenditure. Both varied throughout the winter, for both sexes. Although females did not cover longer distances, they had a higher total energy expenditure. Sex-differences in activity budgets, foraging in particular, were not consistent throughout the whole non-breeding period but only appeared during the second part of the winter, concurrently with the emergence of spatial differences between partners. However, it is unlikely to simply result from experiencing different day lengths due to latitude (longer days may give more opportunities to forage). Both sexes visited similar latitudes, for example both males and females visited the Mediterranean Sea. We did not detect monthly differences in activity budgets apart from November, when females spent more time in sustained flight than males (perhaps linked with the start of the divergence between partner's routes) and January, when females spent more time foraging and less time sitting than males. The lack of significant differences in the other months may not only be due to the lack of actual differences between sexes but also potentially to the relative coarseness of our classification method.

In other words, while pairs followed similar routes and had similar energy expenditures during the first part of the winter, in the second part of the winter they followed more different routes and females had a more energy-demanding behaviour, most likely spending more time flying and foraging. The amount of time spent foraging significantly affected their performance during the following breeding season.

Interestingly, it affected males and females differently. Females which spent more time foraging during the winter laid earlier and had a higher breeding success; males which spent more time foraging during the winter also started incubation earlier (i.e. their partner laid earlier) and the effect was less strong, but they had a significantly lower breeding success. This suggests that during the second part of the winter females started to prepare for the breeding season by increasing their foraging effort, and perhaps visited different, more productive areas than males. The effort females put into gaining a good body condition before breeding seemed to directly affect how early they could lay and how successful their breeding season was. Males, on the other hand, spent less time foraging than their partners, and higher levels of foraging negatively affected their breeding success the following season. This may be because males foraged more as a consequence of poor body condition or exploitation of less productive areas, while females foraged more to build up more reserves.

Recent findings in rockhopper penguins *Eudyptes chrysocome* suggest that mates use different foraging grounds but share the same isotopic niche during the non-breeding season, and that females stay longer at sea than males (Thiebot et al. 2015). In many seabirds species, especially procellariformes, females embark on a pre-laying exodus after mating, presumably due to different and higher nutritional requirements to build an egg (Guilford et al. 2012; Dean 2013; Hedd et al. 2014). Pre-laying exodus has not been reported in auks and is unlikely to occur in puffins; females have not been noticed to be away from the colony after their initial return, or at least not long enough to build an egg, which takes 10-18 days (Astheimer and Grau 1990). However, what we observed could be another way to prepare to lay an egg, by accumulating extra reserves before the start of the breeding season. Unfortunately puffins are extremely sensitive to disturbance so it was not possible to collect data on pre-breeding body condition at the return to the colony to test this hypothesis. Apart from a report of a proportion of male kittiwakes *Rissa tridactyla* taking a separate trip further from the colony just before the breeding season (Bogdanova et al. 2011), we are not aware of similar evidence of temporal variation of sex-related spatial segregation throughout the winter in other species. However, our study is one of the first to investigate within-pair differences in migration strategies in such detail so this may be a common, but yet undiscovered, phenomenon. It would be interesting to extend this study to other auks and make a comparison with birds with a specific pre-laying exodus to prepare for breeding.

It is important to note that two pairs were identified as statistical outliers in terms of within-pair route similarity. These pairs are the only two pairs which had dramatically different routes during the entire breeding season. In one pair the female went to the mid-Atlantic and then to the Mediterranean Sea, while her partner went as far as the Labrador Sea and then remained in the mid-Atlantic, in the other the female remained locally while the male went to the mid-Atlantic. These pairs did not lay substantially earlier or later than others, and had a similar breeding success to others. This shows that even if we found that within-pair similarity in migratory routes seemed to be beneficial to a majority of pairs, it is not a necessity to successful breeding. It would be interesting to know whether these pairs are newly formed and whether their route differences will change over the years; unfortunately we do not have the necessary information to test this.

Another question raised by our results is how within-pair similarity could develop in a dispersive migrant. Although assortative mating (at-sea) could be considered, the number of courtship displays, fights and mating events on puffins colonies at the start of the breeding season strongly suggests that puffins choose their mate at the colony at the start of the breeding season (Harris and Wanless 2011, A.F. *personal observation*). Pairing far at sea seems unlikely. Perhaps birds migrating to similar areas are likely to return near to the colony simultaneously and hence may be more likely to meet close to the colony before the actual return to land. Alternatively, it could be an age-driven process; if same-year fledglings tend to migrate to similar areas, mates available to them later will likely be of the same age and migrate to similar places (what would happen when a bird finds a new partner after a death or divorce is unclear). We do not know the age of our study birds (all but one were ringed as adults) so we cannot currently test this hypothesis. Another possibility is that partners finish breeding together and start their migration together as a result. However, tracking puffins for up to 7 consecutive years showed that individuals are highly conserved in their migratory routes regardless of their breeding success prior to migration (Chapter 2), and so it does not seem a likely explanation. To answer this question additional tracking of birds, ideally from fledging, would be required, as well as tracking of pairs before and after a divorce.

This study reveals the complexity of the within-pair dynamics of migration in a dispersive migrant. We present evidence for a beneficial role of within-pair similarity in migration strategy on subsequent breeding success. However pair members do not seem to migrate together and their routes diverge mid-winter, the opposite of what would be expected if the birds were trying to synchronise returns to the breeding site. This may however not be an issue if, as seems to be the case in puffins, pair synchrony is a by-product of colony-wide synchrony. The within-pair differences in migration route in the second half of the winter are combined with a higher foraging effort of females compared to males, directly related to lay date and breeding success. This suggests that the spatial divergence between pair members may be driven by the need for the female to build up additional reserves in preparation for egg laying. These findings raise key questions about the mechanisms by which such migration patterns develop (pair members following similar routes but likely not together), and why and how within-pair route similarity increases breeding success. They also have important implications for sexual conflict and sex-differences in cost of migration.

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Chapter 4

Migratory strategies of Atlantic puffins across their breeding range: behavioural differences and environmental drivers on a global population scale

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Abstract

While the typical avian migrant travels to a single destination for the winter, dispersive migrants can follow a variety of routes and visit many destinations, sometimes with large variations between populations. The extent to which factors such as intra-specific competition or environmental conditions shape population-specific winter distributions is unknown; and whether and how these factors can affect migratory behaviour, and ultimately fitness, remains to be understood. Here we use a large dataset of 270 geolocator tracks of migrating Atlantic puffins *Fratercula arctica* collected at 9 colonies across their whole breeding range to address these questions on a global population scale. First, we reveal the worldwide non-breeding distribution of puffins, measure inter-colony connectivity, and identify important hotspots. In addition, we use saltwater-immersion data collected by geolocators to estimate individual activity budgets and investigate whether they are influenced by local environmental conditions. Despite some connectivity, spatial segregation between colonies is high. Colonies strikingly differ in range, route diversity, activity budgets and environmental conditions, but these differences cannot be simply explained by colony position or size. Foraging effort decreases with sea surface temperature, but increases with productivity, and puffins seem constrained in their winter temperature range by the latitude of their colony, which we suggest may be a consequence of local adaptation.

Introduction

Avian migration is often defined as a long return journey to a specific overwintering destination following the breeding season (Newton 2008). Often birds migrate to lower latitudes than the ones at which they breed, or to similar latitudes in the opposite hemisphere. However, ringing recoveries over decades, and more recent tracking studies, have started to reveal the diversity of avian long-distance migration strategies, and the need to broaden the above definition to encompass a larger range of migratory patterns. It emerged that while in many species all individuals migrate to a single broad area (sometimes using a variety of routes to get there, e.g. Hake et al. 2003), others use multiple wintering destinations (Jones 1995; Oppel et al. 2008; Hedenström et al. 2013). In particular the latter seems to be a widely-used strategy among seabirds (Shaffer et al. 2006; Gonzales-Solis et al. 2007; Yamamoto et al. 2010; Dias et al. 2011; Kopp et al. 2011; Fort et al. 2012), perhaps because the pelagic environment offers more flexibility in terms of movements and resources, and can be, but is not always, unpredictable (Weimerskirch 2007). Some seabirds exhibit an even greater flexibility by showing high migratory route diversity within a single colony (Weimerskirch et al. 2000; Croxall et al. 2005; Phillips et al. 2005; Guilford et al. 2011).

Among these dispersive pelagic migrants is the Atlantic puffin *Fratercula arctica*, a small auk breeding across the North Atlantic. Puffins from Skomer Island (Wales, UK) show a remarkably dispersive migration (Guilford et al. 2011, Chapter 2). However, the level (or even presence) of dispersion seems to vary between colonies. Puffins breeding in southwest Ireland show similar migratory patterns to Welsh puffins (Jessopp et al. 2013), although no birds seem to remain locally over winter like some Welsh birds do. However, most puffins from the Isle of May in east Scotland seem to remain in the North Sea all winter, with a small proportion of individuals venturing further west to the Atlantic Ocean (Harris et al. 2010). The migratory movements of puffins on other colonies such as Norwegian, Icelandic, and North American colonies, which are home to most of the world population, are currently unreported, apart from a single study tracking movements of Norwegian puffins from Røst in the first post-breeding month (Anker-Nilssen and Aarvak 2009).

What drives such differences in migratory strategies is unclear, although between-colony differences in migratory patterns have been found before (perhaps to a lesser extent) in other species, such as black-legged kittiwakes *Rissa tridactyla* (Frederiksen et al. 2011), Brünnich’s and Common guillemots *Uria lomvia* and *Uria aalge* (Tranquilla et al. 2013), and northern gannets *Morus bassanus* (Fifield et al. 2014). It may be a response to local environmental conditions during the winter, for example poor resource availability around some colonies may force these birds to migrate further. The population dynamics of different Norwegian colonies of kittiwakes were shown to be affected by the environmental conditions of different areas at different times, and populations generally declined with warmer sea surface temperatures (Sandvik et al. 2014). Different migratory strategies could also arise from competition, for example insufficient resources near the colony may allow high-quality individuals to remain close but drive lower quality ones to seek resources elsewhere (Gauthreaux 1982; Gunnarsson et al. 2005). They may be density-dependent, resulting in larger colonies having longer migratory routes (Ashmole 1963). These differences could also be genetic, potentially resulting in closely genetically related colonies having similar migration patterns (Berthold 1996).

Regardless of the mechanisms leading to their development, different migratory strategies could have important fitness consequences (Reynolds et al. 2011; Alves et al. 2013; Weimerskirch et al. 2015). Although the drivers of dispersive migration in puffins are unclear, an in-depth study of a large dataset collected on a single Welsh colony over multiple years revealed that both foraging effort and breeding success differed between routes (Chapter 2). Whether similar differences exist in other colonies is unknown. However, on the potentially much larger scale between colonies, such differences could have important implications for colony breeding success and persistence. For example, birds from colonies with longer migration routes may have to invest more energy in migration and consequently return to the colony in poorer body condition, which could lead to lower reproductive success. Alternatively, colonies where birds travel further to reach more productive areas may have higher breeding success after the birds return in better body condition (on Skomer, birds following the longest migration routes had a higher breeding success, Chapter 2).

Here we investigate these questions using a dataset of over 250 migratory tracks collected with geolocators from 9 colonies of puffins across their entire breeding range, including unpublished datasets from 6 colonies. We carry out a detailed study of the migratory behaviour of puffins, with the objectives of (i) determining the global non-breeding distribution of puffins and the connectivity of puffins from different colonies; (ii) assessing the differences in migratory strategies between colonies by measuring within-colony route similarity; (iii) comparing approximate activity budgets between colonies; (iv) comparing environmental conditions experienced by birds in different wintering areas and testing whether these can help to explain the migratory patterns observed.

Methods

Ethical Note

All work was conducted after ethical approval from the appropriate organisation from each respective country. To avoid disturbance, handling was kept to a minimum. When possible, survival and breeding success of manipulated birds were monitored and compared to control birds. Birds on Skomer (Wales) showed similar breeding success and survival to non-tagged birds. At the time of writing, data were not available from other colonies.

Logger Deployment

Geolocators were deployed and retrieved on 9 colonies across the Atlantic puffin's breeding range between 2007 and 2015: Gull Island, Canada (47°57' N, 53°02' W), Grimsey, Iceland (66°32' N, 18°00' W); Hornøya, Norway (70°23 N, 31°09 E); Isle of May, Scotland (56°11' N, 2°34' W); Papey, Iceland (64°35' N, 14°10 W); Røst, Norway (69°30 N, 12°00 E); Skellig Michael, Ireland (51°77 N, 10°54 W); Skomer, Wales (51°44' N, 5°17' W); Stórhöfði, Iceland (63°38' N, 20°18 W). Colonies vary in size between 1,500 pairs (Skellig Michael) and ~400,000 pairs (Røst) (Figure 1), but some such as Gull Island and Stórhöfði are part of archipelagos with much larger breeding populations.

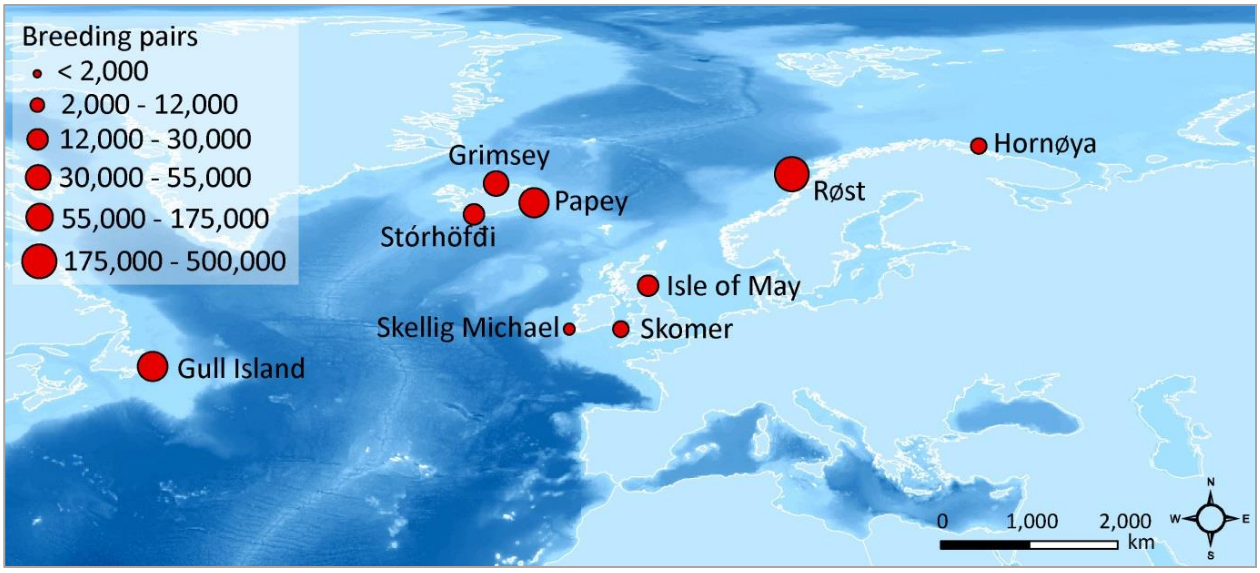

Figure 1. Colonies where geolocators were deployed on puffins between 2007 and 2015, by approximate size of their breeding puffin population (most recent record).

Birds were ringed using a metal ring and a geolocator was attached either to the metal ring or a plastic ring (models Mk13, Mk14, Mk18L or Mk18H - British Antarctic Survey, or Mk4083 or Mk3005 – Biotrack). Birds were recaptured in subsequent years to remove or replace the device. In total 270 migration tracks (including 240 complete ones) were collected (Table 1). Because of the small sample sizes on the 3 Icelandic colonies, of their proximity (323km on average), and of the lack of major differences between tracks (Figure S1), we pooled all tracks together in one "Iceland" group (*n* = 8).

Table 1. Deployments of geolocators on the 9 study colonies.

colony (country)	years	number of tracks (complete)	number of birds
Gull Island (Canada)	2013 - 2014	22 (11)	22
Grimsey (Iceland)	2013 - 2014	4 (3)	4
Hornøya (Norway)	2012 - 2014	53 (42)	38
Isle of May (Scotland)	2007 - 2008 & 2009 - 2010	42 (39)	42
Papey (Iceland)	2013 - 2014	3 (1)	3
Røst (Norway)	2012 - 2013 & 2014 - 2015	5 (3)	5
Skellig (Ireland)	2010 - 2013	35 (35)	31
Skomer (Wales)	2007 - 2014	105 (105)	38
Stórhöfđi (Iceland)	2013 - 2014	1 (1)	1

Spatial data

Light data were decompressed and processed using the BASTrack software suite (British Antarctic Survey) and MatLab R2010b (MathWorks Inc.). Data were filtered using similar criteria to those used in Chapter 2: a 500km/day speed filter, a 15-day filter either side of the two equinoxes, and the breeding season (April - July). We calculated 2-day median positions for all tracks and filtered out those with high standard error ($SE_{longitude}$ > 150 km, $SE_{latitude}$ > 150 km) or unrealistic locations (longitude > 65 or < -73 dd, latitude < 30 or >80 dd). Spatial occupancy kernels were calculated with ArcGIS 10.0 (ESRI) and Geospatial Modelling Environment 0.7.2 (Spatial Ecology LLC) (parameters: bandwidth ~275km, resolution ~20km, similar to those in Chapter 2) and the overlap between colonies was calculated with the {*adehabitat*} package in R (R 3.0.2, R Core Development Team 2014). We estimated distance from the colony as the great-circle distance between the colony and each position. To account for the flight around the Iberia (puffins do not fly over land) for positions in the Mediterranean Sea, distance from the colony was calculated as the distance between the actual position and the Strait of Gibraltar, and added to the shortest distance between the Strait and the colony (~1700 km). Daily average distance and total distance covered were calculated for each track by averaging or summing the great-circle distances between each median between August and February (4-day medians were used instead of 2-day ones in order to reduce the artificial increase in distance covered due to the inaccuracy of the data (± 185km, Phillips et al. 2004).

To compare within-colony levels of route similarity between colonies, we calculated the average nearest neighbour distance (NND, in km, see Chapter 2 for definition and Guilford et al. 2011 for details) of each migration track to all other tracks over a 24-day window (12 days either side of each 4-day median, see detailed methods in Guilford et al. 2011). To partially correct for this, year is controlled for in the models using route similarity as a variable. We also used NND to compare within- and between-individual route similarity for birds from the colonies for which we had multiple tracks per individual (Hornøya, Ireland and Wales).

Activity budgets

We estimated at-sea activity budgets using the same method as in Chapter 2, using salt-water immersion data collected by geolocators. Briefly, each 10-minute interval during daylight between August and March was allocated one of three categories: sustained flight (≥ 98% dry), sitting on the water (≥ 98% wet) or foraging (>2% dry and >2% wet) (Lecomte et al. 2010). Only tracks for which saltwater-immersion data were available for at least 6 of the 8 months of the non-breeding season were included in this analysis, and only complete tracks were used for the calculations of variables summed over the whole winter (e.g. total time spent flying).

Environmental data

Sea-surface temperature (SST, °C) and chlorophyll A concentrations (mg/m^3) were extracted from the NASA OceanColor website using data from the MODIS Terra and Aqua satellites, using a spatial resolution of 50km and a temporal resolution of 8 days. Net primary productivity (NPP, mg C /m^2/day) data (50km resolution), estimated from chlorophyll, light and photosynthetic efficiency values using the Vertically Generalized Production Model algorithm, were obtained from the Ocean Productivity website. Each location from the dataset was assigned a SST, chlorophyll a and NPP value. To test for relationships between at-sea behaviour and environmental conditions, each track was assigned an SST, chlorophyll a and NPP value averaged over the whole track.

Statistics

Linear Mixed-Effects Models (LMMs) including individual identity and year as random effects ({*lme4*} package in R) were used to test for between-colony differences in spatial characteristics (total and daily distance covered, average and maximum distance from the colony), in activity budgets (proportion of time and total amount of time spent in different behavioural states), in energy expenditure, and in environmental conditions. Relationships between at-sea behaviour and environmental factors were tested with LMMs with year, bird and colony as random effects. In these models environmental factors (SST, NPP and chlorophyll A) were included as fixed effects simultaneously to control for potential colinearity. Data were log-, asin- or sqrt-transformed to meet parametric assumptions when necessary. Posthoc pairwise comparisons between colonies were realised with {*lsmeans*} (with adjustment for multiple comparison). Linear models (LM) were used to test for potential effects of colony latitude on the average SST experienced by birds from each colony, and the average proportion of time they spent foraging. Means expressed in the text are ± SE unless stated otherwise. Although sample sizes varied among colonies, most colonies had > 20 tracks which should give a reasonably representative idea of each colony’s distribution (Soanes et al. 2013). At the time of writing fewer tracks were available from Røst and Iceland (n = 5 and 8) than from the other colonies, but they were of good quality and similar (e.g. Figure S1) and so we are confident that the resulting distributions are still relevant, however we emphasize the small sample size when discussing the results of these colonies, and such results should be interpreted with caution.

Results

Winter distributions

Winter distributions differed substantially between colonies (Figure 2a). The latitudinal ranges used by birds (31 to 80 decimal degrees (dd), average latitudinal spread = 32.3 ± 1.4 dd) reflected the latitude of their breeding colony. For example, only birds from the 3 southernmost colonies ventured further than 45° south (northern Spain), and Canadian birds remained south and southwest of their Newfoundland colony. On the east side of the Atlantic, birds from southwest Ireland and Wales went as far south as the Strait of Gibraltar, which some used to enter the Mediterranean Sea. Similarly, only birds from the 2 Norwegian colonies far north spent significant amounts of time at higher latitudes than 68° (northern Iceland), although some birds from the Scotland also seemed to visit these high latitudes for short periods. Differences in longitudinal ranges were more pronounced (-72 to 65 dd, average longitudinal spread = 65.9 ± 10.7 dd). The 2 Norwegian colonies had the largest longitudinal spread (Hornøya: 117.2 dd; Røst: 77.4 dd), followed by the Irish and Welsh colonies with birds wintering across the entire North Atlantic Ocean and nearly as far east as Italy in the Mediterranean Sea (Ireland: 72.3 dd; Wales: 69.5 dd). Canada (28.9 dd), Iceland (51.1 dd) and the Scotland (45.5 dd) were the most longitudinally constrained. It is important to note that the range was not simply proportional to the number of tracks obtained for each colony. For example Røst had the second largest range with the smallest sample size, with an East-West spread over 2.5 times as much as that of Scotland which had over 8 times as many birds tracked.

No colony was totally spatially segregated from the others; the 90% occupancy kernels of all colonies overlapped with 2 to 5 other colonies (Figure 2b). Large areas of the Atlantic Ocean were visited by birds from 2-3 colonies, particularly around Ireland and northwest of Great Britain, and between Greenland and Iceland, as well as a smaller area in the West Atlantic nearer the southern tip of Greenland. Up to 4 colonies overlapped in smaller areas south of Iceland, and a small area near the south tip of Greenland seemed to attract birds from multiple colonies, with a small portion even visited by birds from 5 out of the 7 study colonies. At the 50% occupancy level, three colonies were totally segregated (i.e. did not overlap with 50% occupancy kernels from any other colonies): Canada, Hornøya, and Scotland. Iceland and Røst's overlapped with Ireland but at a low level (2.1 % and 8.7% respectively). The only two colonies with substantial overlap were the Irish and Welsh colonies, whose 50% kernels overlapped by nearly half (22.5%).

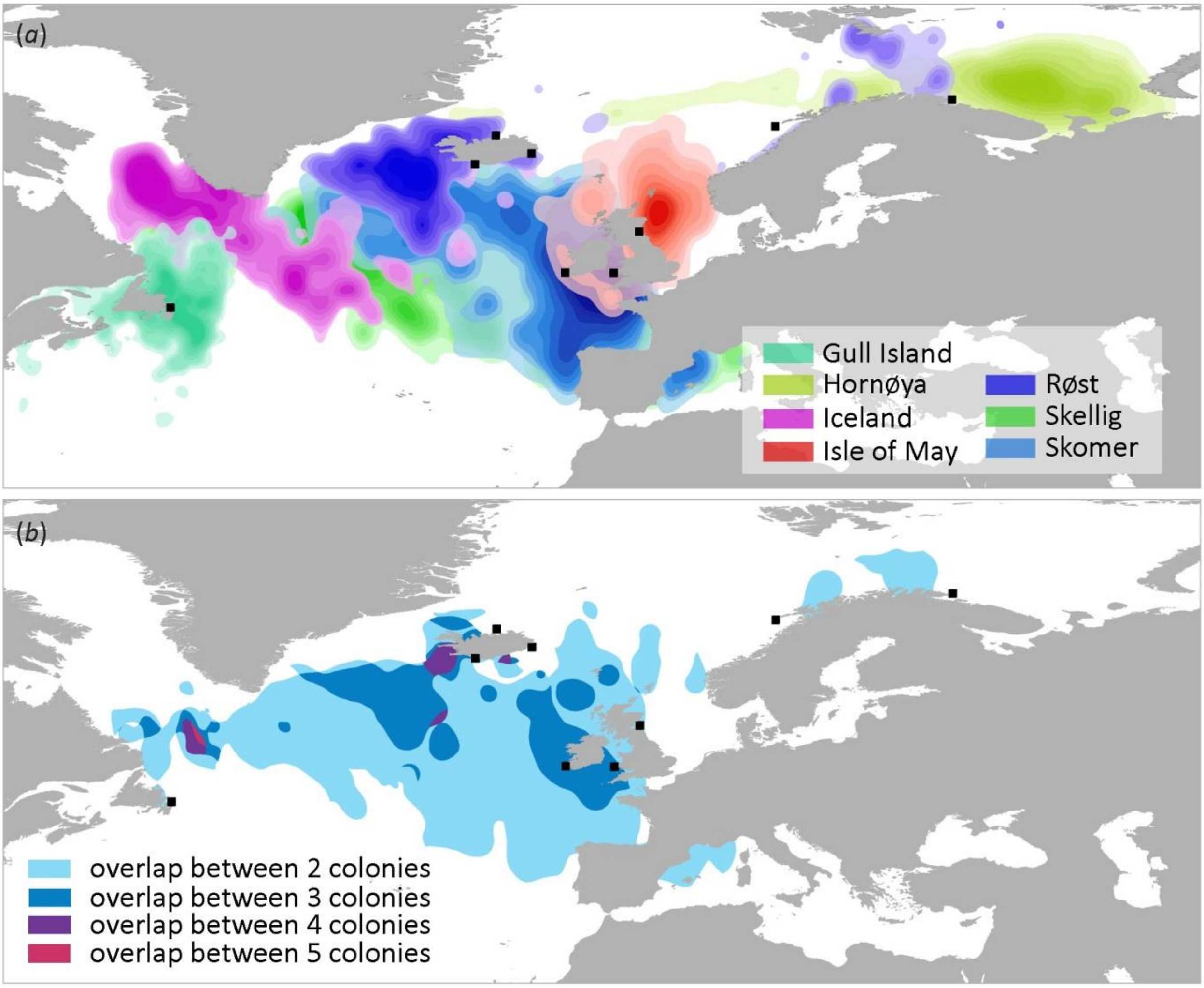

Figure 2. (*a*) Occupancy kernels for each colony across the entire non-breeding season (August to March), with each colony in a different colour. The different shades of a colour indicate different densities of positions (10% to 90%), with darker shades indicating a higher density. (*b*) Overlap between the 90% occupancy kernels of different colonies between 2 (light blue), 3 (dark blue), 4 (purple) or 5 colonies (pink). On both panels colonies are indicated with black squares.

Overlap varied between colonies (Figure 3). Hornøya was the most spatially segregated colony and essentially only overlapped with Røst. The second most segregated was Gull Island in Canada which mainly only overlapped with birds from Icelandic colonies and, for a small part, with Irish birds. In the British Isles the Scottish colony was the most segregated: only 30% of birds left the North Sea to go west of Great Britain and towards the Atlantic, where they overlapped with birds from Ireland and Wales. Ireland and Wales were the least segregated colonies across the whole range, overlapping with all but 1-2 colonies and nearly 60% of their 90% range overlapping with each other. Overlap decreased significantly with distance between the colonies (LM, n = 21, $F_{1,19}$ = 8.2, P = 0.009), however this overall trend does not hold for all colonies. For example, Røst shows almost the opposite pattern, with overlap increasing with distance between colonies, while Iceland did not overlap with its closest colony, the Isle of May in Scotland.

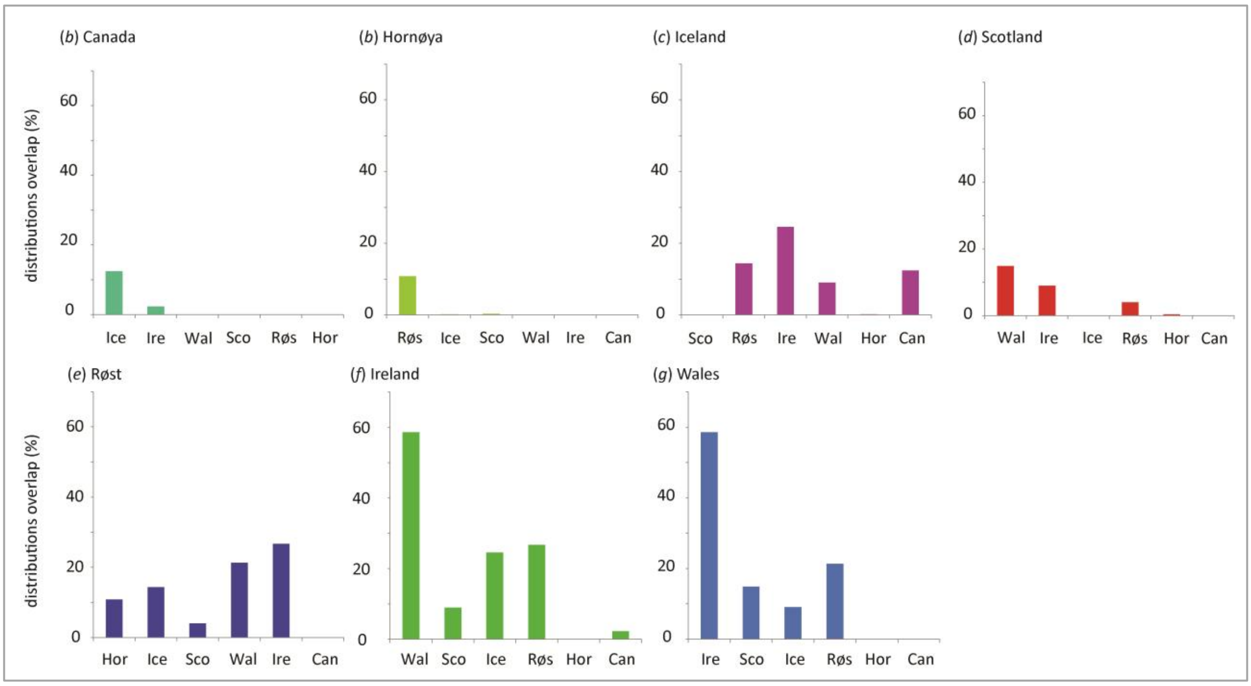

Figure 3. Percentage of overlap between 90% occupancy kernels between each colony, ordered along the x-axis by distance from the focal colony.

The distributions of birds from each colony were not constant but varied throughout the winter (Figure 4), and so did the overlap between them (Figure 5). Overlap between colonies was highest during the first part of the non-breeding season (August-November) when birds from many colonies gathered in the central and west Atlantic and around Iceland. From December-January onwards overlap decreased between colonies, with most colonies being spatially segregated from others, apart from Ireland and Wales which had very similar distributions to each other all year round.

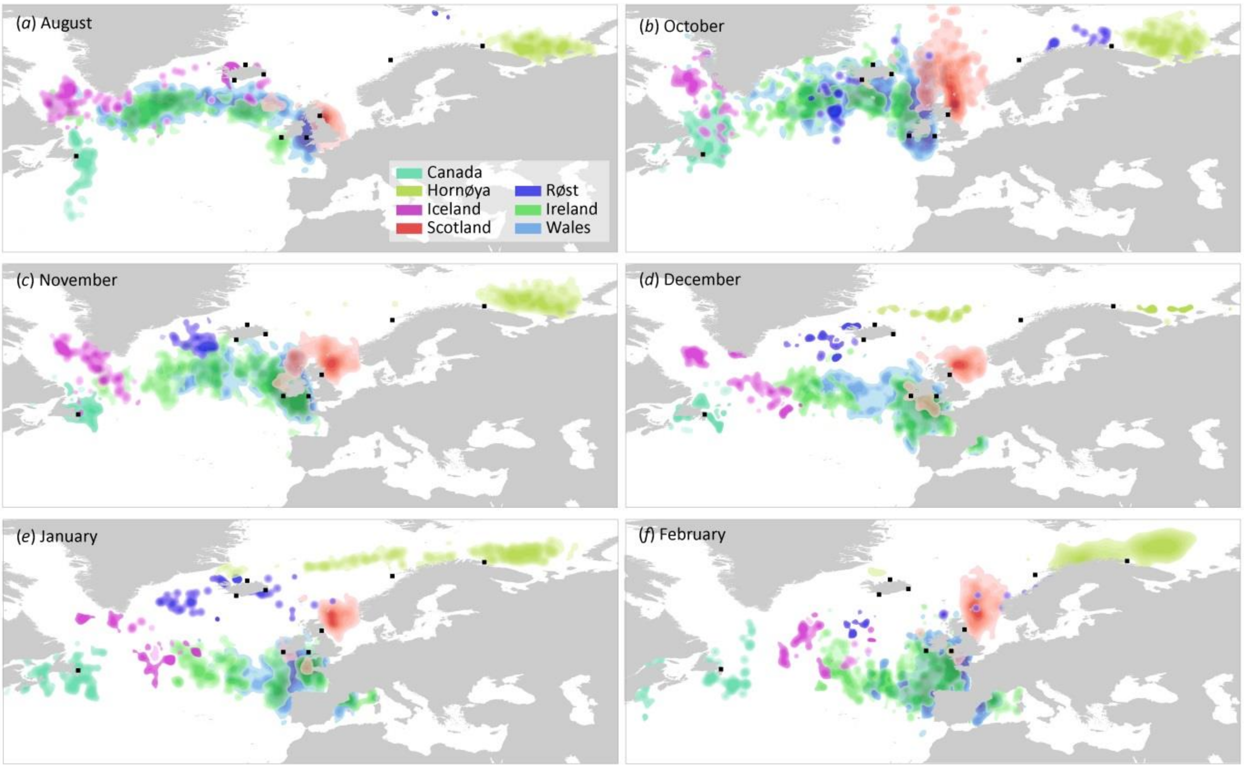

Figure 4. Monthly occupancy kernels for each colony across the non-breeding season, with each colony in a different colour. Different shades of one colour indicate different densities of birds (10% to 90%), with darker shades indicating a higher density. The months of September and March are not presented as most of the data are unusable due to large errors around the equinox. Colonies are indicated with black squares.

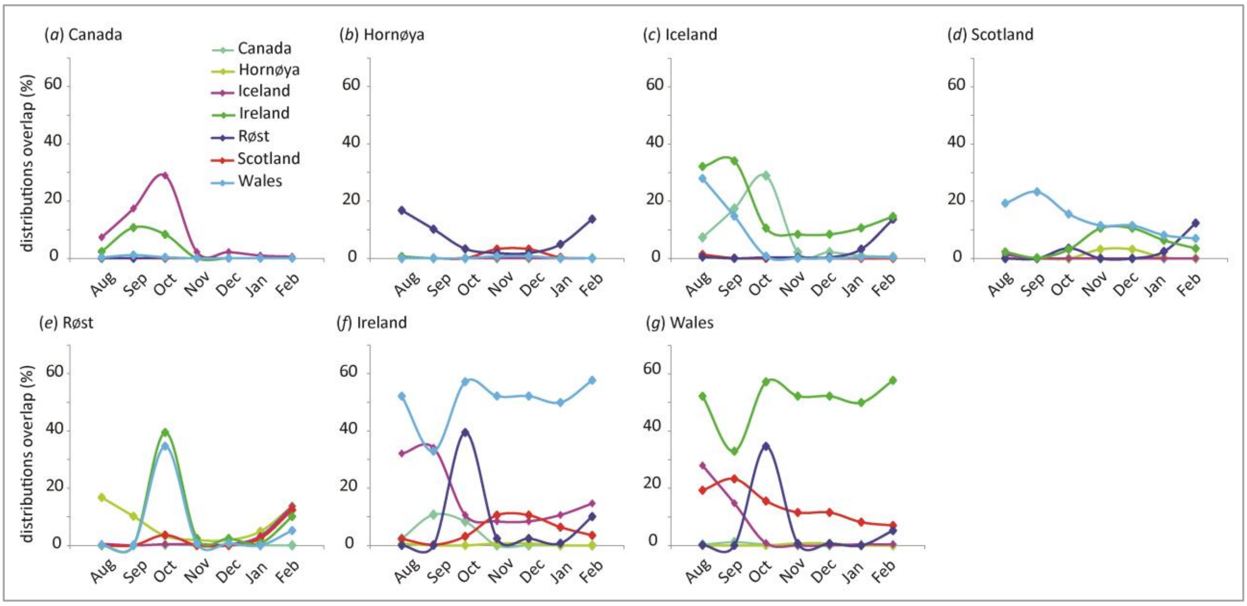

Figure 5. Monthly proportion of overlap between 90% occupancy kernels between each colony. Each colony is represented with a different colour.

Individual variation in migratory route

Individual routes varied between colonies but also between individuals from the same colony (Figure S3). Canadian puffins from Gull Island remained relatively locally, staying around Newfoundland, some birds also migrating further South later in the winter but staying relatively close to the coast. In Hornøya most birds stayed near the colony all winter, reaching western latitudes as far as Røst, but ~ 15% ventured further west, some as far as North Iceland, with one bird even going as far as southwest Greenland. Røst puffins seemed to visit the Barents Sea first at the start of the non-breeding season, then to fly further west and to spend substantial amounts of time southwest of Iceland. Icelandic puffins all went west towards the south and west of Greenland and ~90% visited the Labrador Sea. Many birds from the Isle of May in Scotland either stayed in the North Sea or further North, but ~ 35% went around the UK towards western Ireland during the second part of the winter; one bird ventured to the central North-Atlantic. Irish birds also seemed to follow one of two strategies, all going to the mid- or west Atlantic Ocean first, then either returning towards Ireland or the Bay of Biscay, or going to the Mediterranean Sea (~12%). Birds from Wales had a very similar distribution of routes to Irish birds: ~ 50% of birds visited the mid- or west-Atlantic during the first part of the winter, and then returned towards the UK, the Bay of Biscay or, for a smaller proportion, the Mediterranean Sea (~15%). The main difference between Welsh and Irish birds was that ~50% of Welsh birds did not visit the Atlantic and remained locally, while this did not happen for Irish birds.

These differences in migratory routes resulted in a significant difference in the average total distance covered during the winter between colonies (Table 2; LMM: $n = 247$, $\chi_6^2 = 114.7$, $P < 0.001$). On average birds from Hornøya covered a significantly smaller distance than any other colony, while birds from Ireland covered significantly longer distances than any other colony apart from Røst and the Icelandic colonies (see Table S1 for details of pairwise comparisons). Colonies also differed in how far from the colony their birds went on average, even controlling for total distance covered (Table 2; LMM: $n = 247$, $\chi_6^2 = 97.3$, $P < 0.001$). Birds from Scotland stayed closest to the colony (average distance from the colony < 500km), travelling less far than all other colonies except Canada and Hornøya. On average birds from

Iceland stayed significantly further from the colony (> 1,700km on average) than birds from all other colonies except Røst (see Table S2 for details of pairwise comparisons).

Table 2. Characteristics of migratory routes of puffins from different colonies. Means ± SE.

	Canada	**Hornøya (Norway)**	**Iceland**	**Ireland**	**Scotland**	**Røst (Norway)**	**Wales**
Total distance covered (km)	4445 ± 473	2266 ± 131	6124 ± 491	6810 ± 306	5384 ± 211	7399 ± 842	5686 ± 164
Average distance from colony (km)	527 ± 46	599 ± 83	1759 ± 54	1143 ± 63	496 ± 25	1600 ± 172	904 ± 44

Within-colony route similarity varied significantly between colonies (LMM: n = 251 tracks (7588 pairs), χ_6^2 = 903.4, P < 0.001). Birds from Scotland and Hornøya had the most similar routes within-colony (lowest NND), while the Welsh and Irish colonies had the least, i.e. there was a higher diversity of routes in birds from these colonies. We compared within-individual route similarity (i.e. route fidelity) for the 3 colonies on which birds had been tracked multiple times (Ireland, Hornøya and Wales) to within-colony route similarity. We found that within-individual NND was significantly smaller than between-individual NND from the same colony (within-individual NND = 369.4 ± 16.1 km, between-individual NND = 707.9 ± 4.6 km; LMM: n = 183 tracks (6789 pairs), χ_1^2 = 21.3, P < 0.001); indicating that birds' routes were more similar to their own routes in other years than to other birds' routes from the same colony. There was no significant difference between the degrees of individual route fidelity between the 3 colonies (LMM: n = 115 tracks (150 pairs), χ_2^2 = 0.74, P = 0.688).

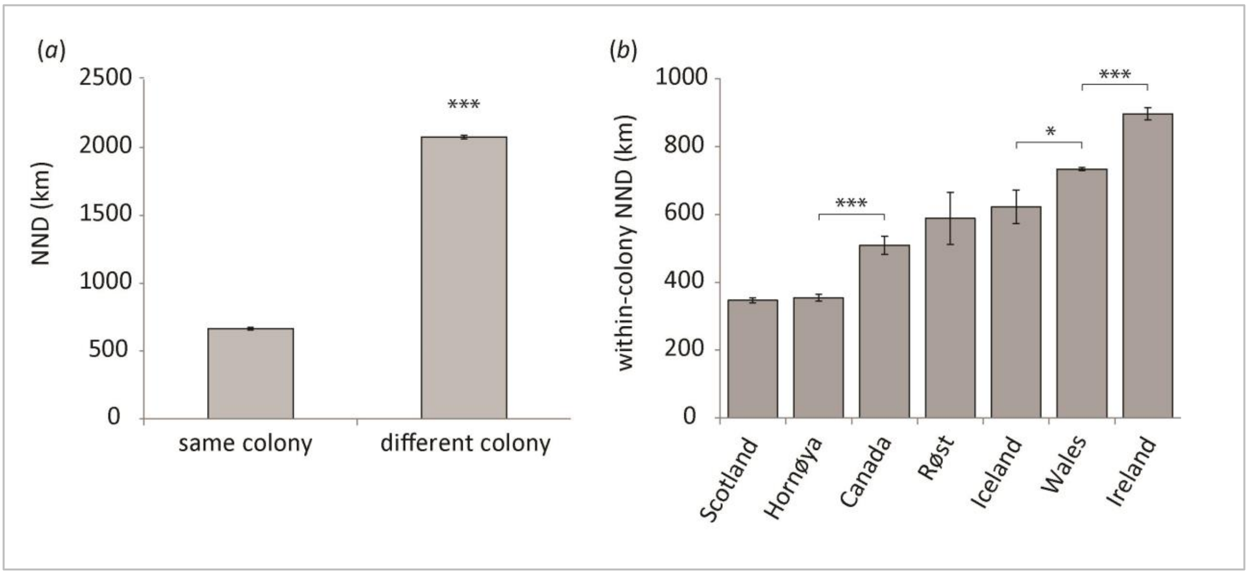

Figure 6. (*a*) NND (the inverse of route similarity) within and between colonies, averaged over all colonies. (*b*) Within-colony NND for each colony, in growing order. Means ± SE. Asterisks represent significant differences between consecutive bars (*: $P < 0.05$; ***: $P < 0.001$).

At-sea behaviour

We compared the activity budgets during daylight between colonies (Table 3). We found significant differences in the total length of time spent engaged in each activity (LMMs, $n = 207$, sustained flight: $\chi_6^2 = 98.9$, $P < 0.001$; foraging: $\chi_6^2 = 74.7$, $P < 0.001$; sitting on the surface: $\chi_6^2 = 161.9$, $P < 0.001$). However, the number of daylight hours that birds from different colonies were exposed to varied, presumably affecting the opportunity to engage in certain behaviours. Hornøya birds spent the winter in areas with significantly longer nights than other colonies, with days almost 3h shorter than for birds from Scotland, which had the longest days.

To correct for difference in day length we also compared the proportion of daylight hours spent in each activity between colonies, and found that the previous results held despite the correction for daylength (LMMs, $n = 236$, sustained flight: $\chi_6^2 = 123.4$, $P < 0.001$; foraging: $\chi_6^2 = 126.9$, $P < 0.001$; sitting on the surface: $\chi_6^2 = 145.5$, $P < 0.001$). Irish birds spent by far the most time in sustained flight (over 11% of their day on average), unlike Scottish and Welsh puffins which spent very little time in prolonged flight (3.2 % and 2.6% of their time on average). All other colonies spent 6-8% of daylight hours flying. On average Norwegian and Irish birds spent more time foraging than others, with Røst birds foraging for over

43% of daylight hours on average, contrasting with birds from Canada and Wales which spent approximately half as much time foraging. These differences were naturally reflected in the time spent sitting on the water surface, with Welsh birds resting the most (nearly 80% of their daylight hours) and Røst birds the least (48% of their day).

Table 3. Activity budgets of puffins from different colonies. The proportions of time represents the percentage of daylight hours spent engaged in a particular behaviour, while total time represents the number of hours spent in this behaviour over the whole non-breeding season (1st August to the 1st March). The average day length (number of daylight hours) during the non-breeding season is indicated in the first row. Means ± SE.

	Canada	**Hornøya (Norway)**	**Iceland**	**Ireland**	**(Scotland**	**Røst (Norway)**	**Wales**
Average day length (h)	10.8 ± 0.5	8.1 ± 0.9	10.8 ± 2.3	10.6 ± 0.9	11.0 ± 0.4	10.1 ± 1.3	11.0 ± 1.3
Proportion time in flight (%)	7.4 ± 2.8	6.3 ± 4.1	7.9 ± 4.0	11.7 ± 5.6	3.2 ± 2.1	8.1 ± 4.3	2.6 ± 2.6
Total time in flight (h)	166 ± 60	122 ± 84	208 ± 112	303 ± 145	86 ± 60	191 ± 73	75 ± 114
Proportion time foraging (%)	21.7 ± 8.7	37.4 ± 9.9	24.3 ± 11.7	37.5 ± 9.9	25.2 ± 9.2	43.7 ± 2.3	18.3 ± 6.7
Total time foraging (h)	561 ± 255	705 ± 237	635 ± 318	968 ± 285	672 ± 249	1070 ± 131	481 ± 183
Proportion time resting (%)	70.9 ± 9.0	56.4 ± 10.9	67.8 ± 11.9	50.8 ± 13.2	71.6 ± 9.6	48.1 ± 5.2	79.2 ± 7.8
Total time resting (h)	1825 ± 257	1077 ± 242	1766 ± 492	1301 ± 339	1922 ± 280	1190 ± 270	2094 ± 274

Environmental conditions

There were significant differences in NPP (LMM, $n = 31478$, $\chi_6^2 = 188.2$, $P < 0.001$), SST (LMM, $n = 33326$, $\chi_6^2 = 572.3$, $P < 0.001$) and chlorophyll a levels (LMM, $n = 16841$, $\chi_6^2 = 209.3$, $P < 0.001$) encountered by birds from different colonies during the winter (see Figure 7 (*c*-*e*) for individual differences between colonies).

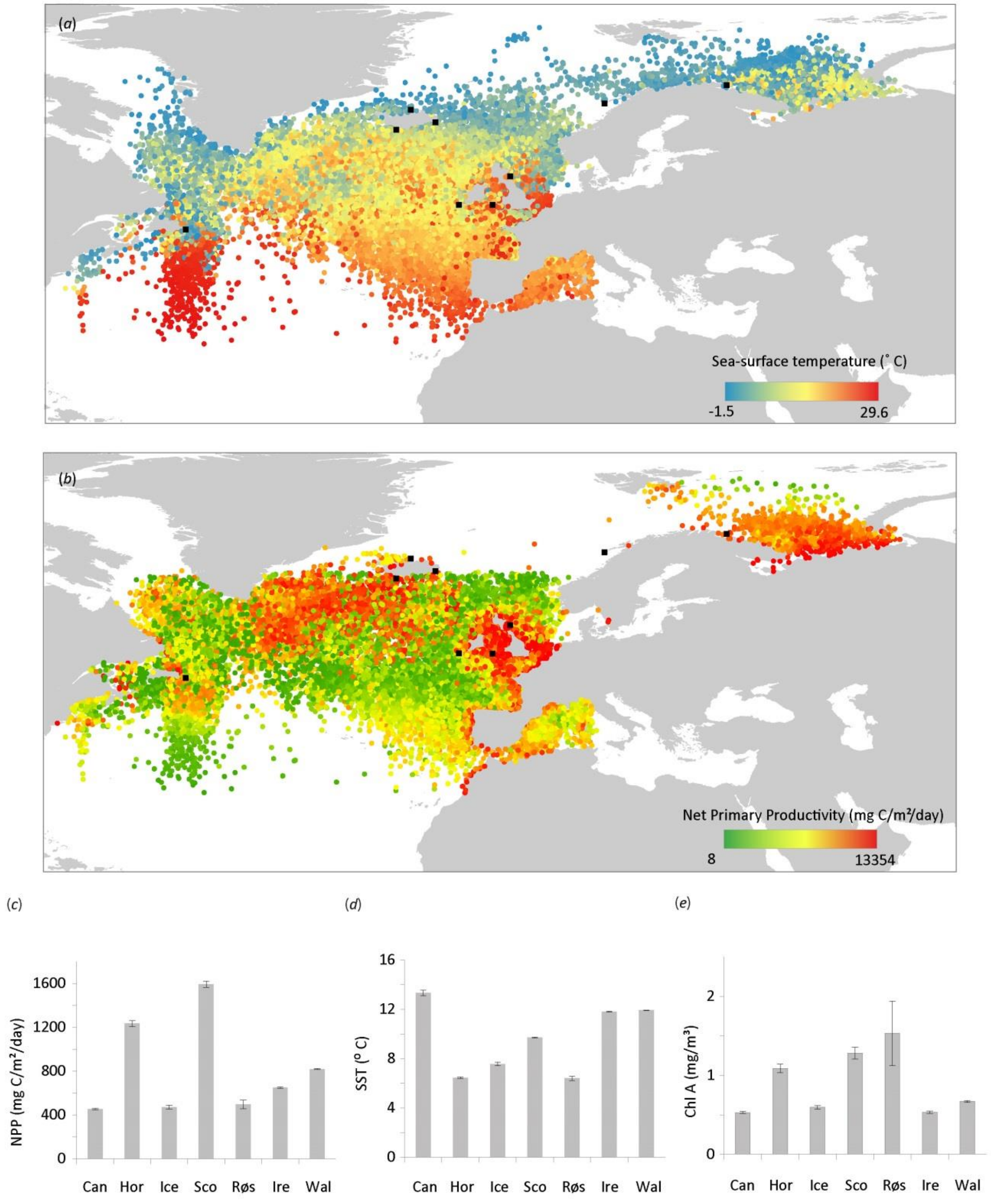

Figure 7. Maps representing the levels of SST (*a*) and NPP (*b*) encountered by all puffins on their migration (positions across the entire non-breeding season). (*c*-*e*) Average levels of NPP, SST and chlorophyll A experienced by birds of different colonies over the winter (means ± SE).

We tested whether environmental variables influenced the at-sea activity budget of birds (regardless of their colony), and varied with distance from the colony (Table 4). The daily proportion of time spent foraging (proportion of daylight hours) significantly increased with NPP but decreased with SST. In other words, birds in more productive areas, and in colder waters, spent a larger proportion of their day foraging. On the contrary, the daily proportion of time spent sitting on the water significantly increased with SST (birds in colder waters sat less), but there was no relationship with NPP. There was no significant effect of environmental variables on the proportion of time in flight. We found similar results when using the total amount of time engaged in an activity over the whole winter (regardless of the length of day), although NNP no longer had a significant effect. There was a negative relationship between NPP and the average distance from the colony, i.e. birds which stayed further from the colony were visiting less productive waters. Finally, there was no significant effect of chlorophyll A on any variable.

Table 4. Relationships between environmental variables and at-sea behaviour for all birds (LMMs, random effects: individual identity, year and colony). p.e. = parameter estimate. Significant relationships (*P* < 0.05) are in bold.

	NPP (mg C/m^2/day)	**SST (° C)**	**Chlorophyll A (mg/m^3)**
Proportion time in flight (%) (*n* = 236)	p.e.: -1.0 E^{-5} ± 2.1 E^{-5} X_1^2 = 0.25, *P* = 0.615	p.e.: -5.1 E^{-3} ± 2.7 E^{-3} X_1^2 = 0.83, *P* = 0.363	p.e.: -1.5 E^{-2} ± 1.8 E^{-2} X_1^2 = 0.67, *P* = 0.415
Proportion time foraging (%) (*n* = 236)	**p.e.: 5.4 E^{-5} ± 2.5 E^{-5}** **X_1^2 = 4.3, *P* = 0.038**	**p.e.: -0.015 ± 0.003** **X_1^2 = 19.6, *P* < 0.001**	p.e.: -0.035 ± 0.021 X_1^2 = 2.8, *P* = 0.093
Proportion time sitting (%) (*n* = 236)	p.e.: -7.3 E^{-5} ± 4.5 E^{-5} X_1^2 = 2.7, *P* = 0.103	**p.e.: 2.4 E^{-2} ± 6.2 E^{-3}** **X_1^2 = 17.0, *P* < 0.001**	p.e.: 6.1 E^{-2} ± 3.6 E^{-2} X_1^2 = 2.8, *P* = 0.095
Total time in flight (h) (*n* = 207)	p.e.: -4.8 E^{-4} ± 1.2 E^{-3} X_1^2 = 0.19, *P* = 0.667	**p.e.: 0.011 ± 0.166** **X_1^2 = 5.1, *P* = 0.024**	p.e.: -0.83 ± 1.01 X_1^2 = 0.61, *P* = 0.432
Total time foraging (h) (*n* = 207)	p.e.: 0.001 ± 0.001 X_1^2 = 0.58, *P* = 0.447	**p.e.: -0.39 ± 0.19** **X_1^2 = 10.1, *P* = 0.002**	p.e.: -1.49 ± 1.16 X_1^2 = 1.7, *P* = 0.192
Total time sitting (h) (*n* = 207)	p.e.: -0.001 ± 0.001 X_1^2 = 0.85, *P* = 0.355	**p.e.: 0.72 ± 0.18** **X_1^2 = 21.9, *P* < 0.001**	p.e.: 0.97 ± 1.0 X_1^2 = 0.88, *P* = 0.348
Average distance from the colony (km) (*n* = 252)	**p.e.: -4.0 E^{-4} ± 1.0 E^{-4}** **X_1^2 = 13.3, *P* < 0.001**	p.e.: -9.8 E^{-3} ± 1.4 E^{-2} X_1^2 = 1.8, *P* = 0.178	p.e.: -4.1 E^{-2} ± 9.1 E^{-2} X_1^2 = 3.2, *P* = 0.075

Finally, we found a strong negative relationship between the average SST experienced by birds from a colony, and the latitude of this colony (LM, n = 7, parameter estimate = 0.28 ± 0.02, $F_{1,5}$ = 152, $P <$ 0.001). In other words birds from more northern colonies foraged in colder waters (Figure 8a).We tested whether this had an effect on the average foraging effort of birds from a colony. We found a positive, but non-significant, relationship between the average proportion of time spent foraging by birds from a colony and its latitude (LM, n = 7, parameter estimate = 0.0.2 ± 0.01, $F_{1,5}$ = 2.6, P = 0.167, Figure 8b).

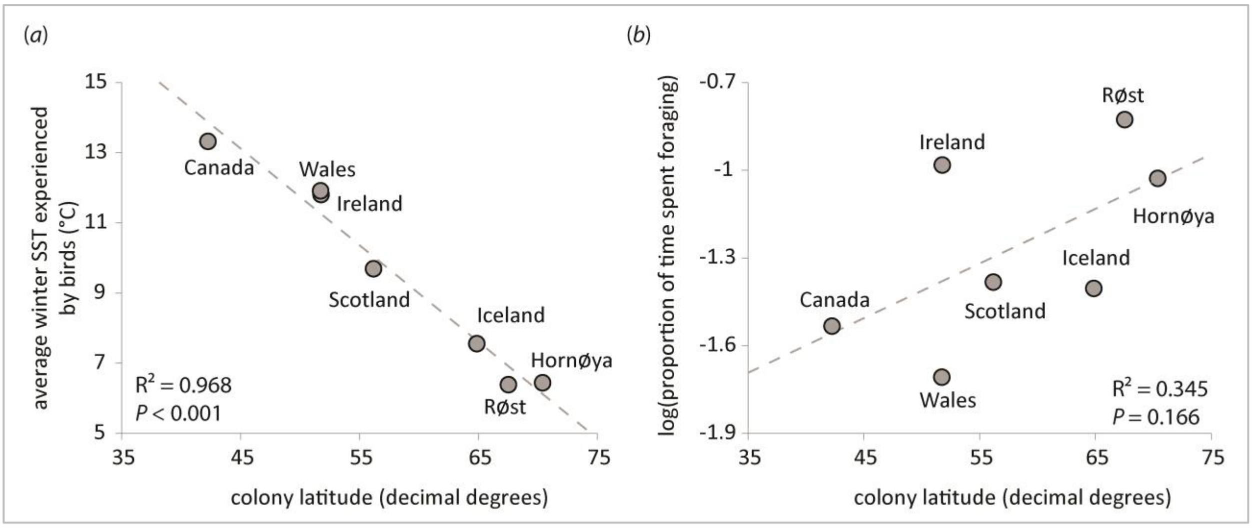

Figure 8. Relationship between colony latitude and (*a*) the average SST experienced by birds from this colony overwinter and (*b*) the average proportion of daylight hours spent engaged in a foraging-related activity overwinter. Regression lines (dashed grey lines) and R^2 and P values are obtained from linear models.

Discussion

In this study we compared the winter distributions of Atlantic puffins from 9 colonies across their breeding range, using a large tracking dataset collected over an 8-year period, including novel data from 6 colonies. We found differences among colonies in the distributions and activity budgets of overwintering birds, and in the environmental conditions they were experiencing.

Although the colonies' distributions overlapped, there was a substantial amount of segregation between colonies. The core occupancy areas (50%) of most colonies did not overlap at all, apart from two colonies in the UK (Ireland and Wales) which had very similar distributions, and a few very restricted overlaps.

Overall, overlap between colonies decreased with the distance between them, with a few exceptions (e.g. Røst). However this was not a result of birds staying close to their colony. In fact, the scale of the migratory journeys varied strikingly between colonies, without following obvious longitudinal or latitudinal patterns: birds from colonies such as Iceland or Røst covered long distances during the winter, while birds from other colonies like Hornøya stayed mostly locally. The differences in the size of the wintering range were not a simple effect of sample size, for example there were almost 8 times as many birds tracked from Hornøya than from Røst. The complex patterns observed, and large differences in migratory strategies between colonies (differences in range, destinations and route diversity) are unusual for seabirds. Species often share one (Guilford et al. 2009; Fort et al. 2012; Freeman et al. 2013) or a few wintering sites (Frederiksen et al. 2011; Tranquilla et al. 2013), apart from perhaps albatrosses which also tend to show highly dispersive migration (Weimerskirch et al. 2000; Croxall et al. 2005; Phillips et al. 2005). By looking at the overlaps between colonies, two areas appear to be of particular attraction to many puffins: southwest of Iceland, and south of Greenland near the Labrador Sea. There is evidence from tracking studies and at-sea surveys that both areas are hotspots for other seabirds and marine species (Gardarsson 1999; Boertmann 2011; Frederiksen et al. 2011; Montevecchi et al. 2012). This is most likely because of highly productive waters (Bennison and Jessopp 2015), which we can also see in our dataset (Figure S4).

In addition to differences in distributions, we found differences in within-colony route similarity. In some colonies (e.g. Scotland, Canada) birds mostly followed similar routes, while in others (Ireland, Wales) routes largely diverged. The potential drivers of dispersion have been investigated on the Welsh colony in Chapter 2, and we found evidence for fitness differences between different routes, suggesting that some routes were better than others, or followed by birds of higher quality. The mechanisms leading to the striking differences we observed between colonies, however, remain unclear. Several explanations could be considered. First, this may be a consequence of density-dependent competition. Higher competition may deplete prey resources near colonies and lead birds from larger colonies to exploit more distant areas and spread more (Alerstam et al. 2003). This is an adaptation of Ashmole’s hypothesis for migratory, non-central place foraging behaviour. This hypothesis predicts that during the breeding season, central-place foraging birds from larger colonies are forced to forage further from the colony because the area around the colony (the Ashmole's halo) has poor resource availability (Ashmole 1963; Ballance et al. 2009). Although our sample size (*n* = 7 colonies) is too small to test this theory formally, it seems unlikely to explain our results. This hypothesis fits the two largest colonies in our dataset, Iceland (which counts over 3 million pairs of puffins across all colonies, Hansen et al. 2011; Harris and Wanless 2011) and Røst, whose birds wintered the furthest from the colony. However these two colonies only had an intermediate within-colony route similarity (i.e. most birds followed similar routes). Furthermore, the hypothesis of density-dependent competition does not fit the other 5 colonies. For example Ireland, the smallest colony (<15,000 pairs, Harris and Wanless 2011) had the highest within-colony NND (i.e. low route similarity) and Irish birds wintered twice as far from their colony as birds from Canada, which come from an archipelago with 500,000 pairs (D. Fifield, personal communication, Harris and Wanless 2011) but showed a significantly lower within-route diversity. Second, route diversity may be driven by environmental conditions near the colony in winter. Birds from colonies where winter conditions are good may remain in the area (which automatically increases their chance of following similar routes), while birds from colonies with poor winter resources are forced to winter further, and possibly explore different areas, leading to wider ranges and different routes. Although at the time of writing this chapter we did not have sufficient data to test this hypothesis, the differences in NPP experienced by birds from different colonies and the negative relationship between NPP and average distance from the colony suggest that it is a likely explanation. For instance, birds from the two colonies with the highest within-colony route similarity, which also have two of the smallest average wintering distances from the colony, winter in the most productive waters.

This raises the question of why Icelandic birds seem to avoid the seabird hotspot visited by puffins from, amongst others, Wales, Ireland and Røst, and which looks like a productive area from our NPP data (Figure 7b), despite its proximity to Iceland. Indeed all 8 Icelandic puffins wintered in the Labrador Sea and in the Davis Strait. Despite the small sample size, this suggests that at least a proportion of Icelandic puffins (which represent > half of the puffin world population) do not visit this hotspot. We suggest that it may be a consequence of local adaptation. Like many animals (Blackburn et al. 1999), puffins follow the Bergmanns' rule and their body size increases with latitude (Blackburn et al. 1999; Harris and Wanless 2011). For instance in our study Icelandic birds were ~20% heavier, and Hornøya birds ~35% heavier, than Welsh birds. The metabolic rate, and therefore the energy expenditure, of puffins from northern colonies should be higher than that of more southern birds, because of their larger body size, and of their exposure to lower temperatures requiring additional energy for thermoregulation (Whittow and Rahn 1984). This should result in an increased foraging effort to catch sufficient prey to compensate for the higher energy demands. Our results support this prediction. First, although the positive relationship we found between colony latitude and proportion of time spent foraging was not significant (perhaps because of the small sample size, n = 7 colonies), we found that birds in colder waters spent significantly more time engaged in foraging-related activity and, consequently, significantly less time sitting on the water. Second, we found a significant negative relationship between the latitude of a colony and the averaged SST experienced overwinter by birds from this colony; this indicates that regardless of how far birds go in the winter, the higher the latitude of their colony, the colder the water they will migrate to. Taken together, these results show that (larger) birds from more northern colonies overwinter in colder waters, where they spend more time foraging. Whilst the higher foraging effort is likely a result of higher energy requirements, the fact that they visit colder waters could have several explanations. First, colder waters may be more productive, but the benefit of foraging in these areas may only outweigh the additional cost incurred by thermoregulation in large birds from northern colonies, which have adapted to cold temperatures. Second, birds may have an optimum window of temperatures for foraging and overwintering, outside of which they may spend too much energy thermoregulating or suffer heat stress (Dawson and Hudson 1970). The former hypothesis seems unlikely to explain why Icelandic birds did not visit the southwestern Icelandic hotspot but went to the Labrador Sea and Davis Strait instead. Indeed, although birds from the most northern colony (Hornøya) stayed in more productive areas than most other colonies, birds from Iceland and Røst experienced less productive waters than birds from colonies further south. Furthermore, Iceland birds had a relatively low foraging effort compared Røst and Hornøya, which suggests that they were in less productive waters (productivity was significantly related to foraging effort). Therefore, our findings suggest that the patterns we observed are more likely to result from local adaptation to temperature. However more data for Icelandic colonies and Røst, unavailable at the time of writing, would be needed to confirm this hypothesis. Similar latitudinal patterns were observed in guillemots *Uria spp.*, where birds from more northern colonies wintered at higher latitudes (Tranquilla et al. 2013), but other less closely-related species visited similar wintering regardless of the latitude of their colony (Frederiksen et al. 2011; Fort et al. 2012).

Colony distributions varied significantly throughout the winter. Overlap between colonies was highest during the first part of the winter (until November-December) and later decreased. From December onwards most colonies were almost completely segregated, apart from the Welsh and Irish colonies which had very similar distributions all winter. In addition to the distributions themselves, the temporal variations of the birds' distribution over the non-breeding season are also interesting. Variability changed between colonies, with some showing little variation over time (e.g. Canada) and others making major movements half-way through the winter. For example in December-January some birds from Hornøya took a long westward movement towards Iceland, while some puffins from Ireland travelled from the central Atlantic to the Mediterranean Sea. The reasons behind these movements are unclear, especially because they are only undertaken by a proportion of birds. The synchrony of these movements between birds suggests that they may be responding to local changes in environmental conditions. In Chapter 2 we showed that Welsh birds visiting the Mediterranean Sea spend more time foraging during their visit (than other birds during that time) and have a higher breeding success on their return to the colony. Influences of migratory strategies on fitness have also been documented in other species (Reynolds et al. 2011; Alves et al. 2013; Weimerskirch et al. 2015). Although we currently do not have the data to test this hypothesis, differences similar to that observed in Skomer birds may occur in other colonies. A more detailed analysis of differences in behaviour and local conditions between different routes across the whole breeding range, combined with information on breeding success, could help understand the drivers of such movements and their fitness consequences. It is however beyond the scope of this study.

Nevertheless, determining how differences in migratory strategies can shape the fitness landscape of a colony, and perhaps of a whole population, is paramount to understanding the population dynamics of colonies. This is particularly relevant in puffins, which have seen steady population declines in the last few decades on some colonies, for reasons still partly unclear, which lead to their new classification on the IUCN European Red List as “endangered” (European Red List of Birds 2015). For example, puffins on Røst have had extremely variable breeding success in the last few decades (Durant et al. 2003), while puffins from Wales showed consistently high breeding success during the study period (Skomer seabird monitoring reports 2008-2015). On Røst, there is evidence that sea-surface temperature and salinity around the colony before and during the breeding season negatively affect fledging success (Durant et al. 2003; Durant et al. 2006), similar finding were also found in kittiwakes breeding in Norway (Sandvik et al. 2014). However, this does not exclude the possibility that winter conditions also affect the birds’ reproductive success. Puffins from Røst spent more time engaged in foraging-related activity than birds from any other colony, while Welsh birds had the lowest foraging effort. Although it is too early to connect the two observations, such differences during the winter may affect population dynamics and colony productivity. Furthermore, if resources are depleted in a wintering area used by a large number of birds, many colonies may be affected during the summer (Reynolds et al. 2011). Increase in SST along the Norwegian coast has been shown to be associated with population declines of kittiwakes (Sandvik et al. 2014); similarly, changes in environmental conditions may have a detrimental effect on puffins. For instance if the hypothesis of local adaptation discussed earlier is correct, puffins from northern colonies may become gradually more restrained in the wintering areas they can exploit. The high within-individual fidelity to a migration route, already established in Welsh puffins in Chapter 2 and now found in the two additional colonies for which data were available, suggests that birds - at least adults - have limited flexibility in their migratory strategy. However it is unknown whether this would increase their vulnerability to sudden changes of their environment, or on the contrary, whether this could potentially increase population flexibility over a genetically determined overwintering strategy (individually established inflexibility is generally a sign of learning based strategies).

In summary, our study revealed for the first time the global winter distribution of puffins and the complexity of colony-specific migratory patterns. Colony size was not an important driver of colony distribution, but resource availability in winter around the colony may affect how dispersive and far ranging birds will be. SST was an important driver of distributions, with birds constrained to a temperature zone by the latitude of their colony, perhaps as a result of local temperature adaptation. At the time of writing, it was not possible to access data on weight and therefore to estimate daily energy expenditure for different colonies (it requires weight-adjusted calculations using allometric equations, Shaffer 2011). Similarly, data on breeding success was unavailable for most colonies, thus we cannot yet test the potential fitness consequences of differences in migratory behaviour and environmental conditions. These seem important directions to follow in the future in order to understand the drivers of seabird colony distribution on large oceanic scales but also for their potential conservation implications.

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Supplementary Material

Supplementary Figures S1 – S4

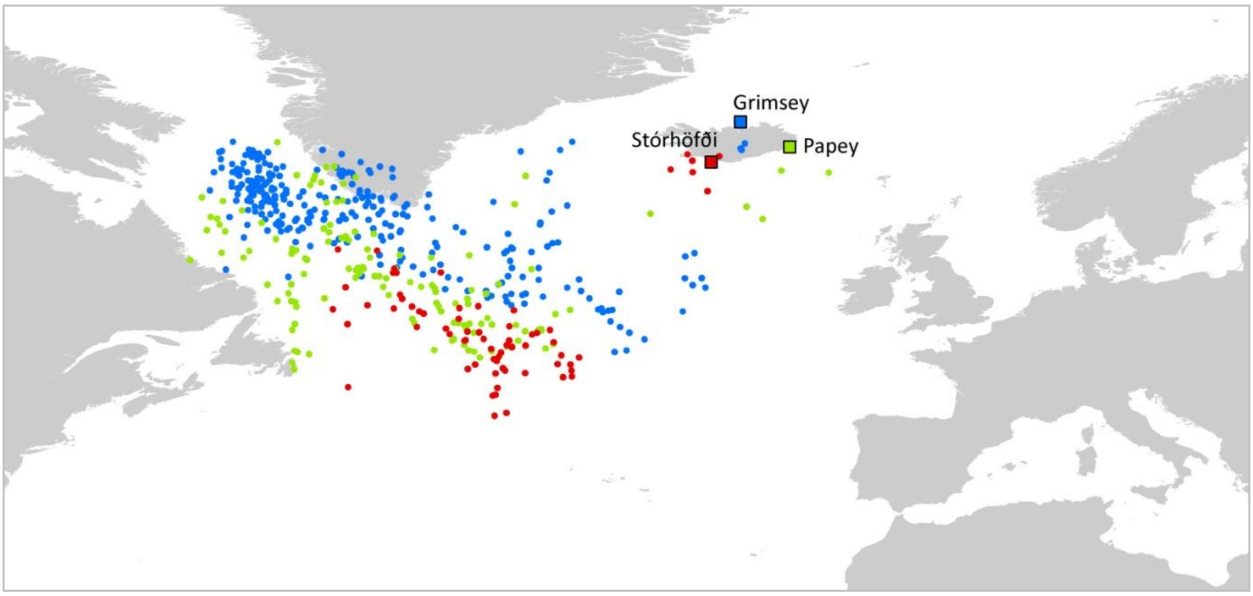

Figure S1. Migratory tracks of 8 puffins breeding on 3 different colonies in Iceland. Each colour represents birds from a different colony (blue: Grimsey, *n* = 4; green: Papey, *n* = 3; red: Stórhöfði, *n* = 1). Colonies are indicated with a square. Because of the small sample sizes, the proximity between colonies and the similarity of the tracks, all 8 tracks were pooled together for the analysis.

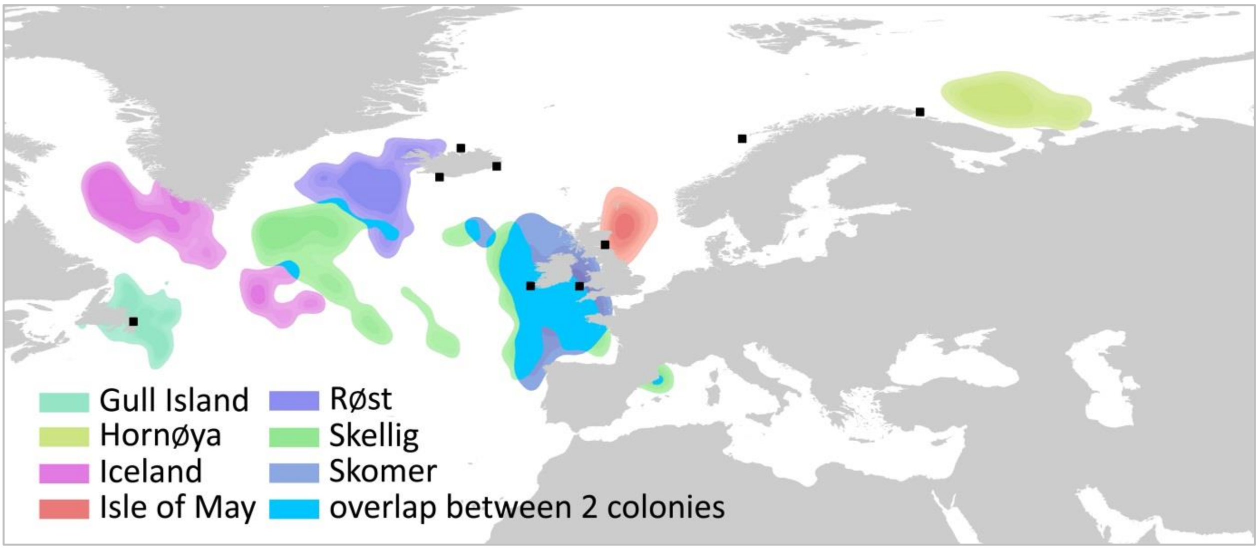

Figure S2. 50% occupancy kernels for all 7 colonies (semi-transparent), and their overlap (bright blue). The only colonies overlapping at the 50% level are Ireland with Iceland, Røst and Wales (separately).

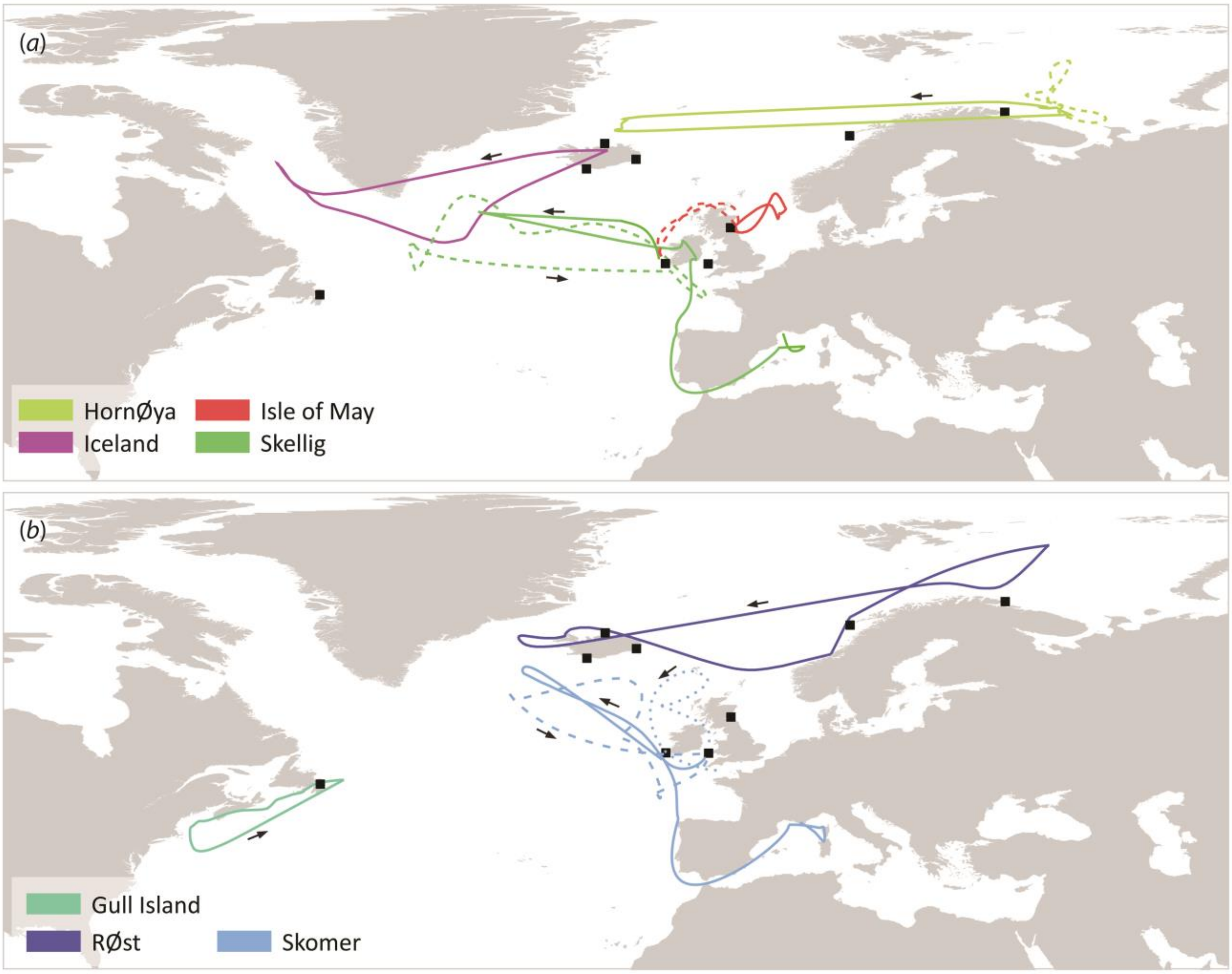

Figure S3. Example tracks from all colonies. For colonies with higher route diversity, 2-3 typical tracks are shown (using continuous, dashed, or dotted lines to differentiate each route). Smoothed trajectories between weekly medians from August to March. The tracks going to the Mediterranean Sea were modified to go around Iberia instead of straight across (puffins do not fly far over land).

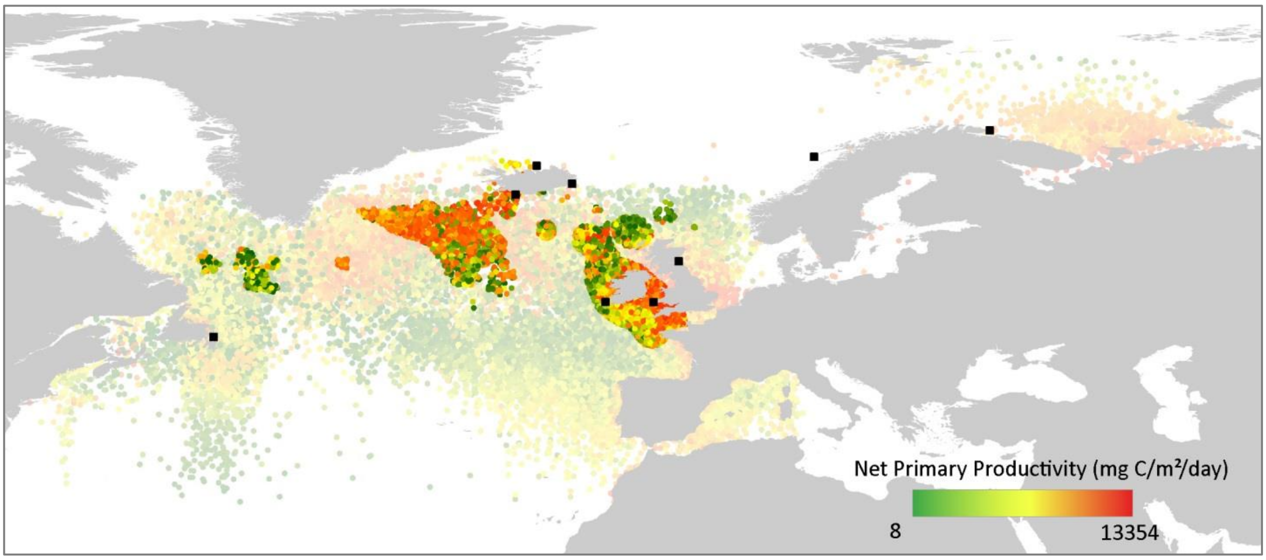

Figure S4. Net primary productivity in the puffin "hotspots", areas where the 90% occupancy kernels of at least 3 colonies overlapped. The productivity in the rest of the range is in semi-transparent to allow for comparison.

Supplementary Tables S1 – S2

Table S1. Pairwise comparisons of the average length of the migratory journey between colonies (obtained with a post-hoc test using {lsmeans}; *P*-values are adjusted for multiple comparisons).

colonies	**estimate**	**SE**	**df**	***t***	***P*-value**
Canada - Hornøya	1659.065	495.785	205.9	3.346	0.0136
Canada - Iceland	-1678.53	649.847	197.73	-2.583	0.1157
Canada - Ireland	-2431.12	559.335	163.73	-4.346	< 0.001
Canada - Scotland	-676.105	588.637	82.28	-1.149	1
Canada - Røst	-2835.23	936.166	103.79	-3.029	0.0372
Canada - Wales	-1263.38	516.981	145.4	-2.444	0.1453
Hornøya - Iceland	-3337.6	611.825	208.88	-5.455	< 0.001
Hornøya - Ireland	-4090.19	377.692	199.91	-10.829	< 0.001
Hornøya - Scotland	-2335.17	447.667	76.26	-5.216	< 0.001
Hornøya - Røst	-4494.29	852.05	102.92	-5.275	< 0.001
Hornøya - Wales	-2922.45	340.342	160.8	-8.587	< 0.001
Iceland - Ireland	-752.588	664.366	190.92	-1.133	1
Iceland - Scotland	1002.429	689.217	124.79	1.454	0.897
Iceland - Røst	-1156.69	1002.464	120.42	-1.154	1
Iceland - Wales	415.1521	629.123	178.62	0.66	1
Ireland - Scotland	1755.018	451.217	106.2	3.89	0.0026
Ireland - Røst	-404.106	857.33	107.24	-0.471	1
Ireland - Wales	1167.741	347.705	155.34	3.358	0.0136
Scotland - Røst	-2159.12	866.87	92.61	-2.491	0.1453
Scotland - Wales	-587.277	382.868	102.3	-1.534	0.897
Røst - Wales	1571.847	835.833	101.03	1.881	0.5033

Table S2. Pairwise comparisons between colonies of the average distance from the colony during migration (obtained with a post-hoc test using {lsmeans}; *P*-values are adjusted for multiple comparisons).

colonies	**estimate**	**SE**	**df**	***t***	***P*-value**
Canada - Hornøya	-0.06976302	0.121009	173.84	-0.577	0.7514
Canada - Iceland	-1.14924979	0.163019	181.67	-7.05	< 0.001
Canada - Ireland	-0.55413319	0.133706	131.76	-4.144	< 0.001
Canada - Scotland	0.146755990	0.126741	77.05	1.158	0.7514
Canada - Røst	-0.91796438	0.219501	157.83	-4.182	< 0.001
Canada - Wales	-0.33788961	0.121883	124.96	-2.772	0.0449
Hornøya - Iceland	-1.07948678	0.155797	192.75	-6.929	< 0.001
Hornøya - Ireland	-0.48437017	0.108702	221.38	-4.456	< 0.001
Hornøya - Scotland	0.216519010	0.101118	104.58	2.141	0.1729
Hornøya - Røst	-0.84820137	0.208269	180.8	-4.073	< 0.001
Hornøya - Wales	-0.26812659	0.093852	193.77	-2.857	0.038
Iceland - Ireland	0.595116610	0.157081	154.22	3.789	0.0022
Iceland - Scotland	1.296005780	0.155101	114.11	8.356	< 0.001
Iceland - Røst	0.231285410	0.233764	160.88	0.989	0.7514
Iceland - Wales	0.811360190	0.149907	152.98	5.412	< 0.001
Ireland - Scotland	0.700889180	0.102743	90.91	6.822	< 0.001
Ireland - Røst	-0.36383120	0.200101	164.1	-1.818	0.2834
Ireland - Wales	0.216243580	0.090203	162.13	2.397	0.1059
Scotland - Røst	-1.06472038	0.201468	153.62	-5.285	< 0.001
Scotland - Wales	-0.48464560	0.088509	101.94	-5.476	< 0.001
Røst - Wales	0.580074780	0.197367	163.71	2.939	0.0339

Chapter 5

Carry-over effects on migration and breeding strategies in a pelagic seabird: an experimental study

Annette L. Fayet, Robin Freeman, Akiko Shoji, Holly L. Kirk, Oliver Padget, Chris M. Perrins, Tim Guilford

Abstract

Long-lived migratory animals must balance the cost of current reproduction with their own condition ahead of a challenging migration and future reproduction. However, whether (and how) the processes by which events in one season can affect the outcome of the subsequent season, called carry-over effects, also affect behaviour during the migratory and non-breeding periods, is unclear. Because of the challenge of studying animals away from their breeding site, most studies to date have only focussed on carry-over effects on reproductive success during the following breeding event, and are mostly observational; very few have attempted to look at the non-breeding period in detail, and even fewer have done so in an experimental setting. Here we investigate the carry-over effects induced by a controlled, bi-directional manipulation of reproductive costs on the migratory, wintering and subsequent breeding behaviour of a long-lived migratory seabird, the Manx shearwater *Puffinus puffinus*. By cross-fostering chicks of different age between nests, we successfully prolonged or shortened the chick-rearing period of 40 pairs by ~25% of the normal chick-rearing duration. We tracked the adults with geolocators for the subsequent year and combined data on their migratory routes and their overwintering locations with a dataset on at-sea activity budgets obtained from high-resolution saltwater-immersion data. We found that all birds cared for their offspring until they reached a normal fledging age, which resulted in birds with a longer breeding period delaying their departure on migration. Birds which put more effort into breeding spent less time at the wintering grounds, where they also spent less time resting daily; the following year they started breeding later and had lighter eggs and chicks, leading to a lower reproductive success. Reduced reproductive effort resulted in less time engaged in energy-demanding activities such as foraging and flight and more time resting during the non-breeding season, but these birds had a similar breeding phenology and success to control birds the following year. Interestingly, birds finishing breeding earlier did not start migrating earlier, which suggests that the timings of migration are mainly limited by external factors rather than internal conditions. Our results shed light on the year-round carry-over effects of breeding on behaviour and fitness in long-lived migratory species, and start revealing how a complex interaction between current and future reproductive fitness, individual condition and external constraints could influence life-history decisions.

Introduction

Animals must weigh the cost of current reproduction against their survival and the cost of future reproduction (Williams 1966). This is especially true in long-lived, K-selected birds which can breed for many years and only raise a small number of offspring at each breeding attempt; this makes the adult's own survival and future ability to reproduce a priority over the success of the current brood. The processes by which the events in one season can affect the outcome of the subsequent season are called carry-over effects, and have been demonstrated in a number of taxa including birds and mammals, but evidence suggests they may also occur in fish, reptiles and invertebrates (Harrison et al. 2011).

Carry-over effects may be exacerbated in migratory species, when the breeding season is followed by a physically demanding and potentially dangerous migratory journey (Alerstam 1990; Gwinner 1990), later on followed by a similar return migration to the breeding grounds. In addition to making the migratory journey more difficult and potentially more dangerous as a result of a poorer body condition, breeding effort may also affect the phenology of migration (Marra et al. 1998). Favourable conditions for the start of migration may be limited in time, and a delayed end of breeding may force animals to migrate in more difficult and dangerous conditions (Richardson 1990; Owen and Black 1991); this could in turn affect their overwinter survival and their body condition at the start of the next breeding season. The timing of departure on migration has been shown to depend on the timing of the end of breeding in some species (Bogdanova et al. 2011; Mitchell et al. 2012; Catry et al. 2013) but not others (Jonker et al. 2011).

Despite a recent increase in studies of carry-over effects, a lot remains to be understood. Many studies are observational (see review in Harrison et al. 2011), which makes it difficult to control for unaccounted parameters. To date there have been few experimental studies, likely because of the challenging involved in manipulating and measuring parental effort. Most experimental studies only investigate the effect of binomial breeding outcomes by inducing breeding failure (Riou et al. 2012; Catry et al. 2013), and so it is unknown whether late breeders would delay their departure on migration or desert their brood. The timing of return migration to the breeding site may also influence the breeding success of animals; many species match their breeding dates to food availability (Ben-David 1997; Regular et al. 2014; Hinks et al. 2015) and early return at the breeding grounds often correlates with higher success (Kokko 1999; Bêty et al. 2003).

In altricial species, feeding young is an important part of the cost of reproduction, and the parents' effort is mediated by their response to the young's demand, which may lead to parent-offspring conflict if the offspring demands more than the parents are ready to give (Trivers 1974). Parent-offspring conflict can be greater earlier in the breeding season when parental investment is small (Coleman et al. 1985), however in migratory species it may also be exacerbated towards the end of the breeding period, when it becomes critical for parents to depart on, or start preparing for, migration, and a delay could have disastrous consequences for future reproduction (Alerstam and Lindström 1990). Then, the benefits of prolonging offspring care may become less than the cost of delaying migration. Prioritising offspring care over favourable timings of migration is therefore likely to have important consequences and could generate carry-over effects. Short-lived altricial species such as golden hamsters *Mesocricetus auratus* and zebra finches *Taeniopygia guttata* have been found to adjust the duration of care to offspring requirements (Swanson and Campbell 1980; Rehling et al. 2012).

However the situation is unclear in long-lived, migratory species: some species with experimentally prolonged parental care adapted their parental effort to chick condition within the natural length of the chick-rearing period, but did not extend its duration and stopped brooding or deserted their chick early (Johnsen et al. 1994; Catry et al. 2006), while others adjusted to the new chick age and continued to feed longer, but reduced their feeding frequency (Riou et al. 2012). Studies investigating the long-term carry-over effect of early/late breeding in migratory species are scarce, mainly due to the challenge of tracking migrants during the non-breeding season; often the studies stop at the end of the breeding season (e.g. (Johnsen et al. 1994; Jonker et al. 2011; Riou et al. 2012)). Although several studies have looked at the future survival and reproductive success of animals with regards to current breeding effort (Erikstad et al. 2009; Catry et al. 2013), few have manipulated reproductive cost in a controlled way (Johnsen et al. 1994; Erikstad et al. 2009; Riou et al. 2012). Studies of naturally early/late breeders may be confounded by individual quality, because early breeders are often of higher quality (Perrins 1970), and studies investigating the impact of breeding failure only look at half of the picture (a decrease, but no increase, in reproductive cost). Furthermore, how the carry-over effects of breeding affect the subsequent behaviour of parents during the non-breeding period (for example whether delayed breeders can compensate by increasing their foraging activity during the winter) has been scarcely studied (Kazama et al. 2013; Daunt et al. 2014; Shoji et al. 2015). Furthermore, whether there are more subtle effects in the next breeding season than breeding success, failure or sabbatical year is poorly understood. Such individual carry-over effects can influence population dynamics, especially in migratory species (Norris and Taylor 2006); it is therefore important to answer these questions, particularly in the current context of rapid changes to the environment due to climate change (Carey 2009; Gremillet and Boulinier 2009; Charmantier and Gienapp 2014).

Here we address these questions in a long-lived pelagic seabird, the Manx shearwater *Puffinus puffinus*, a small seabird breeding along the East Atlantic coast, migrating to the Patagonian shelf in South America every winter (Guilford et al. 2009). Manx shearwaters, like other pelagic seabirds, are long-lived, long-distance migrants, with a long and slow breeding season during which they only raise a single offspring, incubating their egg or feeding their chick for over 100 days. Therefore they exemplify the strategies likely to lead to carry-over effects and their possible influence on migration. This, combined with their high breeding philopatry which allows the monitoring of their breeding behaviour and success over several years, and their relatively large size which makes it possible to track their migratory behaviour over entire winters, makes them ideal to investigate carry-over effects. We cross-fostered young and old chicks between nests to shorten or lengthen artificially the chick-rearing period of 40 pairs of breeding shearwaters, and investigated the carry-over effects of different reproductive costs on the non-breeding and subsequent breeding season by using a combination of three different types of data. First, we used at-colony measurements during the experimental breeding season and the next to measure parental effort (daily chick mass gain), breeding phenology and breeding success. Second, we fitted all adults with geolocators at the end of the manipulated breeding season to record their non-breeding movements, allowing us to measure the phenology of migration, wintering and return to the colony. Third, we used an ethoinformatics approach to analyse the saltwater-immersion data collected by geolocators to identify different behaviours and estimate year-round at-sea activity budgets (Freeman et al. 2013). For a subset of birds we also collected geolocator data during the manipulated breeding season, which allowed us to measure feeding frequency and activity budgets during the chick-rearing period, and during the previous and/or the following breeding and non-breeding seasons. This allowed us to compare carry-over effects not only between groups but also within-groups between years of different conditions and, when sample size allowed, within-individual comparisons to separate carry-over effects from individual quality.

Methods

Study site and model species

The study was carried out on Skomer Island, Wales (51°44’N, 5°19’W), probably the largest Manx shearwater colony in the world (~300,000 breeding pairs; Perrins et al., 2012), between June 2012 and August 2014. Manx shearwaters are c. 400g colonial burrow-nesting monomorphic seabirds that mainly breed on the Northeast Atlantic coast.

All work was conducted after ethical approval by the British Trust for Ornithology Unconventional Methods Technical Panel (permit C/5311), Natural Resources Wales, Skomer Island Advisory Committee and the University of Oxford’s Local Ethical Review Process. Bird handling was kept to a minimum to minimise disturbance. Deploying and retrieval of geolocators did not exceed 10 minutes, and weighing of chicks was <1 minute in most cases.

Chick-swapping

Study burrows were monitored from the start of the breeding season (late April) to measure laying and hatching dates. All breeding adults were ringed with a unique BTO metal ring, and when possible sex was identified on the day of laying by cloacal inspection (37 pairs were sexed with this method, 6 additional pairs which we could not sex this way were sexed from DNA extracted from feathers (Avian Biotech, UK), and the remaining pairs were classified as “unknown sex”). Once hatching date was known, burrows were allocated to a group (control, “higher effort” treatment or “lower effort” treatment), then paired between groups (treatments) or within the control group to receive each other’s chick. In the first few days after hatching, chicks are vulnerable and are often guarded by a parent; therefore no swapping was done before the chicks were 10 days old. Control chicks were swapped with chicks of the same age (age difference 0-1 days, *n* = 20). In the treatment group we chose to swap chicks with an age difference as close as possible to 18 days, which was the largest difference possible given the natural spread of hatching in our study burrows and represents c. 25 - 30% of the whole chick-rearing period (average age difference 17.7 ± 0.3 days, *n* = 20). To minimise noise between burrows and groups, we tried to always swap control chicks at day 10, and to swap treatment chicks when the young chick of the pair reached 10 days old (i.e. the older chick was 28 days old). When there was more than one possibility to pair a burrow (e.g. when several burrows hatched 18 days apart), the choice was made at random. In total 60 chicks were cross-fostered: 30 in 2012 and 32 in 2013 (2012: 10 controls, 10 "old", 10 "young"; 2013: 10 control, 11 "old", 11 "young"). All parents continued feeding their foster chick after swapping, so there was no desertion. One chick was found dead for unknown reasons one week after swapping, despite having been fed regularly by its foster parents, and 2 chicks went missing (at 20 and 43 days old) – they may have ventured closer to the entrance of the burrow and been preyed on by gulls. In both cases they also were fed regularly by their parents. The rate of natural chick deaths and disappearance was similar, or lower, to that of control (non-swapped) burrows (Skomer seabird monitoring reports 2008-2014).

Deployment and retrieval of devices

Geolocators (BAS Mk15 and M19, Biotrack M4083), miniature archival light-loggers (<2.5g) which also measure the proportion of time immersed in saltwater for every 10 minute-bin, were deployed on all adults before they left the colony to start their autumn migration. When possible, they were deployed earlier during the breeding season in order to collect data on the at-sea behaviour and visit rate of adults to their nest. The devices were attached with two lightweight cable ties to a plastic ring around the bird's otherwise unringed tarsus (for detailed methods see Guilford et al. 2009). The following year, birds were caught when they returned to the colony to breed and data were downloaded from their devices. Loggers were left on during the following breeding season to collect data on their breeding behaviour (at-sea activity and visits to the colony) the year after manipulation. In total, 120 devices were deployed, of which 93 were recovered, one was lost at sea, and the remaining 26 birds were not recaptured.

Due to high rates of failure of devices during the winter, our final dataset contained 88 complete autumn migrations (2012: 40; 2013: 48), 82 complete wintering periods (on the wintering grounds; 2012: 36; 2013:46), 6 partial wintering periods, and 82 complete return spring migrations to the colony (2013: 36; 2014: 46). In addition, some of the birds had been tracked the year before or after the experiment (before: $n = 13$, after: $n = 14$. When possible the loggers were also left on the birds during the breeding season (of the experiment or the next) to collect data on their breeding behaviour. We collected data for 128 complete chick-rearing periods (72 in the experiment year, 9 the year before, 46 the year after), and 35 partial ones (12, 4 and 19 respectively).

Chick growth rate and mass gain

All chicks were weighed daily to monitor their growth, until they fledged. Weighing occurred during the day when both parents were at sea. We also estimated the total amount of food brought by parents to a burrow by calculating the cumulative mass gain of the chick in each burrow. This is an underestimation of the actual amount as chicks were weighed ~12 hours after being fed and therefore had already lost some weight by respiration and defecation (Brooke 1990), but the rate of weight loss is approximately constant in chicks (1.7 ± 0.6 g.h^{-1}, (Dean 2013)) and so the estimations should allow for relative comparisons between groups.

Position data processing and analysis

Light data were decompressed and processed using the BASTrack software suite (British Antarctic Survey) and MatLab R2010b (MathWorks Inc.). We calculated average daily positions for all tracks during the non-breeding season, and filtered out those with high standard error (longitude > 40 km, latitude > 30 km), and applied a speed filter of 1000 km per day (18h of sustained flight at average speed 55 km/h (Guilford et al. 2009)). Autumn migration usually starts in September, making it difficult to use latitude to assess departure from the colony (because of the low latitude resolution near the equinox). The start of autumn migration was estimated as the day that each bird crossed the -12° meridian: longitude is more reliable than latitude during the migration period near the equinox, and -12° was chosen to rule out long foraging trips to the Atlantic during the breeding season, observed in a handful of birds. The mean wintering latitude and longitude were assessed for each bird between November and January (when the resolution of the data is at its highest and all birds have finished their autumn migration); the end of autumn migration was calculated as the day of arrival within 500 km of this mean wintering position. Similarly, we identified departure on spring migration as the first day crossing the 500 km boundary around the wintering area, and the end of Spring migration as the first day crossing the -12° meridian again in the colony-bound direction.

Saltwater-immersion data processing and analysis to identify behaviours

For each bird, salt-water immersion data (or "activity" data) were split into "breeding season", "southward migration", "wintering" or "northward migration", using the dates calculated from position data. We identified and classified behaviours for the breeding, migration and wintering periods separately, as different behaviours (e.g. different types of foraging or flight) can be expected to take place during these different parts of the birds' annual cycle. We used Hidden Markov Models (HMMs) to identify and classify behaviours in each of these four parts. For the non-breeding season HMMs were run on (normalised, logit-transformed) activity data and (arcsin-transformed) proportion of each day spent dry. For the breeding season, light data collected by geolocators was added as an extra variable, as it can represent incubation stints or days spent in the burrows (dark period during daylight hours) and not only night time sitting on the water surface. We used the data from the control birds to train the models and then applied them to the data from treatment birds and, when available, to the data corresponding to the year before and after the experiment. The most likely sequence of hidden states was calculated and each data point (corresponding to a ten-min period) was allocated a state. The optimal number of states for each period was first determined by running models (on the control data) with 1 to 10 states. We initialised all models using uniform prior and transition probability matrices (i.e. all states equally probable). The optimal number of states was chosen as the best compromise between minimising the log-likelihood of the model, and identifying behaviours which were sufficiently different to make biological sense (e.g. if 5 states had a slightly lower log-likelihood than 4 but 2 of the 5 states appeared virtually identical, 4 states would be selected as the optimal number). Using this method we found 3 optimum states for the non-breeding season, and 6 for the breeding season (4 in daytime, 2 in night-time). Three states is consistent with other studies of similar datasets analysed with HMMs and other machine-learning techniques and validated by other types of data (Guilford et al. 2009; Dean et al. 2012; Freeman et al. 2013), which identified sitting on the water surface (mostly wet) and sustained flight (mostly dry). The intermediate state (short bouts of dry and wet states) was called “foraging” although this should be interpreted cautiously and may also contain other types of behaviours (especially during migration where it could be interrupted flight). However, using a similar classification combined with diving data, (Dean et al. 2012) showed that the vast majority of diving (>95%) occurred in this state during the breeding season, and so it is likely that it include most foraging activity. During the breeding season we allocated to each of the 6 states the following behaviours using the mean immersion time of the states, and observing temporal patterns: sitting on the water, sustained flight, foraging type 1 (short wet bouts in-between longer dry bouts, perhaps more associated with searching) and foraging type 2 (short dry bouts in-between longer wet bouts) during the day; sitting on the water (mostly wet) and visiting the colony (mostly dry) at night (Figure S1). Unlike (Dean et al. 2012; Freeman et al. 2013) we did not have any other tracking data to validate our classification, therefore we also classified our data in 3 states with simple thresholds (sitting: <3% dry; flight: >97% dry; “foraging”: anything in-between). This method was used in Chapters 2, 3 & 4 and by Lecomte et al. (2010), and similar methods have been used in a number of species (Yamamoto et al. 2008; Catry et al. 2011; Ramirez et al. 2013). All results were comparable, therefore we only present below the results using the HMM classification.

Statistics

To avoid the potentially confounding effects of between-year variation when testing for differences in breeding phenology, each date was formulated as its difference from the median date of the event on the colony that year (e.g. median laying date or median hatching date). All our analyses testing the effect of the chick manipulation on breeding and non-breeding variables (e.g. lay date, start of migration) used Linear Mixed Models (LMMs) or Generalised Linear Mixed Models (GLMMs) (depending on whether normality of the dependent variables could be obtained), and included bird and year as random effects, as well as burrow when separate data were available for the two members of a pair (e.g. migration phenology). Previous reproductive success was also controlled for when we examined within-group differences in winter activity budgets between the experimental and non-experimental years. Dependent variables were transformed to meet normality assumptions when necessary. Paired t-tests were used to compare between-year consistency in laying date and egg mass between groups, and χ^2 tests were used to test for differences in breeding success between groups. LMMs and GLMMs *P*-values were obtained by comparing our models to null models (with the random effects but without the fixed effect of interest) with a χ^2 test. All the analyses were performed using the {lme4} package in R. Due to the failure of some geolocators during migration, some tracks were incomplete, but were still included in the analysis (e.g. the light logger stopped but saltwater-immersion data were still being recorded, or vice-versa), although imcomplete datasets were excluded when testing variables requiring a complete migratory track (e.g. total time spent foraging during the non-breeding season). Therefore, sample sizes vary slightly between models; all sample sizes are indicated for each test.

Results

Natural differences in breeding phenology before manipulation

Because of the design of the experiment, prior to cross-fostering the birds in the "lower effort" treatment group inevitably laid later than control birds (LMM: n_{control}=19, $n_{\text{lower effort}}$=20; parameter estimate = 12.7 ± 1.8, $\chi_1^2 = 30.3$, $P < 0.001$), and birds in the "higher effort" treatment group laid earlier than controls (LMM: n_{control}=19, $n_{\text{higher effort}}$=20; parameter estimate = -3.4 ± 1.6, $\chi_1^2 = 4.3$, $P = 0.037$). Control birds were chosen as randomly as possible, but due to the need to match early birds with late ones for the treatment groups, controls were often the "intermediate" birds which did not lay early or late, but near the peak of the laying date distribution.

Effects of swapping chicks on the current breeding season

There were significant differences in the duration of chick-rearing between groups (LMM: n_{control}=19, $n_{\text{lower effort}}$=20, $n_{\text{higher effort}}$=20; $\chi_2^2 = 163.5$, $P < 0.001$, see Table 1). Adults which raised an older foster chick had a significantly shorter chick-rearing period (from hatching to fledging: 49.8 ± 1.1 days) than controls (68.7 ± 0.8 days; LMM: parameter estimate = -18.9 ± 1.4, $\chi_1^2 = 71.8$, $P < 0.001$), which spent significantly less time rearing a chick than adults with a younger foster chick (85.6 ± 0.7 days; LMM: parameter estimate =

16.9 ± 0.9, $\chi_1^2 = 80.84$, $P < 0.001$). In other words, the manipulation reduced the chick-rearing period by 27.5% on average in the "lower effort" treatment group and lengthened it by 24.6% on average in the "higher effort" treatment group.

Using the saltwater-immersion data to calculate visit rate and at-sea activity budgets during the chick-rearing period immediately following the chick-swapping, we found that there was no difference in activity budgets between groups: all birds spent similar amounts of time in sustained flight, foraging or sitting on the water surface (n_{control}=24, $n_{\text{lower effort}}$=23, $n_{\text{higher effort}}$=37, sitting: GLMM, $\chi_2^2 = 2.1$, $P = 0.354$; foraging: LMM, $\chi_2^2 = 0.10$, $P = 0.952$; flying: LMM, $\chi_2^2 = 1.91$, $P = 0.386$), and the daily total time spent dry (i.e. in a foraging or flying state) did not vary significantly between groups (LMM, $\chi_2^2 = 1.85$, $P = 0.395$). Similarly, the visit rate to the chick did not differ between adults of different groups (control: 0.66 ± 0.02 visits.day^{-1}, $n = 25$; lower effort: 0.68 ± 0.03 visits.day^{-1}, $n = 23$; higher effort: 0.67 ± 0.02 visits.day^{-1}, $n = 37$; LMM, $\chi_2^2 = 0.05$, $P = 0.973$).

However, due to the difference in duration of the chick-rearing period between group, the cumulative amount of time spent in a foraging state during chick-rearing (from the 30th day of chick-rearing until the last feeding event) varied significantly between groups (LMM, n_{control}=18, $n_{\text{lower effort}}$=19, $n_{\text{higher effort}}$=10; $\chi_2^2 = 39.74$, $P < 0.001$). Over this period, birds in the "lower effort" treatment group spent significantly less time foraging than controls (20.1 ± 4.1 hours vs. 59.3 ± 10.9 hours; LMM, parameter estimate = -3.81 ± 1.3, $\chi_2^2 = 22.07$, $P < 0.001$), while birds in the "higher effort" treatment group spent significantly more time foraging during the chick-rearing period (86.3 ± 7.2 hours; LMM, parameter estimate = 1.66 ± 1.1, $\chi_2^2 = 7.41$, $P = 0.007$).

As a result, the total amount of food brought to the burrows over the whole chick-rearing period also varied significantly between groups (LMM: n_{control}=19, $n_{\text{lower effort}}$=20, $n_{\text{higher effort}}$=20; $\chi_2^2 = 108.9$, $P < 0.001$). Adults in the "lower effort" treatment group brought significantly less food to their burrow (628.4 ± 25.2 g) than controls (1077.7 ± 29.7 g; LMM: parameter estimate = -449.4 ± 38.9, $\chi_1^2 = 59.6$, $P < 0.001$), while "higher effort" treatment adults brought significantly more (1279.6 ± 26.1 g; LMM: parameter estimate = 207.6 ± 38.6, $\chi_1^2 = 20.9$, $P < 0.001$).

All chicks fledged at the same age of 68.2 ± 0.5 days old (LMM: $n_{\text{control}}=19$, $n_{\text{lower effort}}=20$, $n_{\text{higher effort}}=20$; $\chi_2^2 = 1.3$, $P = 0.530$). However, there were significant differences between the peak weight, fledging weight and fledging date of chicks in different groups (LMMs: Peak weight: $\chi_2^2 = 6.1$, $P = 0.048$; Fledging weight: $\chi_2^2 = 19.9$, $P < 0.001$; Fledging date: $\chi_2^2 = 63.7$, $P < 0.001$). Chicks in “lower effort” treatment burrows reached a similar peak weight to controls (control: 576 ± 12 g; lower effort: 569 ±7 g; parameter estimate = -9.2 ± 12.8, $\chi_1^2 = 0.5$, $P = 0.483$) but fledged heavier (control: 418 ± 10 g; lower effort: 453 ±10 g; parameter estimate = 37.1 ± 12.9, $\chi_1^2 = 6.7$, $P = 0.009$) and earlier in the season (5.8 ± 1.8 days earlier on average, parameter estimate = -5.8 ± 1.8, $\chi_1^2 = 10.1$, $P = 0.001$). Chicks in “higher effort” treatment burrows on the other hand, reached significantly lower peak weights than controls (538 ± 15 g; parameter estimate = -39.4 ± 18.8, $\chi_1^2 = 4.3$, $P = 0.038$), and fledged lighter (367 ±18 g; parameter estimate = -51.7 ± 19.2, $\chi_1^2 = 6.7$, $P = 0.009$) and later (12.3 ± 1.6 days later on average, parameter estimate = 12.5 ± 1.5, $\chi_1^2 = 36.9$, $P < 0.001$).

Table 1. Summary table of difference in breeding characteristics between groups during the breeding season where the manipulation took place. The numbers show the difference between each treatment group and the control group, significant “positive” differences (i.e. representing a reduced effort for the birds, or a higher fitness – e.g. heavier chick), are underlined in green, while the significant “negative” differences (detrimental to the birds’ fitness) are underlined in red.

	LOWER EFFORT	**CONTROL**	**HIGHER EFFORT**
	(difference from control)		*(difference from control)*
chick-rearing duration	16.8 ± 1.1 days shorter	63.3 ± 0.9 days	15.3 ± 1.4 days longer
total food given to chick	449.3 ± 25.2 g less	1077.7 ± 29.7 g	201.9 ± 26.1 g more
chick peak weight	no difference	576 ± 12 g	38 ± 15 g lighter
chick fledging weight	35 ± 10 g heavier	418 ± 10 g	51 ± 18 g lighter
chick fledging date	5.8 ± 1.8 days earlier	6 Sept. ± 0.8 day	12.3 ± 1.6 days later

Effects of swapping chicks on the adults' migration phenology

All birds followed similar routes during their spring and autumn migrations, and wintered in similar areas (Figure S2), but groups differed significantly in the phenology of their migration (Table 2). There were significant differences in the timing of the start of the autumn migration at the end of the manipulated breeding season (LMMs: n_{control}=30, $n_{\text{lower effort}}$=23, $n_{\text{higher effort}}$=37; $\chi_2^2 = 10.8$, $P = 0.005$). While control birds and birds in the "lower effort" treatment group started their southward migration on similar dates (parameter estimate = -1.3 ± 2.1, $\chi_1^2 = 0.4$, $P = 0.556$), birds in the "higher effort" group left significantly later than controls (parameter estimate = 5.3 ± 2.2, $\chi_1^2 = 6.0$, $P = 0.014$). As a consequence, there was no difference between the timing of arrival at the wintering grounds between control and "lower effort" treatment birds, although there was a non-significant trend for control birds to arrive earlier (LMMs: n_{control}=28, $n_{\text{lower effort}}$=23; parameter estimate = 1.7 ± 1.3, $\chi_1^2 = 3.7$, $P = 0.054$), and birds in the "higher effort" group arrived later than controls ($n_{\text{higher effort}}$=35; parameter estimate = 2.1 ± 1.3, $\chi_1^2 = 9.2$, $P = 0.002$) (Figure 1).

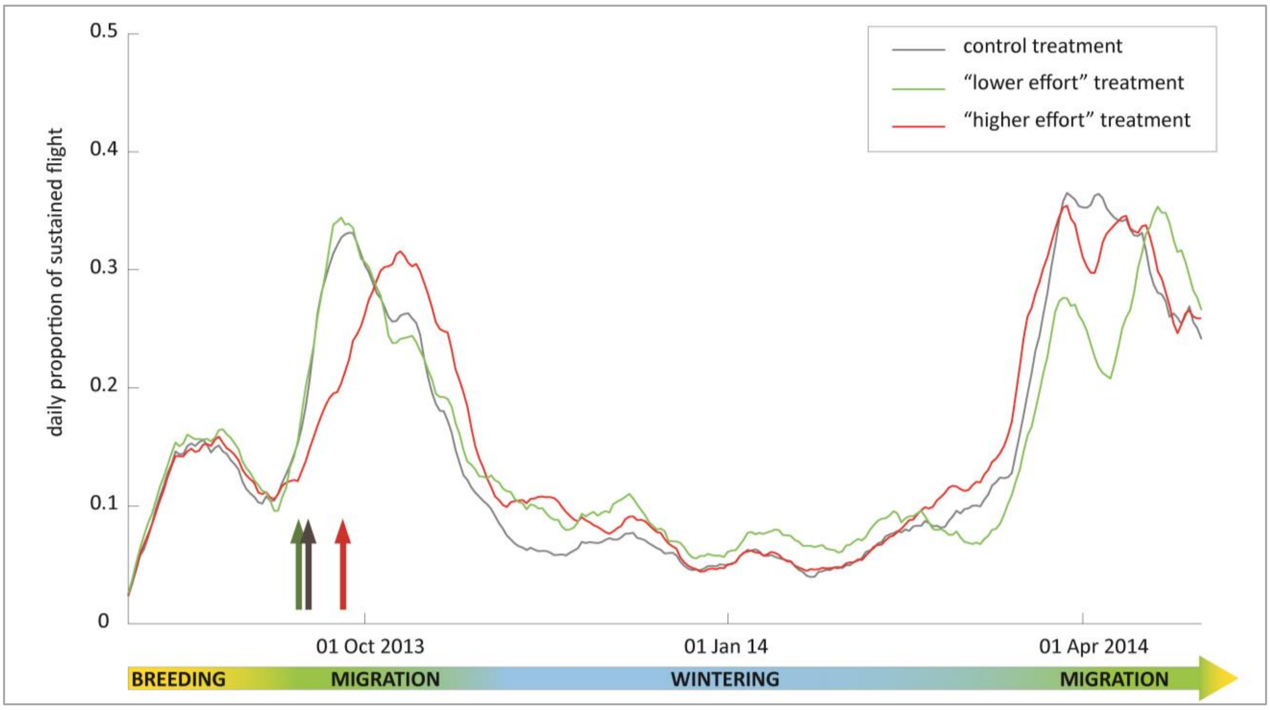

Figure 1. Average proportion of time in flight each day for each group (grey=control, green="lower effort" treatment, red="higher effort" treatment), following chick manipulation. Arrows indicate the average start of migration (crossing of the 12° W) for each group. "Higher effort" birds start fall migration, but not spring migration, late. To facilitate interpretation we used here the 2013-2014 data only, and a 7-day moving average.

We compared these migration timings with the birds' timings the previous or following year (i.e. years without manipulation). We found significant differences between groups in the between-year consistency of the start of migration. While there was no difference in the start of migration between years for "control" birds (LMM, n_{control}=35, parameter estimate -5.3 ± 5.5, χ_1^2 =1.03, P = 0.310), birds in the "lower effort" treatment group started their migration significantly earlier than in non-experimental years (LMM, $n_{\text{lower effort}}$=35, parameter estimate = 8.2 ± 4.1, χ_1^2 = 4.1, P = 0.042). Birds in the "higher effort" treatment group started their migration significantly later in experimental year (LMM, $n_{\text{higher effort}}$ = 47, parameter estimate = -9.5 ± 3.9, χ_1^2 = 4.7, P = 0.029).

There was no difference between groups in timing of departure on spring migration (LMM, n_{control}=28, $n_{\text{lower effort}}$=18, $n_{\text{higher effort}}$=32; χ_2^2 = 4.31, P = 0.116). As a consequence, the total time spent on the wintering grounds (i.e. before the start of the spring migration) differed significantly between groups (LMM, n_{control}=28, $n_{\text{lower effort}}$=18, $n_{\text{higher effort}}$=32; χ_2^2 = 10.5, P = 0.005). Whilst "lower effort" treatment birds stayed on the wintering ground for a similar duration as control birds (139.4 ± 4.3 vs. 142.5 ± 2.2 days, parameter estimate = -3.3 ± 4.5, χ_1^2 = 0.5, P = 0.481), "higher effort" treatment birds had a shorter wintering period than controls (131.5 ± 1.9 days, parameter estimate = -11.9 ± 3.2, χ_1^2 = 13.3, P < 0.001). All birds returned to the colony at similar times (LMM, n_{control}=25, $n_{\text{lower effort}}$=17, $n_{\text{higher effort}}$=28; χ_2^2 = 3.69, P = 0.158). Overall, the total amount of time spent away from the colony differed significantly between treatment and control individuals (LMM, n_{control}=25, $n_{\text{lower effort}}$=17, $n_{\text{higher effort}}$=28; χ_2^2 = 12.78, P = 0.002). "Higher effort" treatment birds spent less time away from the colony than controls (204.9 ± 2.2 vs. 211.2 ± 2.4 days, parameter estimate = -6.8 ± 3.0, χ_1^2 = 5.0, P = 0.025), but there were no significant differences between "lower effort" treatment birds and controls (217.2 ± 2.9 days, parameter estimate = 5.6 ± 3.5, χ_1^2 = 2.7, P = 0.101).

Table 2. Summary table of differences in migration characteristics between groups in the non-breeding season following the manipulation. The numbers show the difference between each treatment group and the control group, significant "positive" differences (i.e. representing a reduced effort for the birds, or a higher fitness – e.g. heavier chick), are underlined in green, while the significant "negative" differences (detrimental to the birds' fitness) are underlined in red. When the differences were not significant most likely due to a small sample size we indicated the numbers followed by ns. In some instances ("comparison with…") the numbers represent within-group differences between years and not differences with control birds.

	LOWER EFFORT *(difference from control)*	**CONTROL**	**HIGHER EFFORT** *(difference from control)*
start of autumn migration	no difference	15 Sept. ± 1.3 days	5.5 ± 1.7 days later
comparison with year -1	11.4 ± 1.5 days earlier in year 0	no difference	5.3 ± 9.3 days later in year 0 (ns)
comparison with year +1	no difference	no difference	no difference
arrival at the wintering grounds	5.7 ± 2.5 days later (ns)	13 Oct ± 1.6 days	9.9 ± 2.1 days later
start of spring migration	no difference	3 Mar ± 1.7 days	no difference
time spent at the wintering grounds	no difference	142.5 ± 2.2 days	11.0 ± 3.2 days less
return to the colony in year +1	no difference	15 Apr ± 2.1 days	no difference

At-sea behaviour during the following migration and wintering periods

We used saltwater-immersion data to estimate activity budgets during the autumn (southwards) migration, the wintering period (at the overwintering grounds) and during the spring (northwards) migration (Table 3, Figure 2). During the autumn migration (~September-October), birds in the "lower effort" treatment spent less time in sustained flight or in a foraging state than control birds (LMMs, foraging: $\chi_1^2 = 22.2$, $P < 0.001$; flight: $\chi_1^2 = 7.7$, $P = 0.005$). We did not find any difference in activity budgets of "higher effort" treatment birds in comparison to controls. During the wintering period (~November-February), "lower effort" birds generally spent more time sitting on the water surface than controls (LMM, $\chi_1^2 = 20.6$, $P < 0.001$). In addition, birds from both treatment groups foraged less than control birds (LMMs, "lower effort" treatment: $\chi_1^2 = 37.7$, $P < 0.001$; "higher effort" treatment: $\chi_1^2 = 7.13$, $P = 0.008$). During the subsequent spring migration (~ March-April): "lower effort" treatment birds still spent less time foraging than control birds each day (LMM, $\chi_1^2 = 21.2$, $P < 0.001$) and nearly significantly less time in sustained flight (LMM, $\chi_1^2 = 2.8$, $P = 0.097$). There was a nearly significant trend for "higher effort" treatment birds to spend more time flying each day compared to controls (LMM, $\chi_1^2 = 3.5$, $P = 0.062$).

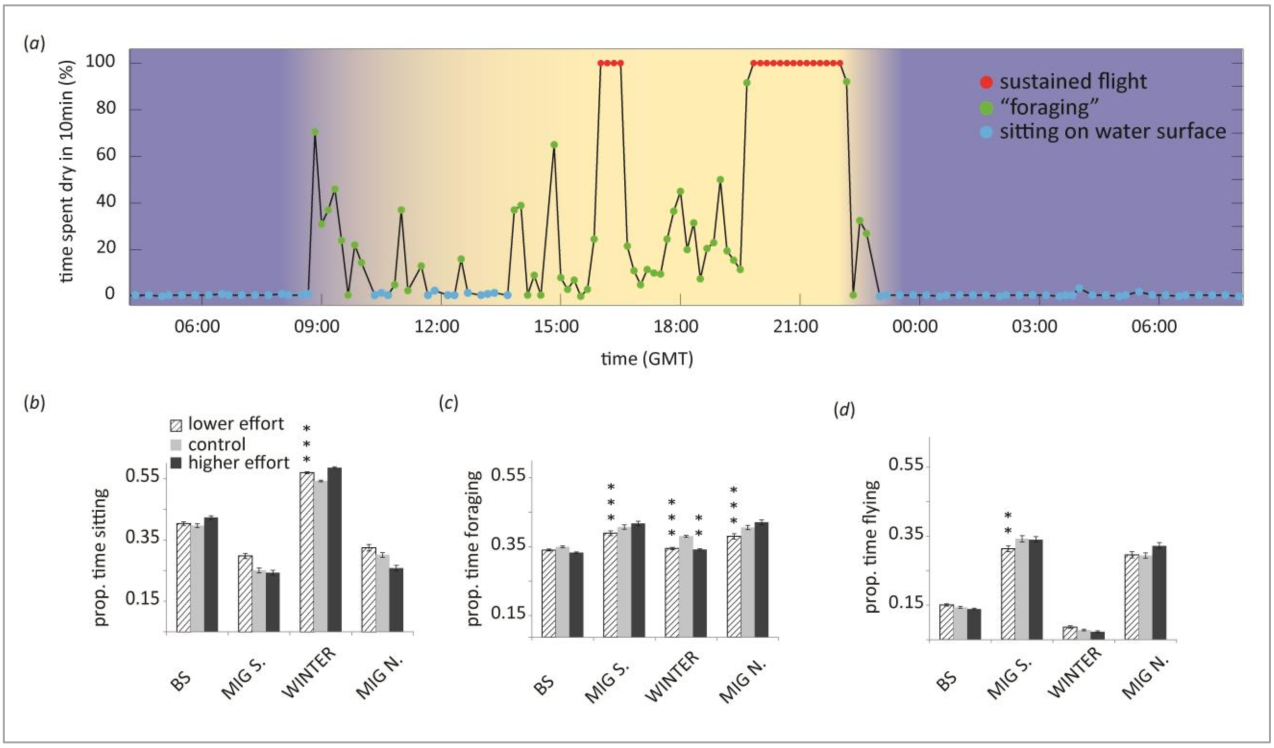

Figure 2. (*a*) Example of behavioural classification of saltwater-immersion data by a HMM for a day in the wintering period of a bird. Each point represents a 10min period. Points of low "dryness" are classified as one state (identified as sitting on the water surface, blue), while points of very high dryness are classified in a separate state (identified as sustained flight, red). Points of intermediate levels are classified in a 3rd intermediate state, which we called "foraging" but may also encompass other behaviours other than sustained sitting/flying. (*b* -*d*) Average proportions of time spent in the three behavioural states as classified by HMMs ((*b*) sitting; (*c*) foraging and (*d*) flying), for the breeding season, autumn migration, wintering and spring migration, for each group ("lower effort" treatment in white and black stripy pattern, control in light grey and "higher effort" treatment in dark grey). Difference with the Asterisks indicate significant differences between a treatment and the control group (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). Means ± SE.

Table 3. Means and statistics for the comparison of activity budgets during the non-breeding season following the cross-fostering experiment, for all three groups, during autumn migration, wintering, and return spring migration. All the statistics (χ^2 and *P* values) come from Linear Mixed Models controlling for individual and year. The sample sizes are given under each treatment group. Means ± SE.

	SITTING		**FORAGING**		**FLYING**	
	mean ± SE (%)	within-year difference	mean ± SE (%)	within-year difference	mean ± SE (%)	within-year difference
Autumn Migration						
Lower effort *n* = 23	28.1 ± 4.7	$\chi_1^2 = 0.3$ $P = 0.584$	36.7 ± 3.9	**$\chi_1^2 = 22.2$** **$P < 0.001$**	29.6 ± 4.7	**$\chi_1^2 = 7.7$** **$P = 0.005$**
Control *n* = 29	25.0 ± 4.2	n/a	40.7 ± 3.3	n/a	34.3 ± 4.7	n/a
Higher effort *n* = 35	23.9 ± 3.9	$\chi_1^2 = 1.1$ $P = 0.29$	41.1 ± 3.1	$\chi_1^2 = 1.1$ $P = 0.307$	33.5 ± 4.1	$\chi_1^2 = 0.3$ $P = 0.563$
Winter						
Lower effort *n* = 20	54.5 ± 3.7	**$\chi_1^2 = 20.6$** **$P < 0.001$**	33.0 ± 3.2	**$\chi_1^2 = 37.7$** **$P < 0.001$**	8.3 ± 1.9	$\chi_1^2 = 0.1$ $P = 0.924$
Control *n* = 26	54.2 ± 2.8	n/a	38.0 ± 2.5	n/a	7.8 ± 1.4	n/a
Higher effort *n* = 30	58.1 ± 2.6	$\chi_1^2 = 1.8$ $P = 0.179$	33.9 ± 2.0	**$\chi_1^2 = 7.13$** **$P = 0.008$**	7.2 ± 1.2	$\chi_1^2 = 0.5$ $P = 0.477$
Spring Migration						
Lower effort *n* = 13	30.9 ± 7.0	$\chi_1^2 = 0.4$ $P = 0.517$	36.2 ± 5.2	**$\chi_1^2 = 21.2$** **$P < 0.001$**	28.9 ± 6.1	$\chi_1^2 = 2.8$ $P =0.097$
Control *n* = 22	29.7 ± 5.0	n/a	40.0 ± 3.9	n/a	30.6 ± 4.9	n/a
Higher effort *n* = 26	25.8 ± 4.3	$\chi_1^2 = 2.6$ $P = 0.106$	42.0 ± 3.5	$\chi_1^2 = 1.1$ $P = 296$	33.0 ± 4.4	$\chi_1^2 = 3.5$ $P = 0.062$

We also found significant differences in the birds' activity budgets during the winter immediately following the manipulation and in other winters (the year before or after) (Table 4). We found a significant interaction between group (control, "lower effort" or "higher effort" treatment) and year (year of the experiment or "control" year (before/after)) in the proportion of time spent sitting on the surface and foraging (LMMs, $n_{\text{control}} = 27$, $n_{\text{lower effort}} = 22$, $n_{\text{higher effort}} = 33$, sitting: $\chi_2^2 = 75.4$, $P < 0.001$; foraging: $\chi_2^2 = 93.5$, $P < 0.001$) but not in sustained flight (LMM, $\chi_2^2 = 2.4$, $P = 0.307$). While there was no difference between experimental and non-experimental years for birds in the "lower effort" treatment group in any behavioural activity, both control and "higher effort" birds spent less time engaged in foraging activity in the experimental year than in other years (LMMs, control: parameter estimate = 0.14 ± 0.05, $\chi_1^2 = 5.5$, $P = 0.019$; higher effort: parameter estimate = 0.08 ± 0.04, $\chi_1^2 = 4.2$, $P = 0.041$). They differed in sitting behaviour, with control birds spending significantly more time sitting on the water surface in the experimental year (LMM, parameter estimate = -0.16 ± 0.06, $\chi_1^2 = 5.1$, $P = 0.023$) and "higher effort" treatment birds spending significantly less time sitting on the water in the experimental year (LMM, parameter estimate = -0.13 ± 0.05, $\chi_1^2 = 4.7$, $P = 0.029$).

Table 4. Means and statistics for the comparison of activity budgets during the winter following cross-fostering for all three groups, compared with winters in other year (year immediately before and/or after). All the statistics (χ^2 and *P* values) come from Linear Mixed Models controlling for individual, year and previous breeding success. The sample sizes are given under each treatment group. Means ± SE (top values are during the experimental year, bottom values are during non-experimental years).

	SITTING		**FORAGING**		**FLYING**	
	mean ± SE (%) exp. year non-exp. year	between-year difference	mean ± SE (%) exp. year non-exp. year	between-year difference	mean ± SE (%) exp. year non-exp. year	between-year difference
Lower effort	54.5 ± 0.3	$\chi_1^2 = 0.3$	33.0 ± 0.3	$\chi_1^2 = 0.5$	8.3 ± 0.2	$\chi_1^2 = 0.1$
n = 20	58.0 ± 0.5	*P* = 0.609	34.6 ± 0.3	*P* = 0.461	7.4 ± 0.2	*P* = 0.767
Control	54.2 ± 0.2	$\boldsymbol{\chi_1^2 = 5.1}$	38.0 ± 0.2	$\boldsymbol{\chi_1^2 = 5.5}$	7.8 ± 0.3	$\chi_1^2 = 0.1$
n = 26	53.9 ± 0.6	***P* = 0.023**	38.3 ± 0.5	***P* = 0.019**	7.8 ± 0.1	*P* = 0.803
Higher effort	58.1 ± 0.2	$\boldsymbol{\chi_1^2 = 4.7}$	33.9 ± 0.2	$\boldsymbol{\chi_1^2 = 4.2}$	7.2 ± 0.1	$\chi_1^2 = 0.5$
n = 30	59.3 ± 0.5	***P* = 0.029**	34.6 ± 0.4	***P* = 0.041**	6.1 ± 1.9	*P* = 0.494

Effects on the next breeding season

The breeding success of control birds in the year following the manipulation was similar to that of non-manipulated birds (Skomer seabird monitoring reports 2008-2014). We found significant differences between groups in the phenology and outcome of the breeding season the year following the manipulation (Figure 3, Table 5). Although there was no difference in actual lay date between groups (LMM, $n_{\text{control}} = 12$, $n_{\text{lower effort}} = 8$, $n_{\text{higher effort}} = 14$, $\chi_2^2 = 3.5$, $P = 0.169$), the difference in laying date between the experimental year and the next differed between groups. There was no difference in control birds ($n_{\text{control}}=10$, lay date = 0.7 ± 2.9 days later in the following year, paired T-test, $t_9=1.28$, $P = 0.234$), while “higher effort” treatment birds laid significantly later after the experiment than before ($n_{\text{higher effort}}=10$, lay date = 4.3 ± 3.2 days later after the experiment, paired T-test, $t_9=2.26$, $P = 0.050$). On average “lower effort” treatment birds laid 3.7 ± 1.7 days earlier in the year following manipulation but this was not significant, perhaps because of the small sample size ($n_{\text{lower effort}}=6$, paired Wilcoxon test, W=9, $P = 0.843$).

Additionally, control birds laid eggs of similar size as the year before manipulation (control: $n_{\text{control}}=10$, eggs 0.1 ± 1.2 g lighter, paired T-test, $t_9=-0.09$, $P = 0.933$); “lower effort” birds’ eggs were 3.4 ± 3.9 g heavier but the difference was not significant ($n_{\text{lower effort}}=5$, paired T-test, $t_4=0.86$, $P = 0.440$); birds in the “higher effort” treatment laid eggs significantly lighter than in the previous season ($n_{\text{higher effort}}=10$, eggs 3.2 ± 1.1 g lighter, paired T-test, $t_9=-2.84$, $P = 0.019$). In the breeding season after the experiment, chicks from “higher effort” treatment birds reached lower peak weights than chicks from control birds (520.2 ± 34.7g vs. 586.8 ± 22.9g, $n_{\text{control}}=4$, $n_{\text{higher effort}}=5$, LMM: $t_8=2.14$, $P = 0.0321$) while chicks from “lower effort” treatment birds also tended to reached lighter peak weights than controls but this was not significant (546.5 ± 20.8g, $n_{\text{lower effort}}=4$, $t_7=1.74$, $P = 0.0819$). There was no difference in fledging date between groups (LMM, $n_{\text{control}}=4$, $n_{\text{lower effort}}=4$, $n_{\text{higher effort}}=5$; $\chi_2^2 = 0.42$, $P = 0.812$).

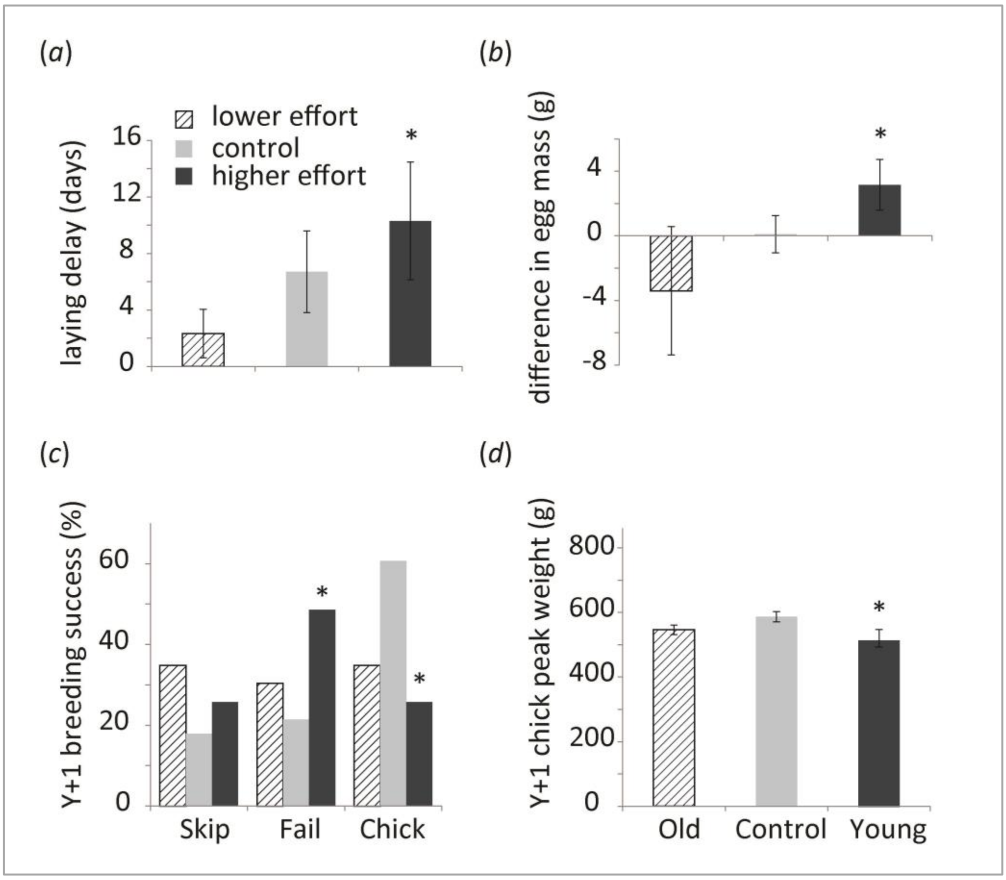

Figure 3. (*a*) Difference in laying date between Y0 (manipulation) and Y+1 (paired test), for all groups ("lower effort" treatment in white and black stripy pattern, control in light grey and "higher effort" treatment in dark grey). Note that the (colony) median hatch date in 2013 was slightly later than 2012, and 2014 was even later than 2013. (*b*) Difference in egg mass between Y0 (manipulation) and Y+1 (paired test), for all groups. (*c*) Breeding success of each group in the year following the manipulation (birds not recaptured not included). "Skip" refers to birds present on the colony but not breeding, "fail" refers to any bird which laid an egg and then failed at egg or chick stage, "chick" refers to birds which successfully fledged a chick. (*d*) Chick peak weight in Y+1 (a year after manipulation of the adults). Differences with the asterisks indicate significant differences between a treatment and the control group (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). Means ± SE.

Finally, we found significant differences in breeding success between the groups ($\chi^2_4 = 9.88$, $P = 0.042$). There was no difference in the proportion of birds skipping breeding the year after the experiment (13.9, 20.5 and 22.5% respectively for control, lower effort and higher effort treatments, $\chi^2_2 = 1.90$, $P = 0.386$). Out of 16 pairs which skipped breeding the next year, 6 did so in their usual pair (i.e. both members were present at the colony but did not breed); in the remaining 10 nests one of the two birds was not seen on the colony all year, and the missing partner was female in 8 of the 10 cases. Among the birds who bred, there were significant differences in breeding success between groups: controls had the highest breeding success (73.9 %), followed by "lower effort" (53.3 %) although the difference was not significant ($\chi^2_1 = 0.92$, $P = 0.384$). "Higher effort" treatment birds had a significantly lower success (34.6 %) than control birds ($\chi^2_1 = 6.07$, $P = 0.014$). The main results of the study are summarised in Figure 4.

Table 5. Summary table of difference in breeding characteristics between groups during the breeding season following the manipulation (year +1). The numbers show the difference between each treatment group and the control group, significant differences are underlined. When the differences were not significant most likely due to a small sample size we indicated the numbers followed by ns. In some instances ("comparison with…") the numbers represent within-group differences between years and not differences with control birds.

	LOWER EFFORT *(difference from control)*	**CONTROL**	**HIGHER EFFORT** *(difference from control)*
laying date (comparison with year 0)	3.7 ± 1.7 days earlier in year + 1 (ns)	no difference (<1 day)	<u>4.3 ± 3.2 days later in year+1</u>
egg mass (comparison with year 0)	3.4 ± 3.9 g heavier in year +1 (ns)	no difference (0.1 g)	<u>3.2 ± 1.1 g lighter in year+1</u>
chick peak weight	40.3 ± 20.8 g lighter (ns)	586.8 ± 22.9g	<u>66.6 ± 34.7 g lighter</u>
chick fledging date	no difference	7 Sept ± 2.7 days	no difference
birds skipping breeding	no difference	20.5 %	no difference
breeding success	53.3 % (ns)	73.9 %	<u>34.6 %</u>

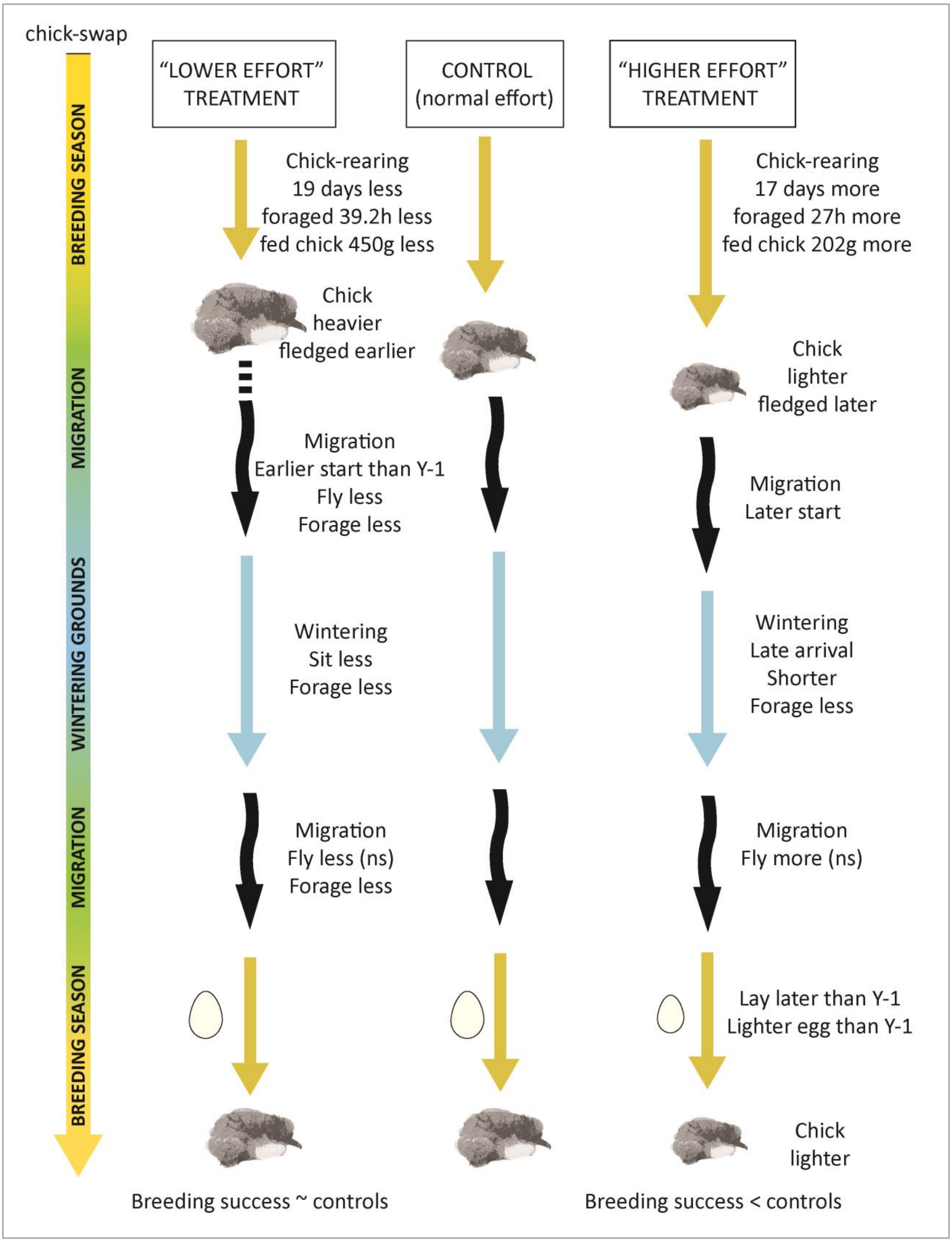

Figure 4. Summary figure of the observed effect of the chick-swapping manipulation on the breeding season, following non-breeding season and subsequent breeding season of all three groups. Only significant differences between treatment and controls are indicated, unless the trend was nearly significant ($P \leq 0.097$, indicated by ns).

Discussion

In this study we manipulated the duration of the chick-rearing period in Manx shearwater nests by cross-fostering chicks of different ages, and examined the immediate consequence of the manipulation on the parents, as well as the carry-over effects of this reduced or increased reproductive cost on their migratory and wintering phenology and behaviour during the subsequent non-breeding and breeding seasons.

As predicted, parents did not feed their chick for a fixed period of time but responded to the chick's needs (presumably via responsiveness to the chick begging), which resulted in all chicks fledging at a similar age and treatment birds finishing the chick-rearing period earlier or later than control birds. Swapping chicks resulted in an extension or shortening of the normal chick-rearing duration of about 25%. Despite being a much more subtle change than breeding failure used to study carry-over effects in other studies (Bogdanova et al. 2011; Catry et al. 2013), this was sufficient to generate significant differences in reproductive costs and detectable carry-over effects. Adults in manipulated nests invested different levels of effort into rearing their presumed chick. This is clearly illustrated by the significant differences in the total amount of food brought to the nest over the entire duration of chick-rearing by both members of a pair; our calculations are an underestimation as chicks were weighed several hours after feeding, however this should not affect relative comparisons between groups. Taken together, these results show that parents responded to the sudden change in chick age by adapting their chick-rearing period to match the demands of the chick, and did not simply feed the chick in their burrow for a fixed period of time after hatching. In a similar cross-fostering experiment in Atlantic puffins, Johnsen (1994) found that a higher proportion of adults with a prolonged chick-rearing period deserted their nests, which we did not observe here. However, this result may be more likely an effect of disturbance than a strategic decision not delay their migration, since puffins are known to be very sensitive to human intervention (Rodway et al. 1996).

Riou et al. (2012) found that Manx shearwaters manipulated in a similar way lowered their frequency of feeding during the season, regardless of having received a younger or older chick. We found no difference in the feeding frequency of the manipulated parents compared to controls; and there was no significant difference in the activity budgets of chick-rearing birds between groups. This suggests that adults did not alter their chick-rearing behaviour significantly despite the sudden change in chick condition after cross-fostering, but simply continued to feed at the same rate until the chick reached an acceptable condition for fledging. The different result obtained by Riou et al. (2012) may be due to their way of measuring feeding frequency, using an increase in daily weight of the chick as an indication of feeding. This is in an estimation of a joint feeding frequency for the pair, which heavily depends on the synchrony of the pair (e.g. a pair always feeding on alternate nights would have a feeding frequency twice as high as a pair feeding the same number of times but on simultaneous nights). Our method, using saltwater-immersion loggers, directly calculates the visit rate of each parent separately.

The chicks in the "lower effort" treatment group fledged earlier and heavier than control chicks, which themselves fledged earlier and heavier than chicks in the "higher effort" treatment group. The difference in fledging date is a direct result of the fact that in order to cross-foster old and young chicks, the old chicks had to hatch earlier than the young ones: with all chicks fledging at a similar age, this therefore resulted in differences in fledging date between groups. The difference observed in fledging weight (earlier fledglings, from the "lower effort" treatment group, were heavier, while late chicks in the "higher effort" group tended to be lighter) is naturally observed in Manx shearwaters, with earlier chicks having higher chances of survival and earlier breeders being more successful (Perrins 1966). The lack of difference in foraging effort between groups does not allow us to conclude that adults in the "lower effort" treatment group worked harder than in the control and "higher effort" treatment groups; it may simply be a consequence of a better match between resource availability and chick demand, as observed in many species (Ben-David 1997; Regular et al. 2014). Resource availability may quickly plummet towards the end of the breeding season and parents still foraging for their chick after mid-late August may catch less food per unit of time spent foraging; this would be reflected in the chicks' weight.

Manipulating chick-rearing duration affected the timing of adult migration. While control birds started their migration at similar times in all years, those with an extended chick-rearing period left later than in non-experimental years, and also later than control birds. However, although birds with a shortened chick-rearing period started their migration earlier than in other years, they did not leave significantly earlier than the control birds in the experimental year, despite finishing breeding earlier. Furthermore, all birds started the spring migration at similar times despite reaching the wintering grounds at different times. While

Jonker *et al.* (2011) found no link between the end of breeding and the start of migration in geese, previous studies of seabirds have found that the timing of departure on migration depended on the end of breeding (Bogdanova et al. 2011; Catry et al. 2013). These two latter studies showed that (natural or induced) failed breeders started migration earlier than breeders. In our study, birds which finished breeding early did not start to migrate earlier; however shortening the breeding season by less than three weeks is less dramatic than breeding failure which can occur several months before migration. We found a link between the end of breeding and the start of migration, but only in birds breeding late; this is consistent with results in short-lived species (Rehling et al. 2012), but to our knowledge had not been shown in long-lived migratory species.

Theoretical models suggested that the decision to start migration heavily depends on the bird's body condition, and that birds which migrate late after breeding may not have enough time to recover sufficient reserves in time for the following breeding event (McNamara et al. 1998). However they also show that different selection pressures may apply on spring and autumn migration and that the timing of migration is more critical in spring. This is consistent with our findings that "higher effort" birds delayed their autumn migration but not their spring migration, despite reaching the wintering grounds later. Taken together, our results suggest that there is no benefit to leaving on migration as early as possible, but rather that there is an ideal timing of migration, which is followed by birds which finish breeding early enough, but missed by late breeders. Perhaps resources at the wintering grounds are not good enough earlier in the season, or perhaps the conditions are only favourable to the long trans-equatorial migratory journey during a specific seasonal time window (Felicísimo et al. 2008). This could help explain why despite early breeders rearing heavier and earlier fledglings with higher survival rates, there does not seem to be a selection pressure to lay ever earlier (Price et al. 1988). Perrins (1966) and Brooke (1990) proposed that the lack of food resources at the breeding site earlier in the season prevents females from laying or incubating an egg any earlier. Our results suggest that the conditions at the breeding site may not be the only determinants of the timings of events in the annual cycle, but that conditions during migration and at the wintering grounds may also play a role. External factors such as weather conditions or food availability may constrain the timings of migration, and could prevent birds from starting their spring migration early enough to breed as soon as the conditions at the breeding grounds allow. Theory predicts that penalties for early or late arrival in spring migration are higher than in autumn (McNamara et al. 1998), while environmental factors and quality of the wintering grounds have been shown to affect migratory timings in passerines and waders (Marra et al. 1998; Forchhammer et al. 2002; Hüppop and Hüppop 2003; Gunnarsson et al. 2006). Constraints of external factors on migration and wintering phenology are not mutually exclusive with Brooke's and Perrins' theory of unfavourable early conditions at the breeding site in Manx shearwaters, but these early conditions may never be experienced by birds if they occur before the earliest possible return to the colony. External constraints on timing of spring migration as the main limiting factor to early breeding in Manx shearwaters would explain why we do not observe a normal distribution of success in relation to laying date (which would be expected if early laying was only limited by conditions at the breeding site), but a truncated distribution which only decreases with date.

There was no obvious difference in the spatial distribution of the different groups of birds during the winter, and all birds followed similar migratory routes. However, our classification of saltwater-immersion data revealed differences in the activity of birds in different treatment groups. Throughout the non-breeding season, birds in the "lower effort" treatment group, which finished breeding earlier than others, spent less time engaged in energy-demanding activities such as foraging (throughout) and sustained flight (both migrations), and more time sitting on the water surface (winter). This suggests that overall they spent less energy travelling and searching for food, perhaps because they were in better condition. There was no difference between these birds' behaviour during the experimental and non-experimental years, however this may be due to the smaller sample size in non-experimental years. Two studies found a positive correlation between the amount of time spent foraging during the non-breeding season and lay date (Daunt et al. 2014) or the likelihood of skipping breeding (Shoji et al. 2015), suggesting that birds which forage more in winter do less well the following breeding season. Some of our results are in agreement with these findings ("lower effort" birds foraged less than controls and had a higher breeding success than "higher effort" birds the next season). However, "higher effort" birds, which started migrating later, also spent less time foraging than controls during the winter, despite laying later the next season. Why this is the case is unclear. Comparing the activity budgets of these birds with non-experimental years showed that they spent less time sitting on the water surface during the winter of the manipulated year than in other years, suggesting that they had a more energy-demanding non-breeding season following manipulation, which also resulted in later laying, which supports findings from Daunt et al. (2014). This may indicate an attempt to regain condition after a more costly breeding season induced by the extended chick-rearing period. The reason why control birds spent less time foraging and more time sitting during the experimental winter than during the other winters is also unclear, but could be due to a difference in resources availability between years. For example, it is possible that the experimental years were "good" years with high resource availability; this would presumably reduce differences between groups and could potentially explain why the main differences in at-sea activity we observed between groups were between experimental and non-experimental years and not within experimental years. Alternatively, it might be possible that birds recognized that it was not their chick in the burrow and all decreased their parental effort. This seems unlikely however, as several species of shearwaters have been shown to provision a foster chick normally (Hamer and Hill 1994), and even try to provision a second chick when placed in the burrow (Perrins et al. 1973).

Carry-over effects from the manipulation were visible during the next breeding season despite similar return dates to the colony between groups, usually a strong predictor of breeding performance in migratory species (Kokko 1999; Bêty et al. 2003). In the experimental year, prior to chick manipulation, birds from the three groups laid eggs at significantly different times (the "higher effort" treatment group was the earliest, followed by the control group and then the "lower effort" treatment group). The following year there was no difference in laying dates between any of the groups, indicating that some birds had changed their lay date with respect to the previous year. Indeed, while control birds laid at a very similar date the year after the experiment, birds which had a higher reproductive effort the previous year laid significantly later than before manipulation. They also laid smaller eggs, which was not the case in control birds. Although there were trends for birds with a lower reproductive effort the previous year to lay larger eggs earlier, the difference was not significant, perhaps because of issues with statistical power. We also found differences in the peak weight of chicks, usually a good proxy for survival (Perrins et al. 1973)). Adults which had to invest more in chick-rearing the previous season reared significantly lighter chicks; there was no difference between the chicks of control birds and those whose parents had an easier season the year before. However fledging date, which is also a proxy for survival but can be influenced by external factors such as moon phase, was similar across all groups. Egg size is usually associated with egg quality, hatching and fledging success in several species of birds, including seabirds (Parsons 1970; Schifferli 1973; Croxall et al. 1992), although a similar effect has not yet been shown in Manx shearwaters (Brooke 1977). Studies showing that female shearwaters tend to lay eggs of similar size, at similar dates, each year (Brooke 1990), led to claims that birds are "programmed" to do so. Our results demonstrate that this is not the case and that the previous year's reproductive effort (and most likely the previous winter) can significantly affect laying date, egg size, and chick quality. The consistency observed in natural conditions may result from a constant individual quality across the years which may act as a virtuous/vicious cycle: earlier, good quality breeders can start migration earlier and have more time to regain condition during the winter, therefore being in a better position for the following year; while the opposite happens in lower-quality breeders. Our results demonstrate that this can be changed if breeding is disrupted.

The carry-over effects observed during the breeding season following the manipulation also directly affected breeding success. While the manipulation did not seem to affect the probability of skipping breeding (our skipping rate was similar to the ~20% usually observed, Brooke 1990), it did affect the probability of fledging a chick. Birds with higher reproductive costs in the experimental year had a lower breeding success the following year, with many laying a (smaller, later) egg and failing to hatch it. This could be a consequence of a lower quality egg, and/or of an inadequate incubation due to the adults being in a poorer body condition. Control birds had the highest breeding success, but although the breeding success of the birds with a lower reproductive cost the previous year was not significantly different, it was lower and the lack of significance may be due to a small sample size. Taken together, these results suggest that a higher reproductive cost one year can significantly decrease reproductive success the following year, and that a lower reproductive cost may have opposite, but not necessarily symmetrical, effects. The lack of significant differences observed between control and "lower effort" treatment birds could be due to the fact that the latter may inherently be lower quality breeders; indeed they were naturally late breeders to be able to be matched with early breeders from the other treatment group. Therefore, the positive carry-over effects from the shortened chick-rearing duration could have been masked by lower parental quality. It is important to note that the results observed in this study are not an artefact due to treatment groups containing mostly late or early breeders: indeed, the effects which could have been caused by this bias would have been the opposite of what we observe here (i.e. "higher effort" birds, natural early, high-quality breeders, would have done better than controls, while “lower effort” birds, naturally late, poorer-quality breeders, would have done worse). Therefore, if the experiment were to be repeated with each treatment group perfectly randomly sampled from the population, the same results should be found, only stronger (and the trends we observe in the “lower effort” group to do better than controls following the manipulation may become significant). It is also interesting to note that while approximately half of the birds which skipped breeding did so in pairs, the rest were missing a partner, and most of these missing birds were female. This suggests that females may be more sensitive to changes in reproductive costs and more subject to carry-over effects. Because females lay eggs and therefore are more likely to dictate the phenology of breeding, it is possible that the carry-over effects observed in the breeding season the year after the manipulation were mainly occurring in females, and that males were less affected. Disentangling the sex-effects from the carry-over effects of the previous breeding events would require further experimentation, for example by targeting a single member of a pair when modifying reproductive cost.

In summary, by manipulating the cost of reproduction in two opposite ways in a long-lived bird and tracking its breeding, migratory and wintering behaviour for the following year, our study measures the carry-over effects of breeding on future reproductive events, but also starts shedding light on how these effects develop, and modify the animal’s behaviour year-round. Birds with a lower reproductive effort generally spent less time the following non-breeding season engaged in foraging and flight, and spent more time engaged in resting (sitting) behaviour; their breeding phenology and reproductive success the following year was similar to that of control birds. On the other hand, birds which invested more effort in breeding delayed their migration and shortened their stay at the wintering grounds; they spent less time engaged in resting behaviour than in normal years, also spending more time in flight during migration. They started breeding later the following season, their brood was of poorer quality and their reproductive success was significantly lower. Interestingly, the manipulation did not change the proportion of birds skipping breeding the following year, perhaps because the change in reproductive cost was too small (increase or decrease of chick-rearing period by ~25%) to prompt such a dramatic shift, or because the conditions at the wintering grounds were good enough to allow the birds to regain enough condition to attempt breeding the next year. Another interesting point is that birds which finished breeding early did not start their migration earlier than control birds, which suggests that the limitation of early breeding, despite its positive effect on fitness, may be driven by constraints on the non-breeding season and not only, as previously thought, by conditions at the breeding region. This study is to our knowledge the first to examine and measure in detail the carry-over effects of breeding throughout the following annual cycle in an experimental setting, and our results shed light on a currently poorly understood phenomenon but also reveal the complexity of the mechanisms behind carry-over effects, which we are just starting to unveil.

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Supplementary Material

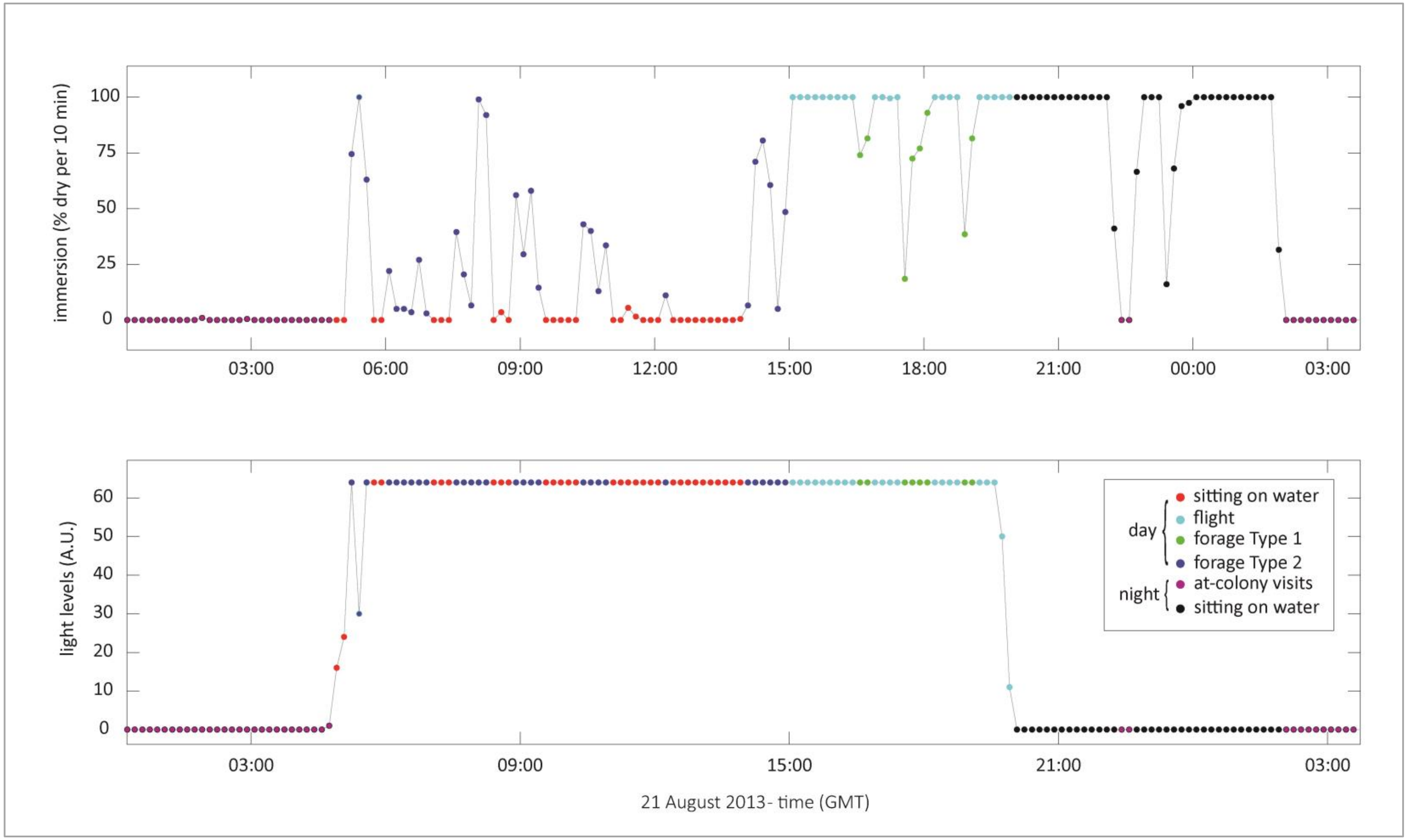

Figure S1. Example of the classification in 6 states of a 24h-period during the breeding season.

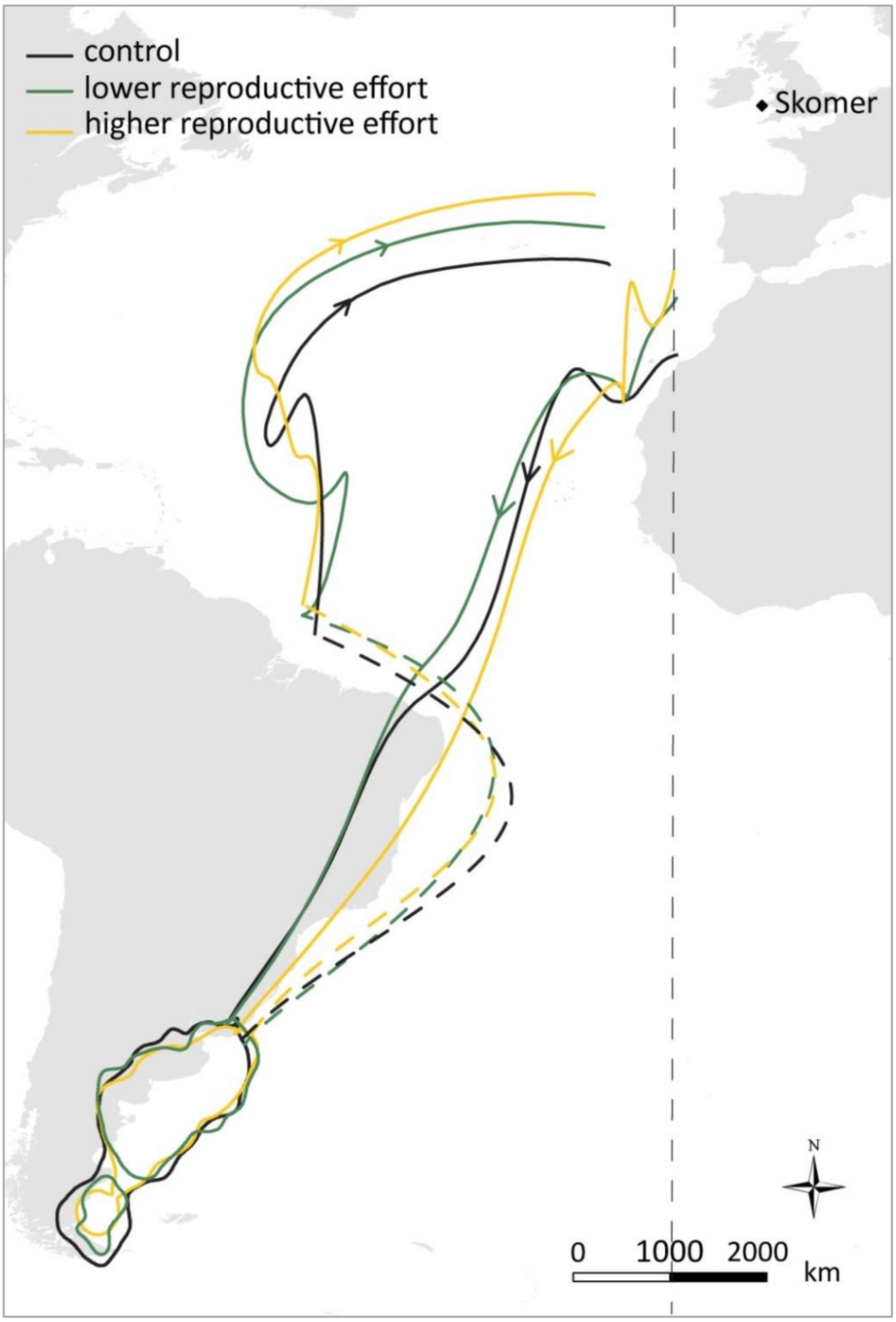

Figure S2. Mean autumn and spring migration routes of the three treatment groups (black: control, orange: "old" treatment i.e. lower reproductive effort, green: "young" treatment i.e. higher reproductive effort) in the non-breeding season following the chick cross-fostering. The black dashed vertical line across the Atlantic Ocean is the -12 degrees meridian which was used to quantify the start of the autumn (southwards) migration. The dashed parts of the spring (northwards) migration routes represent the approximate routes followed by the birds during the first part of the journey around south America (the data are made inaccurate by proximity to the equinox). The 95% occupancy kernels for each group during the wintering period are shown with the same colours (kernels calculated in ArcGIS 10 with a cell size of 25km and a bandwidth of 225km.

Chapter 6

Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird

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Fayet AL, Freeman R, Shoji A, Padget O, Perrins CM, Guilford T. 2015. Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird. Animal Behaviour 110: 79-89.

Abstract

Competition, and ultimately adaptive specialisation, are the major ecological forces behind spatial segregation in foraging distributions, and are commonly driven by size-related differences in competitiveness between sex, ages or social status. However such segregation can also be observed in long-lived monomorphic species, often between immature and breeding individuals. In many of these species, individuals often forage in patchy and potentially unpredictable environments where resources can be spread over large scales and be difficult to find, and efficient foraging may require advanced cognitive skills (for example in navigation and memory). Particularly in species with deferred breeding, experience rather than size may be an important driver of segregation and lead to differences in competitiveness between young and old, but whether there is a relationship between age, foraging efficiency and spatial segregation has never been properly investigated. Here we test this hypothesis by simultaneously tracking individuals at different life stages in a long-lived seabird, the Manx shearwater *Puffinus puffinus*, during a period of central-place foraging around the colony, to investigate spatial segregation, and by measuring foraging efficiency by combining an etho-informatics approach and mass gain. We find substantial spatial segregation between immature and breeding adults, and we find that immatures gain less mass per unit of time spent foraging than adults, foraging in less productive waters than adults, suggesting lower foraging efficiency, most likely due to inexperience.

Introduction

Spatial segregation in foraging distributions driven by competition, which can eventually lead to adaptive specialisation, is observed in a wide range of animal taxa, and often arises from size-related differences in competitiveness between sex, ages or social status (e.g. Harcourt et al. 1976; Gosler 1987; Durant et al. 2004; Webb et al. 2012). Long-lived animals with advanced cognitive capacities (vertebrates) may be able to exploit patchy, expansive, and potentially unpredictable environments using individual memory and experience. This could provide a different mechanism driving spatial segregation - even in monomorphic species - if older, more experienced individuals competitively displace younger cohorts through enhanced foraging efficiency. Higher adult foraging efficiency could result from two (not mutually exclusive) mechanisms: first, adults could have superior hunting skills, resulting in a higher food gain per unit of time spent foraging in areas of similar productivity; second, adults may exploit areas of higher productivity. Either hypothesis would lead to age-related differences in space use correlated with differences in foraging efficiency.

Spatial segregation between immature (non-breeding) and breeding adults during all or part of the year occurs in many species (e.g. in primates, Harcourt et al. 1976; other mammals, Jarman 1974; Cheney and Seyfarth 1983, Durant et al. 2004; birds, Webb et al. 2012; and insects, Robertson and Cushing 2011). Immatures have been found to disperse more and cover greater ranges than breeders, although in some species they have been reported to undertake smaller-scale movements than adults (Field et al. 2005). Understanding such differences is of paramount importance when considering the demography of a species or its conservation needs. It has been suggested that spatial segregation between immature and adult individuals may be due to differences in foraging experience (Lack 1954), and lower foraging efficiency has been documented in some species(Maclean 1986; Lefebvre 1995; Daunt et al. 2007; Le Vaillant et al. 2012), however the relationship between efficiency and spatial segregation has never been properly tested.

Here we investigate this relationship in a long-lived pelagic seabird, the Manx shearwater *Puffinus puffinus*. Pelagic seabirds, like many other marine animals, are long-lived, with a prolonged immature period. They forage in an open and patchy environment which can be unpredictable, depending on the type of marine habitat used and the spatial and temporal scales of their foraging trips (Weimerskirch 2007). This may not only give them more opportunities to segregate, but may also make learning and experience particularly important in the development of the skills necessary to forage effectively, e.g. to navigate to distant areas in a featureless environment, to identify and memorise productive areas and often ephemeral prey distributions. This makes them particularly useful model organisms to study stage-related spatial segregation and changes in foraging skills over time; however few studies to date have attempted to do so, mainly because of the logistical challenges involved with tracking non-breeding individuals. Very little is known about the behaviour and distributions of immature pelagic seabirds (Lewison et al. 2012; Shillinger et al. 2012). Studies in penguins, albatrosses and a few large procellariiformes have found that immature seabirds may be more flexible in their destinations and cover a greater spatial range during non-breeding (usually long-scale) movements in the winter (Kooyman et al. 1996; Clarke et al. 2003; Kooyman and Ponganis 2007; Trebilco et al. 2008; Péron and Grémillet 2013; Sherley et al. 2013; Pelletier et al. 2014; Thiebot et al. 2014). However, few have investigated their foraging movements during the breeding season when both adults and immatures act as central-place foragers (Votier et al. 2011; Péron and Grémillet 2013; Riotte-Lambert and Weimerskirch 2013). During this period, stage-related spatial segregation is likely to arise: parental duties force adults to return to the colony regularly because of changes in the cost-benefit trade-offs of different foraging locations. While immatures are not constrained to a colony, they tend to visit their natal colony (or others), generally during a restricted part of the breeding season, to prospect for future nest sites and mates (Harris 1966; Perrins et al. 1973; Dittmann and Becker 2003; Major and Jones 2011). Immature Scopoli's shearwaters *Calonectris diomedea* showed some spatial segregation from breeding adults, but the sample size and resolution of the data are too low to make any strong conclusion (Péron and Grémillet 2013). Votier and colleagues (2011) showed that immature gannets *Morus bassanus* went further on longer foraging trips and visited other colonies on the way, unlike immature wandering albatrosses *Diomedea exulans* which engaged on shorter trips (in duration and distance) (Riotte-Lambert and Weimerskirch 2013). However, although both studies suggested that these differences could be a consequence of differences in foraging abilities, they did not test this hypothesis, which is our aim here.

Immature Manx shearwaters start to return to the colony in large numbers in their third year, and for 2-3 years spend over a month each summer regularly visiting the colony (Perrins et al. 1973). This makes them an ideal species to realise simultaneous comparisons of the central-place foraging behaviour of immature and breeding adults. Here we investigate the relationship between efficiency and spatial segregation in Manx shearwaters by tracking simultaneously immature and breeding individuals with a mix of archival and remote-download GPS loggers to investigate potential spatial segregation, while inferring individual foraging efficiency by combining an etho-informatics analysis of the high-resolution GPS logs to identify different behaviours at sea and estimate foraging effort, and at-colony measurements of foraging success (daily mass gain). We also examine proxies of marine productivity for the areas in which birds foraged to determine whether any segregation is related to potential differences in habitat quality.

Methods

Ethical Note

All work adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, and was conducted after ethical approval by the British Trust for Ornithology Unconventional Methods Technical Panel (permit C/5311), Natural Resources Wales, Skomer Island Advisory Committee and the University of Oxford's Local Ethical Review Process. To minimise disturbance, handling was kept to a minimum (<10 min for each deployment/retrieval). Similar techniques and loggers have been deployed on adults Manx shearwaters on this colony since 2007 and no significant effect was recorded (Freeman et al. 2013; Shoji et al. 2015). When possible lighter devices were deployed on immatures, on average the devices represented an extra 0.4% (~1.4g) of the immatures' body mass compared to adults, less than the 5g accuracy of our weight measurements and equivalent or less than loads shown to have no significant short-term effect in closely related species (Igual et al. 2004; Passos et al. 2010). Therefore we are confident that our results are not biased by a greater impact on immatures. It was not possible to monitor the survival of immature birds as they do not return to a specific nest, but all adults had a similar or higher breeding success than the rest of the colony after the experiment (Skomer Island seabird monitoring reports 2013-2014).

Study site and model species

The study was carried out on Skomer Island, Wales (51°44'N, 5°19'W), probably the largest Manx shearwater colony in the world (~300,000 breeding pairs; Perrins et al. 2012), in June - July 2013 and 2014. Manx shearwaters are c. 400g colonial burrow-nesting monomorphic seabirds which mainly breed on the Northeast Atlantic coast. The peak of attendance of immatures at the colony is between mid-June and mid-July (Harris 1966; Perrins et al. 1973), which coincides with the end of the incubation period and the start of the chick-rearing period. Although hundreds of thousands of immatures visit the colony every year, their at-sea movements and behaviour during this period are currently unknown.

Deployment of devices

Since immatures appear similar to adults they were identified first by their behaviour on the surface – e.g. prolonged amounts of time on the surface, long periods of immobility, prospecting movements, no strong directional movement towards a particular burrow, quick exploration of many burrows (Brooke 1990) - and then by the absence of a brood patch, having been caught by hand. Breeding adults in study burrows were monitored regularly, via an access hatch, from the start of the breeding season. 50 immature birds (20 in 2013, 30 in 2014), 14 adults at the end of their incubation shift (4 in 2013, 10 in 2014) and 13 chick-rearing adults (2013) were selected for simultaneous device deployment (breeding was later in 2014, therefore all adults were still incubating during the peak of immature attendance at the colony, while in 2013 many nests had already hatched at the peak attendance and so we were able to track simultaneously incubating and chick-rearing adults). All birds were weighed and ringed with a metal ring from the British Trust for Ornithology. IgotU GT-120 (Mobile Action Technology Inc., both years) and remote-download Mataki trackers (Mataki.org, 2013) stripped of external casing and waterproofed in heatshrink tubing were configured to record positions every 15min (IgotU) or 60min (Mataki). The latter were also configured to emit a radio signal and look for a download base station every 30min. Devices, made visible with retro-reflective tape for retrieval, were attached to birds' backs using thin strips of marine tape (Tesa 4651 with water-soluble adhesive, see Guilford et al.(2008) for details of the methods), and designed to fall off within 2-3 weeks if the bird is not recaptured. Devices (including waterproofing and tape) weighed <19g (IgotU) or <17g (Mataki), which is under 5% of the average total individual body mass. A mix of Mataki and archival GPS loggers were deployed on immatures, while all adults carried an archival logger. Handling time was kept to a minimum (~10min) and birds were released on the colony after deployment.

Retrieval of devices

In the 3 weeks following deployment, 3 observers were posted each night in the capture area, using low intensity red light and night-vision scopes to observe the colony and look for immature study birds. In 2013, 2 remote-download base stations were also installed, each able to detect a radio-signal from any devices within ~200m. Birds seen with a device were caught by the closest observer. In total 20 immatures were recaptured, their device retrieved and data successfully downloaded. At least 2 more birds were seen but evaded recapture. For adults, burrows were inspected at regular intervals every night and birds returning had their device removed after 7 or more days or deployment, were weighed then replaced in the burrow. In the case of chick-rearing adults, they were first left for 30min in the burrow to feed their chick. All 27 adults returned but 6 had lost their GPS, so in total we retrieved 21 trackers and successfully downloaded data from 19.

All birds were weighed after device removal using a spring balance (±5g). For chick-rearing adults the return mass was estimated as the mass of the adult after feeding its chick plus the overnight mass gain of the chick (x 0.5 when both parents visited the nest that night).

Data processing and analysis

Only at-sea data (>5km from the colony) were considered (apart from at-colony behaviour analyses), and interpolated to 1-min positions using piecewise cubic hermite polynomials in MatLab (version R2013a, The MathWorks), as in Tremblay et al. 2006). Ground speed was calculated and a 90km/h threshold applied to remove erroneous positions (Guilford et al. 2008). Average flight speed was calculated on data >7km/h (threshold obtained from our bimodal distribution of speed). Individual foraging trips were identified (range: 1-5 trips per individual).

Statistics

We used Linear Mixed Models (LMMs) to test the effect of breeding stage on foraging trip length, daily distance covered, maximum distance from the colony, and average flight speed, and Generalised Linear Mixed Models (GLMMs) to test for differences in minimum and maximum latitudes (Gamma distribution) and trip duration (Poisson distribution), with individual and year as random factors included in all models. In addition, using the bimodal distribution of trip length to choose a threshold of 3 days, we identified short and long trips and tested them separately, using the same models, to test whether the differences observed could be accounted for entirely by trip length alone. Because all incubating trips are >3 days, and to avoid potential issues with statistical power, breeding stages were not separated in this part of the analysis. P-values were obtained by comparing our models to null models (with the random effects but without the fixed effect of interest) with a χ^2 test.

Density kernels representing the core foraging distributions were calculated using a cell size of 2km, with an optimal bandwidth of 86km estimated by a least-squares cross-validation ({*sparr*} package, R) (Geospatial Modelling Environment, Spatial Ecology Ltd). Distribution overlaps were estimated with the {*adehabitat}* package in R, and significance levels were assessed using bootstrapping (i.e. each trip was randomly allocated to the adult or immature group, a new overlap was computed and compared to the observed value; this was repeated 1000 times for each of the 25, 50 and 95% kernels).

Distinctly different activities at sea, such as active foraging, resting, or sustained flight, are reflected in distinguishable distributions of variables derived from the precision GPS tracks, such as speed and turning angle. These states can be statistically determined using Gaussian mixture models (GMMs). GMMS are hierarchical models which, given variables (here speed and turning angle) and a number of states, identify the most likely parameters (means and (co)variances and weights) of these states; the models then assign each datapoint with a probability of having been generated by each state and these can then be classified to their most probable state (see Bishop 2006 for more details on the methods and Guilford et al. 2009; Freeman et al. 2010) for examples of use to classify animal behavioural states). We used AIC to select the optimal number of states, 3, which is consistent with other mixture models run on similar datasets for the same species (Figure S1, Dean et al. 2012; Freeman et al. 2013).

Differences in the proportion of each behaviour between breeding stages were tested with LMMs. Differences in daily patterns of the 3 states between stages were tested with Kolmogorov-Smirnov tests. We tested the effect of mass on trip duration and potential differences in daily mass gain between stages with LMMs.

Sea-surface temperature (SST, °C) and chlorophyll A concentrations (mg/m^3) were extracted from the NASA OceanColor website using data from the MODIS Terra and Aqua satellites, using a spatial resolution of 4km and a temporal resolution of 8 days. Net primary productivity (NPP, $mg/m^2/day$) data (8km resolution), estimated from chlorophyll, light and photosynthetic efficiency values using the Vertically Generalized Production Model algorithm, were obtained from the Ocean Productivity website. Each location in our tracking dataset was assigned a SST, chlorophyll a and NPP value, and after log-transformation of NPP and chlorophyll a concentration, LMMs were used to test for differences between groups, with individual and year included as random effects.

Results

Differences in foraging trips

We compared 29 trips from 6 incubating and 13 chick-rearing adults and 36 trips from 20 immatures. The foraging trips of immatures were significantly shorter than those of incubating adults (3.7 ± 0.6 vs. 9.3 ± 1.2 days, GLMM (Poisson): $n = 42$ Z = 3.17, $P = 0.002$) but not of chick-rearing adults (4.9 ± 0.7 days, GLMM (Poisson): $n = 59$, Z = 1.55, $P = 0.121$, Figure 1a). Immatures also covered less distance than chick-rearing adults each day (LMM: $n = 59$, t = 2.72, $P = 0.028$, Figure 1b), and stayed closer to the colony than all adults, even after removing one extraordinarily long incubating adult trip to the Atlantic (LMM: Imm:Egg: $n = 41$, t = 2.49, $P = 0.035$; Imm:Chick: $n = 59$, t = 2.30, $P = 0.035$, Figure 1c). Chick-rearing adults' mean flight speeds were also significantly higher than immatures' (23.0 ± 0.7 vs. 18.2 ± 0.6 km/h, LMM: $n = 59$, t = 5.25, $P < 0.001$, Figure 1d).

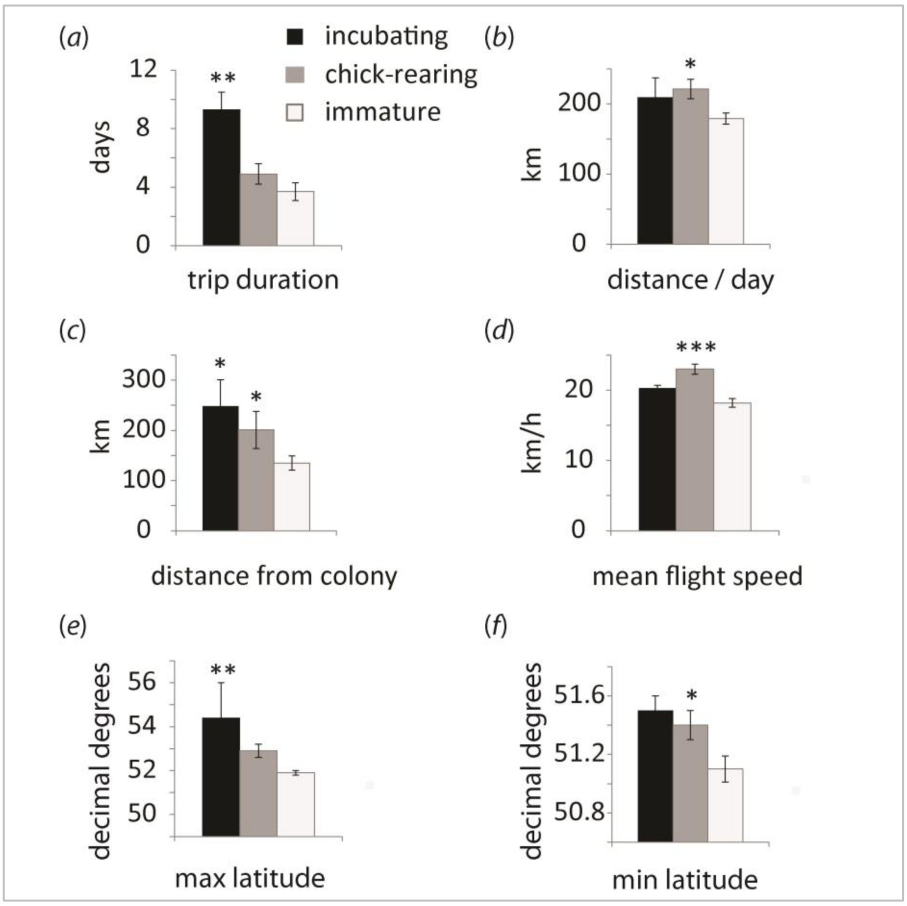

Figure 1 – Trip characteristics of immatures (white), incubating (black) and chick-rearing (grey) adults: (*a*) trip duration, (*b*) distance covered per day, (*c*) ,maximum distance from the colony, (*d*) mean flight speed, (*e*) maximum latitude and (*f*) minimum latitude (mean ± SE). Asterisks represent significant differences between adults and immatures (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). For significance levels between incubating and chick-rearing adults see Table S1.

To investigate these differences further and test whether they could be accounted for entirely by trip length (which varied substantively between immatures: range 1-15 days), we analysed short and long trips separately. The distribution of trip durations was bimodal, which allowed us to identify a threshold of 3 days to classify trips as long (> 3 days, $n_{\text{immature}} = 15$, $n_{\text{adult}} = 19$) or short (≤ 3 days, $n_{\text{immature}} = 21$, $n_{\text{adult}} = 10$). Adults covered more distance each day but the difference was only significant on short trips (LMMs: short trips: $n = 31$, $\chi^2 = 9.04$, $P = 0.003$; long trips: $n = 34$, $\chi^2 = 3.75$, $P = 0.052$). They still travelled further from the colony but only on long trips, even without the long adult trip to the Atlantic (LMMs: short trips: $n = 31$, $\chi^2 = 0.01$, $P = 0.919$; long trips: $n = 33$, $\chi^2 = 6.36$,

$P = 0.012$). Adults' mean flight speed remained higher than immatures' in both short and long trips (LMMs: short trips: $n = 31$, $\chi^2 = 15.94$, $P < 0.001$; long trips: $n = 34$, $\chi^2 = 5.55$, $P = 0.018$) (see Table S1 for all means and statistics).

Spatial segregation

We found significant differences between the destinations of adult and immature birds. On average, adults went to significantly higher latitudes than immatures (GLMM (Gamma): $n = 65$, parameter estimate: 5.4 E-4 ± 2.6E-4, t = 107.4, $P = 0.029$, Figure 1e); while immatures went significantly further south (GLMM (Gamma): $n = 65$, parameter estimate : 2.0 E-4 ± 0.8E-4, t = 200.1, $P = 0.013$, Figure 1f). This held when we looked at short and long trips separately (Table S1). There were differences between the occupancy contours of adults and immatures, at the 95%, 50% and 25% density levels. The overlap of the core distributions of adults and immatures, which was below 20% at the 50% occupancy level and below 5% at the 25% occupancy level, was significantly lower than expected by chance at the 25% and 50% level (25%: 4% overlap, $P = 0.020$; 50%: 19% overlap, $P = 0.045$, 95%: 83%, $P = 0.377$, P-values obtained from bootstrapping with 1000 iterations, Figure 2). These differences were not due to different trip durations between groups, as the overlap between adults and immatures remained small when looking at short and long trips separately (Figure 2c). Overlap of core distributions occurred near the colony, near the southern Irish coast and in the middle of the Celtic Sea. The most striking segregation was in the Irish Sea, which was visited by a single immature but over 50% of adults. This was not due to the Irish Sea trips taking too long for immatures: all adult trips in the Irish Sea lasted 6-12 days and only one of seven immature trips in this range of duration was to the Irish Sea (vs 10 of 18 for adults). Rather than the Irish Sea, the south Celtic Sea and around the Cornish peninsula were used disproportionally by immatures; over 40% ventured south of the Bristol Channel and even south of the UK into the Channel, while only 10% of the adults went to such low latitudes (and none to the Channel). Both groups foraged in the Celtic Sea, but more adults favoured the Irish south coast while more immatures foraged along the coast of North Wales.

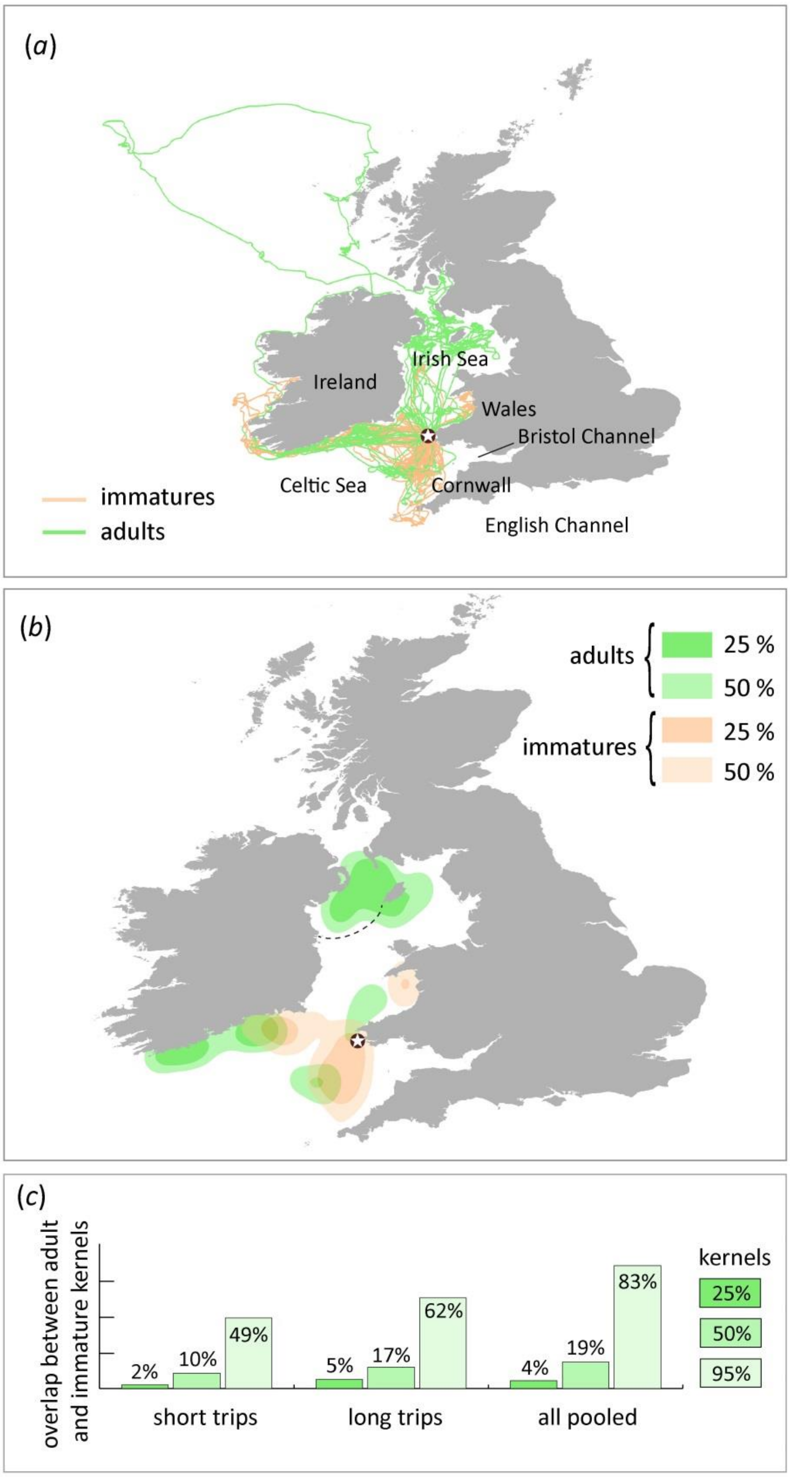

Figure 2. (*a*) Raw tracks from the 20 immature (orange) and 19 adult (green) shearwaters in 2013 and 2014. (*b*) 50% and 25% occupancy kernels of immatures and adults calculated on the whole dataset. The colony is indicated with a star, and the approximate position of the Irish Sea Front with a dashed line. (*c*) Overlap between 25%, 50% and 95% occupancy kernels of adults and immatures, with all trips pooled (n = 65) or separated by trip duration (short: n = 31; long: n = 34).

At-sea behaviour

The optimum number of behavioural states identified with our Gaussian mixture model was 3. The three states are taken to identify approximately foraging (low speed, high turning angle), sustained flight (high speed, low turning angle) and resting (low speed, low turning angle) (Table 1, Figure 3).

Table 1. Metrics of the 3 classes of behaviour as identified by a Gaussian mixture model.

	Ground speed (km/h)	Turning angle (°)	% of time in incubating adults	% of time in chick-rearing adults	% of time in immatures
Class 1: "foraging"	5.85 ± 0.10	129.56 ± 0.52	17.5 ± 0.1	14.0 ± 0.8	14.1 ± 0.5
Class 2: "sustained flight"	34.19 ± 0.20	19.32 ± 0.47	13.8 ± 3.1	16.0 ± 1.6	11.1 ± 1.0
Class 3: "resting"	4.01 ± 0.04	21.35 ± 0.21	68.6 ± 3.2	69.9 ± 1.4	74.7 ± 1.0

Birds spent most of their time "resting" on the water, with "foraging" the second and "sustained flight" the least common behavioural class at sea. All adults and immatures spent similar proportions of time flying (LMM: Imm_Egg: parameter estimate 0.03 ± 0.03, t = 0.92, P = 0.60; Imm_Chick: parameter estimate 0.04 ± 0.02, t = 2.4, P = 0.51; Egg_Chick: parameter estimate -0.02 ± 0.03, t = -0.63, P = 0.70). However, immatures spent less time foraging and more time resting than incubating adults (LMMs: foraging: Imm_Egg: parameter estimate 0.03 ± 0.01, t = 2.34, P = 0.023; Imm_Chick: parameter estimate -0.005 ± 0.01, t = -0.06, P = 0.33; Egg_Chick: parameter estimate -0.03 ± 0.02, t = -2.33, P = 0.07; resting: Imm_Egg: parameter estimate -0.06 ± 0.02, t = -2.24, P = 0.044; Imm_Chick: parameter estimate -0.05 ± 0.02, t = -2.56, P = 0.134; Egg_Chick: parameter estimate 0.006 ± 0.03, t = 0.23, P = 0.65).

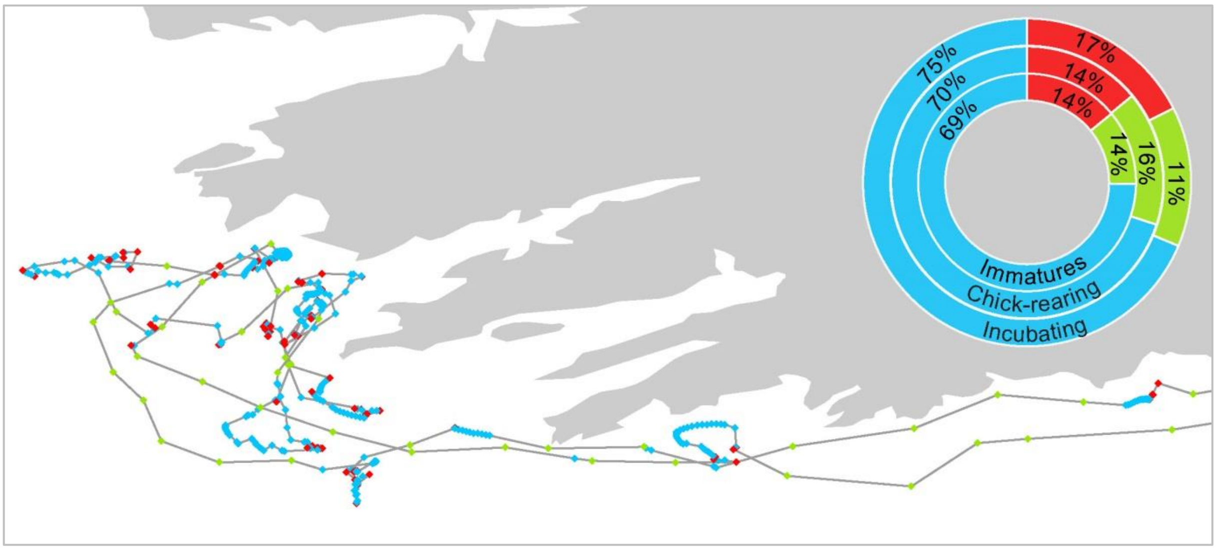

Figure 3. Example of behavioural classification of part of a foraging trip, and percentage of time spent foraging (red), flying (green) and resting (blue) for immatures, incubating and chick-rearing adults across whole dataset.

Despite adults and immatures travelling to largely separate locations, the patterns of daily activity were similar between stages (KS tests, $n_{imm} = 16$, $n_{egg} = 6$, $n_{chick} = 13$: foraging: $D_{\text{imm:egg}} = 0.17$, $P = 0.89$, $D_{\text{imm:chick}} = 0.20$, $P = 0.67$, $D_{\text{egg:chick}} = 0.25$, $P = 0.44$; flying: $D_{\text{imm:egg}} = 0.25$, $P = 0.44$, $D_{\text{imm:chick}} = 0.33$, $P = 0.14$, $D_{\text{egg:chick}} = 0.25$, $P = 0.44$; resting: $D_{\text{imm:egg}} = 0.25$, $P = 0.44$, $D_{\text{imm:chick}} = 0.13$, $P = 0.99$, $D_{\text{egg:chick}} = 0.21$, $P = 0.67$) (Figure 4), and were also similar to timings previously found in this species (Dean et al., 2012). Foraging occurred across daylight hours with a slight increase towards the end of the afternoon. Resting occurred most at night, but also occupied a significant part of the day, especially the middle. Flying occurred predominantly by day, with distinct peaks around sunrise and before sunset, when birds left or arrived near the colony.

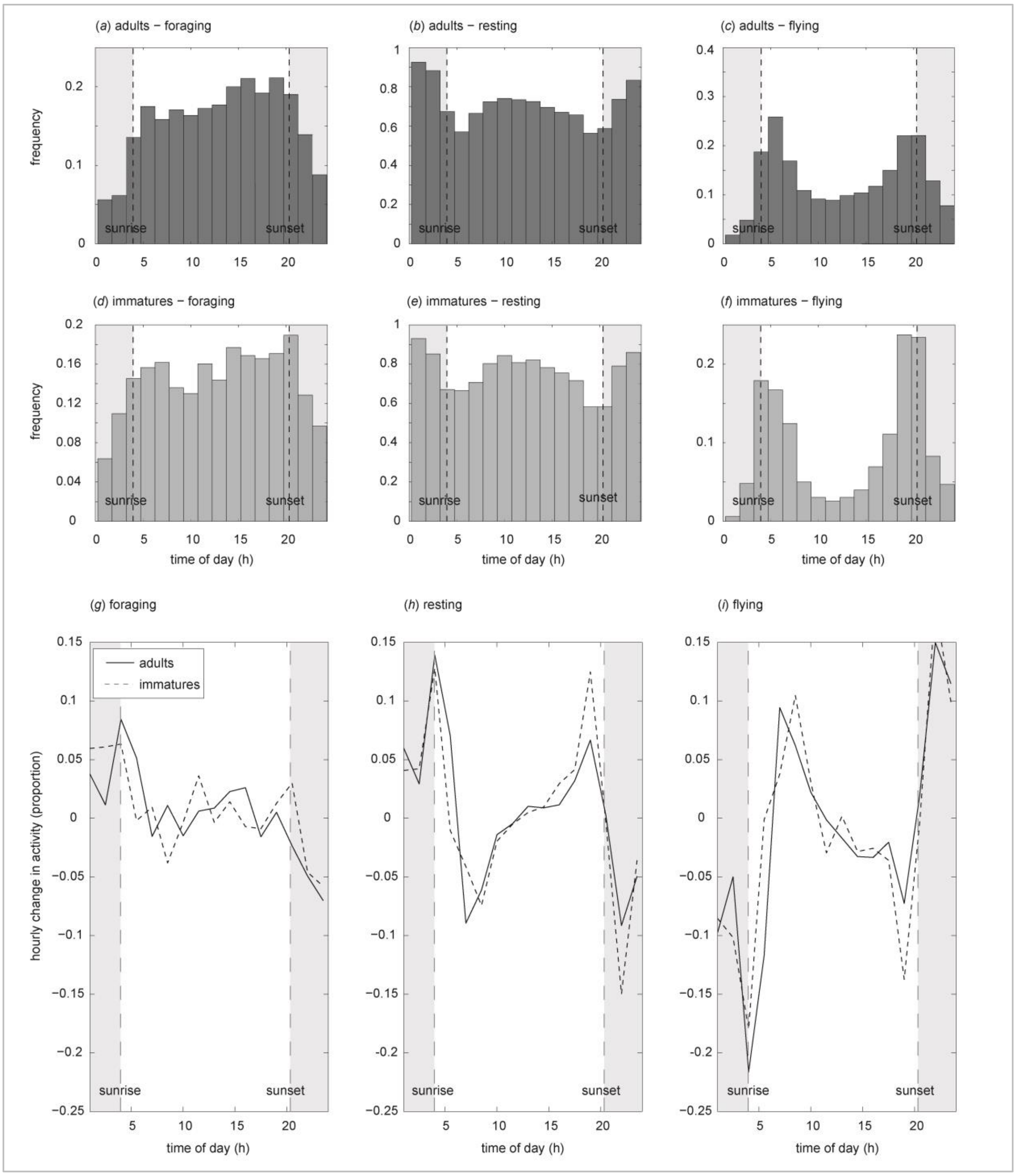

Figure 4. Stacked histograms of (*a*) foraging, (*b*) resting and (*c*) flying behaviours against time of day for adults (dark grey) and immatures (light grey), and their hourly variation (d), (e), (f) for adults (continuous lines) and immatures (dashed lines). The y-axis represents a change in proportion, e.g. if the percentage of adults flying is 10% between 4-5pm and 25% between 5-6pm, the value for 5pm will be 0.15. On all 6 panels night time is represented with a light grey background, and sunrise and sunset with grey dashed vertical lines.

Daily mass gain

Immature birds were significantly lighter than adults prior to tracking (364 ± 5g vs. 405 ± 5g; n_{imm} = 20, n_{ad}=19; T-test: $t_{36.9}$=5.59, $P < 0.001$). Lighter immatures tended to go on shorter foraging trips (LMM, $n = 20$, parameter estimate: 0.01 ± 4.1E-3, Z=3.17, $P = 0.002$), but this was not the case in adults, even when controlling for breeding stage (LMM, $n = 19$, parameter estimate: 0.002 ± 0.004, Z=-0.56, $P = 0.58$). In addition, immatures gained significantly less mass per day (-0.59 ± 0.7 g/day on average) than incubating birds (5.6 ± 1.8 g/day on average; LMM: parameter estimate: 6.22 ± 1.69, t = 3.7, $P < 0.001$) and chick-rearing-birds (2.0 ± 0.9 g/day on average; LMM: parameter estimate: 2.59 ± 1.29, $t = 2.0$, P =0.05), while adults also differed significantly between stages (LMM: parameter estimate: 3.63 ± 1.79, $t = 2.0$, P =0.05). The difference between adults and immatures held when looking at daily mass gain per unit of time spent foraging: while there was no significant difference between chick-rearing and incubating birds (LMM: parameter estimate: 0.02 ± 0.64, $t = 0.47$, P =0.161), immatures gained significantly less mass per unit of time spent foraging than either incubating or chick-rearing adults (LMMs; incubating: parameter estimate: -1.25 ± 0.36, $t = -3.47$, P =0.001; chick-rearing: parameter estimate: -0.62 ± 0.26, $t = -2.37$, P =0.026). To check whether the differences in efficiency were simply an effect of body condition, we tested whether bird mass had an effect on efficiency (mass gain per unit of time spent foraging) in adults and immatures: we did not find any significant differences in adults and a nearly significant trend in immatures (LMMs: immatures: $n = 20$, parameter estimate: -0.01 ± 0.005, $\chi^2_1 = 3.76$, P =0.053, adults: $n = 19$, parameter estimate: -0.11 ± 0.8, $\chi^2_1 = 2.21$, P =0.137). The trend was negative, i.e. heavier immatures tended to be less efficient than lighter immatures.

Marine productivity

Immatures foraged in areas of significantly lower estimated net primary productivity than adults (1873 ± 8 vs 2349 ± 10 mg/m^2/day, LMM: $n_{immature}$ = 20 (9844 locations), n_{adult} = 19 (15912 locations), parameter estimate: -0.21 ± 0.08, $\chi^2_1 = 6.61$, P =0.010). When looking at breeding stages separately, we found that the difference was significant between immatures and chick-rearing birds (1873 ± 8 vs

2453 ± 12 mg/m^2/day, LMM: $n_{chick\text{-}rearing}$ = 13 (10950 locations), parameter estimate: -0.30 ± 0.08, χ^2_1 = 10.03, P =0.002), but not incubating birds (LMM: $n_{incubating}$ = 6 (4962 locations), parameter estimate: -0.11 ± 0.11, χ^2_1 = 1.11, P =0.291). There was no difference between incubating and chick-rearing adults (parameter estimate: -0.19 ± 0.14, χ^2_1 = 1.99, P =0.159). We obtained similar results by looking at the foraging, flying and sitting states separately, although the effect was less obvious in flying (Table 2). Differences in chlorophyll a levels were the same as those obtained with net primary productivity, with immatures generally exploiting areas of lower chlorophyll a concentrations; the only difference with net primary productivity being a lack of difference in flying locations between any stages. Although adults seemed to occupy areas of slightly lower SSTs, there were no significant differences with immatures (Table 2).

Table 2. Differences in net primary productivity, chlorophyll a and sea-surface temperature between locations visited by immatures (IMM), incubating (INC) and chick-rearing (CR) adults for each behavioural state. The numbers presented are means ± SE, and the statistics are issued from LMMs. Significant differences are in bold.

	Foraging	**Sitting**	**Flying**
	(n_{IMM} = 1811, n_{INC} = 1048, n_{CR} = 2052)	*(n_{IMM} = 7105, n_{INC} = 3172, n_{CR} = 7547)*	*(n_{IMM} = 928, n_{INC} = 742, n_{CR} = 1351)*
Net Primary Productivity (mg/m^2/day)	Imm: 1843 ± 18	Imm: 1866 ± 10	Imm: 1983 ± 27
	Inc: 2106 ± 37	Inc: 2142 ± 21	Inc: 2121± 39
	CR: 2526 ± 28	CR: 2443 ± 15	CR: 2401 ± 34
	Imm:Inc : χ^2_1 = 1.2, *P* =0.269	Imm:Inc : χ^2_1 = 1.4, *P* = 0.238	Imm:Inc : χ^2_1 = 0.2, *P* = 0.682
	Imm:CR : χ^2_1 = 18.7, *P* < 0.001	**Imm:CR : χ^2_1 = 9.9, *P* = 0.002**	**Imm:CR : χ^2_1 = 4.2, *P* = 0.040**
	Inc:CR : χ^2_1 = 2.2, *P* =0.139	Inc:CR : χ^2_1 = 1.9, *P* = 0.172	Inc:CR : χ^2_1 = 1.1, *P* = 0.269
Chlorophyll a (mg/m^3)	Imm: 1.08 ± 0.02	Imm: 1.13 ± 0.02	Imm: 1.23 ± 0.04
	Inc: 1.53 ± 0.10	Inc: 1.51 ± 0.06	Inc: 1.58 ± 0.08
	CR: 2.30 ± 0.07	CR: 2.11 ± 0.04	CR: 1.67 ± 0.03
	Imm:Inc : χ^2_1 = 3.3, *P* = 0.068	Imm:Inc : χ^2_1 = 2.8, *P* = 0.094	Imm:Inc : χ^2_1 = 1.0, *P* = 0.318
	Imm:CR : χ^2_1 = 10.5, *P* = 0.001	**Imm:CR : χ^2_1 = 9.8, *P* = 0.002**	Imm:CR : χ^2_1 = 2.7, *P* = 0.097
	Inc:CR : χ^2_1 = 1.14, *P* = 0.285	Inc:CR : χ^2_1 = 1.0, *P* = 0.313	Inc:CR : χ^2_1 = 13.7, *P* = 0.711
SST (°C)	Imm: 17.2 ± 0.03	Imm: 17.1 ± 0.1	Imm: 16.7 ± 0.04
	Inc: 16.4 ± 0.05	Inc: 16.4 ± 0.03	Inc: 15.8 ± 0.06
	CR: 16.9 ± 0.04	CR: 16.9 ± 0.02	CR: 16.6 ± 0.05
	Imm:Inc : χ^2_1 = 1.5, *P* = 0.228	Imm:Inc : χ^2_1 = 1.7, *P* = 0.190	Imm:Inc : χ^2_1 = 2.5, *P* = 0.111
	Imm:CR : χ^2_1 = 0.1, *P* = 0.718	Imm:CR : χ^2_1 = 0.05, *P* = 0.825	Imm:CR : χ^2_1 = 0.03, *P* = 0.873
	Inc:CR : χ^2_1 = 0.4, *P* = 0.515	Inc:CR : χ^2_1 = 0.6, *P* = 0.435	Inc:CR : χ^2_1 = 0.7, *P* = 0.473

Discussion

By comparing simultaneously precision tracked foraging trips of different life-stages we were able to investigate the foraging distributions of immatures and breeding adults under identical environmental circumstances. At the same time, we used an etho-informatics analysis, and a proxy for foraging success (mass gain), to estimate individual foraging efficiencies. We found that immatures were substantially spatially segregated from adults in their foraging destinations, and that this was not an effect of constraints on trip duration or flight distance: on average immatures foraged closer to the colony than adults, their trips were of similar duration than the trips of chick-rearing adults (but shorter than incubating trips). In addition, they covered similar distances per day, and at similar flight speed, to incubating birds (but shorter distances and at lower flight speed than chick-rearing adults). Although there are small differences in measured speeds and trip durations between immatures and chick-rearing (though not incubating) adults, which may indicate that immatures are less efficient in sustained flight, these differences are not sufficient to deny immatures access to the core areas exploited by adults in our study.

Critically, we found that immatures gained less mass per unit of time spent engaged in foraging-related behaviour, suggesting that they are less efficient at foraging than adults. There are several potential causes of this effect. One possibility is that immatures are inferior competitors because they are lighter than adults (~10% lighter in our dataset), and are competitively excluded from the best foraging areas. However we found no evidence that heavier birds were better at foraging – we found no effect of mass on foraging efficiency in adults, and only a nearly-significant trend in immatures, but negative, indicating that heavier immatures do not forage more effectively. Furthermore, we found that whilst lighter immatures did go on shorter trips, this was not the case in adults, whether they were incubating an egg or rearing a chick. Thus, the differences we observe between adults and immatures cannot be readily explained by differences in body condition alone. Alternatively (or in addition), immatures may be less effective foragers because they lack individually acquired experience which may enable adults to recall the locations of the best foraging areas under different conditions, recognise the signals indicative of prey presence, or hunt prey more effectively (e.g. by diving at different depths; Le Vaillant et al. 2012), in an environment where prey is patchy, often ephemeral, and predictable only on a complex spatio-temporal scale (Weimerskirch 2007). We found that immatures exploited areas significantly less productive than chick-rearing adults, with lower primary productivity and chlorophyll a levels. Incubating adults also visit areas of higher productivity than immatures (although less so than chick-rearing adults), but the differences were not significant, which could result from our small sample size of incubating adults. These results support the idea that the lower foraging efficiency of immatures is at least partly due to their exploitation of less productive areas; however this does not rule out the possibility that they are also less skilled at hunting which could itself push them into less productive waters through competition with adults.

In our dataset, the clearest segregation occurred in the Irish Sea: over 50% of adults visited the Irish sea front (a known seabird hotspot for several species including Manx shearwaters; Begg and Reid 1997; Pollock et al. 1997), but no immature did, even though it was well within their range (in duration and distance); it seems unlikely that this absence can simply be explained by their inability to find this area, where large flocks of Manx shearwaters can be seen flying to and from during the breeding season (Durazo et al. 1998). This suggests that immatures were competitively excluded from this area. The only immature going to the Irish Sea (which did not reach the front) was one of the heaviest (3rd/20) and within the range of adult mass; furthermore unlike the other immatures we tracked it shared the same burrow each night with the same bird (with a small brood patch), and remained in a burrow for 24h on two occasions during the tracking period. This suggests that this bird was most likely a pre-breeder with a newly established burrow or a breeder who failed early enough in the season for its brood patch to disappear. There may be a threshold (triggered by mass, age or experience) above which it becomes worth facing intraspecific competition in the Irish Sea. This may also be the same threshold which triggers the start of breeding, as is also observed in albatrosses (Weimerskirch 1992). Displacement of immatures from the Irish Sea is unlikely to occur by direct aggression from the adults, but is more likely to result from differential competitiveness: immatures visiting the Irish Sea could be outcompeted by adults and their superior foraging skills, and therefore the gain from foraging in areas less exploited by adults may outweigh the cost of the lower productivity of these areas.

Poorer foraging ability in immatures has often been invoked as the main reason for the higher immature mortality observed in many species (Lack 1954; Ashmole 1963). Immatures' improvement of foraging with experience has been suggested in several taxa (Lefebvre 1995; Mazur and Seher 2008) including seabirds (Yoda et al. 2004; Daunt et al. 2007), and may continue after reaching adulthood (Haug et al. 2015). Furthermore, despite a lack of difference in bill and wing length with age ruling out the physical inability to catch the same prey as adults, Manx shearwaters are known to increase in mass until at least age 6 (Brooke 1978). Tracking data of immature wandering albatrosses visiting their colony during the breeding season revealed that immatures, like our shearwaters, took shorter trips than breeding adults and covered shorter distances; the authors suggested that immatures may stay nearer the colony (where they are likely to experience higher competition for resources) to learn how to deal with the competition constraints of central-place foraging near the colony, which they will have to deal with once they start breeding (Riotte-Lambert and Weimerskirch 2013; Weimerskirch et al. 2013). On the other hand, a study in gannets found that immature gannets covered longer distances and went on longer trips than chick-rearing adults between regular visits to the colony, interestingly also visiting other colonies during their trips (Votier et al. 2011). Here, the authors argued the longer trips of immature gannets were a way to avoid high intra-specific competition near the colony. The limitation of these studies is that the tracking of immatures and adults was not simultaneous but occurred in different years, and so the differences may be masked or enhanced by different environmental conditions. Although our results strongly indicate a lower foraging efficiency of immature shearwaters, they have a tendency to go on shorter trips and to spend less time foraging than some adults, despite being lighter. They may be under less pressure than adults to exploit the most profitable areas because they do not need to build reserves for incubation shifts or to feed a chick. This would imply the existence of a cost or risk to travel to more productive areas, which breeders benefit from paying or taking. During the short period during which they visit the colony each year, immatures may also prioritise frequent colony visits to prospect for burrows and improve their social skills over foraging. Therefore, the spatial segregation we observe in our study may result not only from the inexperience of immatures at foraging, but also from their inexperience at adult life in general.

In summary, our study reveals for the first time the simultaneous foraging movements of adult and immature seabirds during the breeding season, hereby addressing the issue of between-year differences in environmental conditions potentially confounding the findings of previous studies. In addition, by measuring the foraging success of the birds, we can estimate and compare foraging efficiency between immatures and breeders. Our findings highlight substantial spatial segregation between adults and immatures during central place foraging around the colony, and lower foraging efficiency in immatures, which is not driven by differences in body condition and therefore most likely due to inexperience. This is driving the spatial segregation we observe by excluding the inferior competitors (immatures) from the foraging areas visited by adults, which are significantly more productive. Our findings provide the strongest evidence to date that within-species spatial segregation in long-lived animals can be driven by differences in foraging experience, which may in turn lead to intra-specific competition.

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Supplementary Material

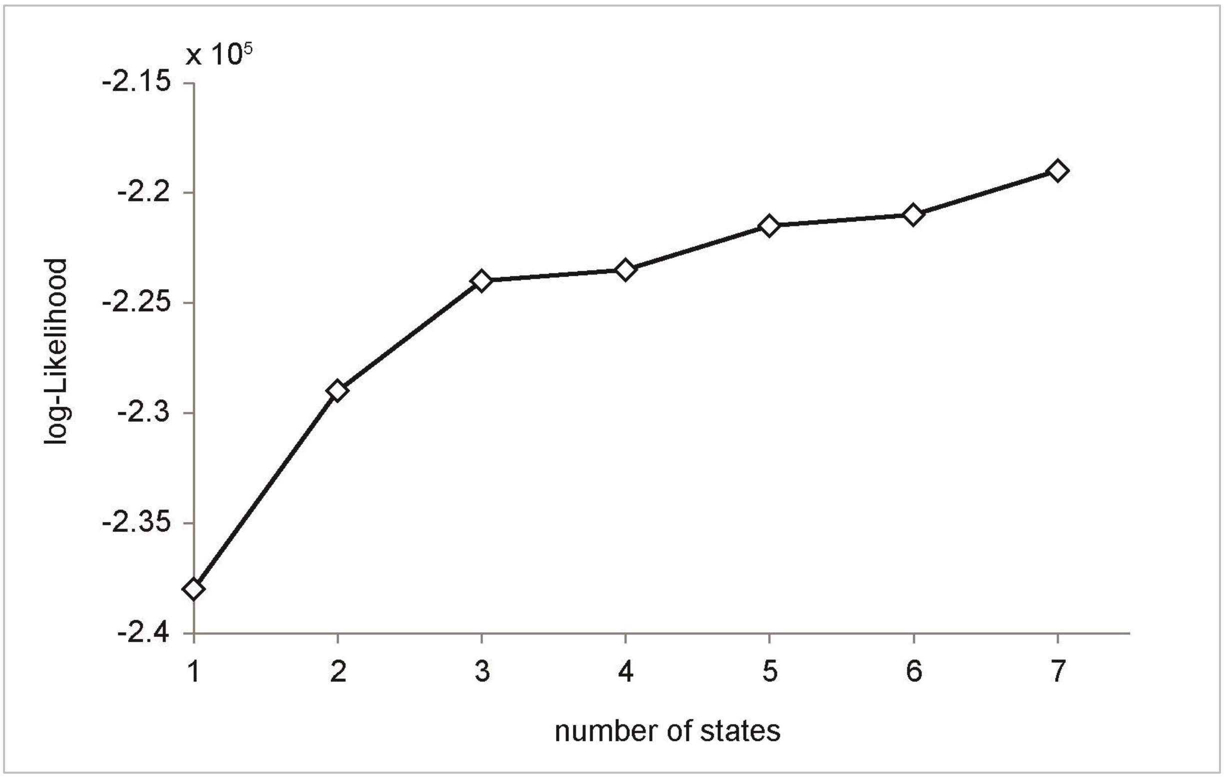

Figure S1. Log-likelihood of Gaussian mixture models with different number of states, used to identify the optimum number of behavioural states (3).

Table S1. Details of the mixed models comparing trip metrics between adults and immatures. For each test we indicate the mean ± SE of the dependant variable, the type of model, the test statistics, the parameter estimates, and the *P*-value. Significant values ($P < 0.05$) are in bold.

	All trips pooled				**Short trips (≤ 3 days)**				**Long trips (> 3 days)**			
	mean ± SE	param. est.	stat	*P*	mean ± SE	param. est.	stat	*P*	mean ± SE	param. est.	stat	*P*
Trip duration (days) GLMM (Poisson distribution)	Egg = 9.3 ± 1.2 Chick = 4.9 ± 0.7 Imm = 3.7 ± 0.6	Imm:Egg: 0.9 ± 0.1 Imm:Chick: 0.3 ± 0.2 Egg:Chick: 0.5 ± 0.3	Z = 3.17 Z = 1.55 Z= 1.86	**0.002** 0.121 0.012	A = 1.1 ± 0.1 I = 1.6 ± 0.2	n/a	n/a	n/a	A = 8.3 ± 0.5 I = 6.5 ± 0.9	n/a	n/a	n/a
Distance / day (km) LMM	Egg = 209 ± 28 Chick = 221 ± 14 Imm = 179 ± 8	Imm:Egg: 28.8 ± 25.6 Imm:Chick: 49.1 ± 18 Egg:Chick: 20.3 ± 28.6	t = 1.12 t = 2.72 t = 0.71	0.499 **0.028** 0.659	A = 275.6 ±18.4 I = 193.2 ± 11.8	-1.51 ± 0.11	ΔlogLik = 4.52 ΔAIC = -7.04 $\chi^2_1 = 9.04$	**0.003**	A = 188.9 ± 10.9 I = 160.4 ± 10.4	-1.26 ± 0.10	ΔlogLik = 1.88 ΔAIC = -1.75 $\chi^2_1 = 3.75$	0.052
Max distance from colony (km) LMM	Egg = 248 ± 53 Chick = 201 ± 37 Imm = 135 ± 14	Imm:Egg: 1.8 ± 1.5 Imm:Chick: 6.7 ± 1.3 Egg:Chick: 0.5 ± 0.3	t = 2.49 t = 2.30 t = 1.02	**0.035** **0.035** 0.312	A = 99.5 ± 6.0 I =92.5 ± 8.7	-1.03 ± 1.06	ΔlogLik = 0 ΔAIC = 1.99 $\chi^2_1 = 0.01$	0.919	A = 309.6 ± 44.4 I = 194.0 ± 22.7	1.5E-3 ± 0.8E-3	ΔlogLik = 2.84 ΔAIC = -4.63 $\chi^2_1 = 6.36$	**0.012**
Mean flight speed (km/h) LMM	Egg = 20.3 ± 1.4 Chick = 23.0 ± 0.7 Imm = 18.2 ± 0.6	Imm:Egg: 2.4 ± 1.3 Imm :Chick: 1.5 ± 1.2 Egg:Chick: -4.9 ± 1.9	t = 1.16 t = 5.25 t = -2.65	0.230 **< 0.001** 0.230	A = 25.2 ± 1.16 I = 17.9 ±0.9	-11.1 ± 1.8	ΔlogLik = 7.97 ΔAIC = -13.93 $\chi^2_1 = 15.94$	**< 0.001**	A = 21.0 ± 0.6 I = 18.5 ± 0.8	-2.41 ± 1.0	ΔlogLik =2.78 ΔAIC = -3.56 $\chi^2_1 = 5.55$	**0.018**
Max latitude (°) GLMM (γ - distribution)	Egg = 54.4 ± 1.6 Chick = 52.9 ± 0.3 Imm = 51.9± 0.1	Imm:Egg: -7.8 ± 2.7 E-4 Imm:Chick: -3.8 ± 2.2 E-4 Egg:Chick: 0.9 ± 1.8 E-4	t = -2.92 t = -1.75 t = 0.47	**0.004** 0.080 0.341	A = 52.3 ± 0.1 I = 51.8 ± 0.04	1.7E-4 ± 0.4E-4	t=4.3	**< 0.001**	A = 53.7 ± 0.5 I = 52.2 ± 0.1	4.7E-4 ± 2.3E-4	t=1.97	**0.049**
Min latitude (°) GLMM (γ - distribution)	Egg = 51.5 ± 0.1 Chick = 51.4 ± 0.1 Imm = 51.1 ± 0.09	Imm:Egg: -1.7 ± 1.0 E-4 Imm:Chick: -2.4 ± 1.1 E-4 Egg:Chick: -0.7 ± 1.4 E-4	t = -1.63 t = -2.21 t - =0.54	0.104 **0.027** 0.589	A = 51.5 ±0.1 I = 51.1 ± 0.09	1.9E-4 ± 1.1E-4	t=1.74	0.081	A = 51.4 ± 0.1 I = 51.0 ± 0.2	1.8E-4 ± 1.1E-4	t=1.65	0.098

Chapter 7

General Discussion

Introduction

This thesis provides new insights into the behaviour of pelagic seabirds on their journeys at sea, and their life-history consequences. As proposed in the opening chapter, I combined high-resolution tracking data and etho-informatics analysis techniques to examine the fine-scale behaviour of these elusive species over days, months or even years, across species, sexes, ages, and colonies. I investigated the ecological drivers of individual variations in behaviour and how these variations may affect fitness. In this chapter I shall summarise and link together my main findings, and propose directions for future research, but also examine ideas that emerge more anecdotally from several chapters and are therefore not explicitly discussed earlier. I also discuss limitations of the methods used in this thesis, and propose potential paths for further improvement. Finally, I take the opportunity to examine in further detail a topic only briefly addressed in previous chapters: the conservation implications of this work.

Main results & Future directions

Individual variation in behaviour and consequences for fitness

Throughout this thesis I have studied the at-sea behaviour of pelagic seabirds at the individual level. I combined tracking data and analytical methods to estimate the fine-scale behaviour (5-15 min resolution) of individual birds over week-long foraging trips or month-long migratory journeys. In all chapters I found significant differences in at-sea behaviour (activity budgets) among individuals. Determining how and why such individual behavioural idiosyncrasies develop and how they may affect individual fitness is essential to understand how they may ultimately affect population dynamics and the evolution of life-histories (Bowlin et al. 2010). Therefore, I investigated the drivers of these individual differences in at-sea behaviour, and whether such differences affected individual fitness. Life-history theory predicts that virtually every event in the life of an animal will affect future events, by the process by which allocating resources to a present event (e.g. spending energy rearing current offspring) will make these resources unavailable for allocation to future events (Bell 1980; Stearns 1989). In long-lived iteroparous animals like the pelagic seabirds studied in this thesis, which can rear over 20-30 chicks over as many years, it is essential to balance carefully current with future resource allocation (Williams 1966). For these species, life-history theory predicts a relatively low and slow reproductive effort, and the adults' survival having priority over offspring survival (Hirshfield and Tinkle 1975). In Chapter 5 I showed that manipulating the cost of reproduction in one year, even by a relatively small amount, had consequences on the birds' reproductive success the next season ("carry-over effects", Harrison et al. 2011). Birds which invested more in the experimental breeding season had a lower breeding success the next year, and those which attempted to breed did so later and laid smaller eggs than they normally do. There was also a non-significant trend across all measures of breeding success for birds which invested less in the experimental year to do better the next season. This is consistent with another study in this species, which found that adults which fledged a chick earlier did better the following season (Shoji et al. 2015). However, the lower winter foraging effort after manipulation was not comparable to this study, perhaps because the manipulation (25-30% increase or decrease in chick-rearing duration) led to more subtle effects than the events studied in the other study (sabbatical year vs. breeding success).

Migration may lead to a significant energy expenditure during the non-breeding season, and sub-optimal migration caused by delays due to late breeding, or poor condition at the end of breeding, may incur significant risks to the adults' survival (Richardson 1990; Owen and Black 1991). As a result, long-distance migration may require particularly careful resource allocation (Norris and Taylor 2006). Therefore, the timing, as well as the energy expenditure and the foraging effort (to maintain or regain body condition) during migration, is likely to be of significant importance for the outcome of the subsequent breeding events (Alerstam and Lindström 1990; McNamara et al. 1998). This was the case in our studies. First, we found that the timing of breeding and parental effort during the breeding season affect individual behaviour during the non-breeding season, as has already been suggested in several species (e.g. (Inger et al. 2010; Sedinger et al. 2011)) including seabirds (Catry et al. 2013; Daunt et al. 2014). Shearwaters whose reproductive effort had been extended did not desert their chick early but instead delayed their fall migration, and spent less time sitting on the water surface overwinter than in non-experimental years (Chapter 5). Puffins have different migratory strategies from shearwaters and do not have a single wintering ground but instead disperse to multiple destinations, furthermore they have a higher flight cost than shearwaters (Elliott et al. 2013). As a result, one could expect large individual differences in the energetic cost of migration leading to differences in individual fitness. Indeed, I found that birds which migrated to the Mediterranean Sea in the second part of the winter spent more time foraging while visiting the Mediterranean Sea than birds elsewhere, and had a higher breeding success the subsequent year (Chapter 2). In addition, female puffins which spent more time foraging during the winter had a higher reproductive success the next season, while I found the opposite effect (but less strong), in males (Chapter 3). Unfortunately individual breeding success of puffins was not available for most colonies studied in Chapter 4, and colony-wide productivity values were not yet available at the time of writing, so we could not investigate the potential fitness consequences of different migratory strategies. However, using the same behavioural classification method as in Chapter 2 and 3, we found a significant relationship between the time engaged in foraging-related activity and net primary productivity. It seems likely that birds wintering in productive areas would be in better condition when returning to the colony to breed, and so we can hypothesise that even across colonies and across birds of different sizes wintering in different areas, the time spent engaged in foraging-related activity may have direct consequences for fitness. However, such conclusions should be taken carefully as NPP may not be reflecting actual prey availability, and so this would need validating with data on breeding success or body condition pre-breeding.

Overall, across these 4 Chapters, our results indicate that (i) individual variations in non-breeding behaviour are affected by the investment in the previous breeding season, and (ii) such variations have important implications for the individual’s fitness. However, these results remain to be confirmed at wider scales (e.g. across several colonies) and in other species. Combining the methods we used with measures of age, body condition and individual quality would greatly improve the clarity of the results obtained.

Environmental drivers of behaviour

Besides the condition of the animal at the end of the breeding season, which I showed affects the behaviour (e.g. the foraging effort) of individuals during the non-breeding season, external ecological factors such as environmental conditions are likely candidates as other important drivers of fine-scale changes in animals’ individual behavioural states (Navarro and Gonzalez-Solis 2009; Goyert 2015). Migration can only occur if the benefits outweigh the cost of travelling, and this can only happen if resource availability at the wintering site(s) is higher than at the breeding site (Alerstam and Högstedt 1982; Alerstam et al. 2003). A wealth of studies have investigated how resource availability affects routes and stopover decisions in long-distance migrants, with the overwhelming majority indicating that animals chose routes and stopover in areas of higher resource availability (Farmer and Parent 1997; Buler and Moore 2011; Cohen et al. 2012; Chudzińska et al. 2015; McCabe and Olsen 2015) and that depleted wintering food resources have negative impacts on fitness (Baker et al. 2004; Newton 2006; Norris and Marra 2007; Aharon-Rotman et al. 2015). In marine ecosystems, the difficulty of measuring prey abundance lead researchers to use proxies of prey availability, such as measures of chlorophyll A, net primary productivity (describing temperature-dependent photosynthetic efficiency) and zooplankton (Morel and Berthon 1989; Kiorboe and Nielsen 1994; Behrenfeld and Falkowski 1997; Behrenfeld et al. 2005), along with physical variables such as sea-surface temperature and bathymetry (Lyle et al. 1992; Sarmiento et al. 2004). A multitude of studies have used these variables to explain or predict the foraging and migratory movements and distributions of marine predators (Ballance et al. 1997; Pinaud and Weimerskirch 2007; Suryan et al. 2012; Anguita and Simeone 2015; reviewed in Tremblay et al. 2009; Wakefield et al. 2009). In this thesis I found that puffins spent more time foraging in cold and productive waters (Chapter 4), and that immature shearwaters foraged in less productive waters than breeding adults, which resulted in lower foraging efficiency (Chapter 6). We do not know whether immature shearwaters chose to exploit less productive waters perhaps to avoid competition, or whether they failed to locate more productive waters because of inexperience, so we cannot conclude whether the productivity levels exploited by different ages was a driver of age-related spatial segregation, or a simple consequence of competition. However, our results in Chapter 4 strongly suggest that sea-surface temperature is a driver of puffin non-breeding distributions. The latitudinal window exploited by birds was strongly related to the latitude of their colony but was not simply a result of the birds staying close to their colony, and our findings suggest that local adaptation to water temperature may define the temperature zones birds can exploit during the winter. Sea-surface temperature and salinity at the start of the breeding season have been shown to negatively affect the reproductive success of puffins on Røst (Durant et al. 2003; Durant et al. 2006). To complement these results, it would be interesting to test the potential links between productivity levels exploited during the winter and breeding success, and to expand the analysis across puffin colonies. This would perhaps help understand the large differences in productivity European colonies currently experience.

In this thesis, linking at-sea behaviour with environmental variables provided interesting results and helped understand differences in habitat use between different age-classes and colonies of seabirds. However, it is important when interpreting such results to remember that seabirds do not feed on chlorophyll and that environmental factors used to estimate prey availability are proxies, and not actual measures, of prey availability (Gremillet et al. 2008). Furthermore, these variables are temporal composites, because snapshots taken by satellites are often obstructed by cloud cover. The inaccuracy arising from the low temporal resolution of environmental data and the low spatial resolution of geolocation data may be minimised in studies like chapter 4 where animals remain in the same area for long periods. However in studies where environmental data are linked to fast moving animals or high-resolution temporal data (as in Chapter 6), negative results should be interpreted with caution. While they could indicate that the environmental variables considered do not affect the animals' distributions, they could equally result from a spatio-temporal mismatch between tracking and environmental data (Suryan et al. 2012), or from a mismatch between prey availability and the proxy measure used (Gremillet et al. 2008). This could partly explain why, for example, multiple studies find correlates between net primary productivity and animal presence, foraging activity or breeding success (Shaffer et al. 2006; Navarro and Gonzalez-Solis 2009; Chapter 4; Chapter 6) while others do not (Bailleul et al. 2005; Anguita and Simeone 2015). Combining tracking devices with small depth-recorders or miniature cameras could potentially help resolve this issue, with dive frequency and dive profiles helping to determine prey abundance (Watanabe and Takahashi 2013; Shoji et al. 2014).

Spatial segregation and intra-specific competition

Competition is often invoked to explain differences in migratory patterns between individuals of different age, sex, social status or from different populations (Alerstam and Hedenström 1998; Alerstam et al. 2003). Typically, dominant individuals (e.g. males or breeders) displace subdominant ones (e.g. females or non-breeders) (Cristol et al. 1999; Phillips et al. 2011; Akesson and Weimerskirch 2014; Gutowsky et al. 2014; van den Hout et al. 2014). Throughout this thesis we found evidence for spatial segregation between sexes (Chapter 2 & 3), age classes (Chapter 6) and populations (Chapter 4). In all cases this spatial segregation was accompanied by behavioural differences. Female puffins spent more time foraging and had a higher energy expenditure than males in the second part of the winter (Chapter 3), when most spatial segregation occurred between sexes (Chapter 2) and partners (Chapter 3). Substantial spatial segregation also occurred between colonies during the non-breeding season, concurrent with significantly different activity budgets, with up to twofold variations in average foraging effort between colonies (Chapter 4). Immature shearwaters were spatially segregated from breeding adults during central-place foraging around the colony, and spent less time foraging and more time sitting on the water surface than adults (Chapter 6). All these results support other examples found in the literature or theoretical predictions, and suggest that intra-specific competition is an important driver of spatial and behavioural differences between individuals of the same species. In Chapter 6, segregation between adults and immatures was combined with lower foraging efficiency and a significant difference in the productivity of exploited areas, even though the productive areas in which adults foraged where geographically within reach of immatures, suggesting that competition was a likely driver of the spatial patterns observed.

However, competition *per se* is extremely difficult to measure in natural settings, especially in the marine environment where manipulating resources seems unachievable. There are other potential explanations besides competition for differences between individuals, especially in monomorphic species, and therefore conclusions must be made carefully. For example, our results in Chapter 2 suggest that there is intraspecific competition between sexes in puffins during the non-breeding season, resulting in partial sex-segregation especially during the second part of the winter. However, once activity budgets were examined, we found that this spatial segregation was combined with a difference in foraging effort pre-breeding, and that females which spent more time foraging during the pre-breeding period had a higher reproductive success the following season (Chapter 3). This suggests that females were unlikely to be suffering displacement by males but instead were trying to improve their body condition in order to increase breeding success. Similar sex-differences are found in many petrels during the pre-laying season (Hedd et al. 2014), and sex-specific energy requirements and foraging strategies have been reported in numerous species, although not always associated with spatial segregation (Weimerskirch, Cherel, et al. 1997; Lewis et al. 2002; Forero et al. 2005; Bearhop et al. 2006; Elliott et al. 2010; Alves et al. 2013; Duijns et al. 2014). Similarly, in Chapter 4, the differences in distributions among puffin colonies could seem partly driven by intra- and/or inter-colony competition, indeed birds from the two larger colonies migrated the furthest, but not did not showing the patterns usually observed in leap-frog or chain migration (Alerstam and Högstedt 1980; Newton 2008; Fort et al. 2012). However, once sea surface temperatures were considered, these differences in distributions among colonies were better explained by local adaptation to environmental conditions. Overall, our results show that intra-specific competition plays a role in driving at-sea distributions of seabirds, but that combining measures of segregation with other variables such as measures of behaviour, environmental conditions or foraging efficiency can help to understand the most likely mechanisms behind the observed segregation.

Flexibility in individual strategies and the role of learning

While the genetic control of migratory routes is well documented in small, short-lived migrants with relatively simple migration routes (Perdeck 1958; Helbig 1991; Berthold et al. 1992; Berthold and Helbig 1992; Liedvogel et al. 2011), the mechanisms controlling the development of migratory routes in long-lived animals are less understood (Bowlin et al. 2010; Scott et al. 2014). The latter will repeat their migratory journeys multiple times, and often have a long immaturity period before starting to breed. This may give them scope for more flexibility and for experience to play a role. In seabirds, the migratory movements of immatures have been only rarely tracked, because of the logistical challenges involved with tracking a small, elusive bird with high mortality. However, young albatrosses have been shown to follow an innate direction when first leaving their natal colony and to progressively improve their flight performance (Weimerskirch et al. 2006; Riotte-Lambert and Weimerskirch 2013), similar reduced flight or orientation skills were also documented in other seabirds (Yoda et al. 2004; Péron and Grémillet 2013). This suggests that in these species learning plays a part in the development of migratory routes. Another manifestations of learning is often high individual inflexibility, demonstrated by homing pigeons *Columba livia* using memory to retrace their routes in familiar areas (Meade et al. 2005; Guilford and Biro 2014). High route fidelity in pelagic species is common (Hunter et al. 2003; Broderick et al. 2007;

Yamamoto et al. 2010; Fifield et al. 2014), although it is not always the norm (Dias et al. 2013; Müller et al. 2014). Puffins showed high route fidelity across colonies (Chapter 4), even over long periods (up to 6 years, Chapter 2), and the striking route diversity among individuals makes their migratory routes unlikely to be controlled genetically. So how do puffin migratory routes develop? Cultural inheritance, the other established mechanism by which some birds which do not inherit their migration route genetically can learn their route by following their parents (Chernetsov et al. 2004; Harrison et al. 2010; Palacin et al. 2011), is also unlikely to explain the migratory patterns observed in puffins, because fledging occurs at night and parents and most adults remain at the colony long after the chicks have fledged. Another hypothesis is that juvenile and immature puffins explore the ocean in their first few years and gradually refine their route using memory – this is the exploration-refinement theory developed by Guilford et al. (2011). Although my thesis did not aim to, and does not have the data to test this hypothesis, some results emerging from my work suggest that it may be a valid hypothesis. When Guilford et al. developed their hypothesis they only had tracks of puffins for 2 consecutive years. My results show that this striking route fidelity lasts for at least a quarter of their average lifespan (25 years, Harris and Wanless 2011). Furthermore, one of the birds switched migration route after 2 years of tracking, and switched back again two years later. Although this may be anecdotal, this suggests that (i) genetic inheritance of migration route in puffins can be ruled out and (ii) memory is likely to play a strong part in route development. In a changing, patchy but often predictable environment (Weimerskirch 2007), using a repertoire of reliable, individually idiosyncratic routes developed by exploration in the early years of life, and switching between them when conditions change, seems like an optimum solution. However, to test this hypothesis properly it is necessary to track juvenile and immature individuals. I deployed geolocators on 55 puffin fledglings in 2012 and 2013; unfortunately a single one has been recovered so far. Although this is not sufficient to make any conclusions, the movements recorded are not incompatible with the exploration-refinement hypothesis. Real-time satellite tracking, although more expensive, may be a more sensible solution to track the migratory movements of young individuals in the future (Votier et al. 2011, Péron and Grémillet 2013; Riotte-Lambert and Weimerskirch 2013).

Another important aspect of learning in animals, which may have important consequences for life-history theory, is the acquisition of foraging skills. Inferior immature foraging skills have been invoked to explain high immature mortality (Lack 1954; Ashmole 1963) and have been studied in several taxa, including seabirds (Yoda et al. 2004; Daunt et al. 2007; Riotte-Lambert and Weimerskirch 2013). By combining a proxy of foraging effort and a measure of foraging success, I demonstrated in Chapter 6 that immature Manx shearwaters had a lower foraging efficiency than breeding adults, during central-place foraging around the colony. Here again, using real-time tracking would allow to compare immature with juveniles and compare foraging behaviour across ages, which has so far been rarely attempted (Weimerskirch et al. 2013).

Although this is not one of the main objectives, several findings across this thesis suggest that learning plays an important part in driving individual movements and behaviour in seabirds. It is only a matter of time until it becomes possible to track individuals throughout their life. Examining how routes and behaviour develop and evolve throughout an animal's life would be of invaluable help to understand the role of learning in shaping seabirds' at-sea movements and behaviour, and their life-history traits.

Limitations

Impact of tracking

Advances in tracking technology and miniaturisation of devices have allowed researchers to track a multitude of species throughout the animal kingdom, including birds, fish, reptiles, mammals and even insects, during various parts of their annual cycle, from natal dispersal to foraging trips or migratory journeys (reviews in (Hussey et al. 2015; Kays et al. 2015; Kissling 2015)). The explosion in the number of tracking studies in the last two decades has been staggering, and lead to a wealth of information which would have seemed impossible to obtain 50 years ago (reviews in Webster et al. 2002; Wilson et al. 2002; Bowlin et al. 2010; Robinson et al. 2010; Tomkiewicz et al. 2010). In elusive marine species particularly, tracking a dozen individuals can often lead to a better understanding of the species' migration than decades of tagging and ringing of tens of thousands individuals (see reviews in Bowlin et al. 2010; Robinson et al. 2010; Bridge 2011). The tremendous advances in our understanding of animal migration, but also foraging strategies, navigation, habitat use and other aspects of movement ecology due to tracking studies are undeniable. However, tracking animals is not without limitations. The impact of attaching a logger to a wild animal is unavoidable (McIntyre 2015), and needs to be minimised, firstly for ethical reasons and secondly to minimise the potential bias on the data collected (Robinson and Jones 2014; Heggoy et al. 2015). The impact of devices depends on the sensitivity of the species, its size, the medium in which the animal moves (air/water/ground), the size and position of the device on the animal, the duration of deployment, and the amount of handling needed to catch the animal, deploy and retrieve the device (see Burger and Shaffer 2008 and Walker et al. 2012 for a reviews of impact in marine species). Multiple studies have revealed effects of data loggers on the movements (Wilson et al. 1986; Vandenabeele et al. 2014), behaviour (Harris et al. 2012; Blanchet et al. 2014), physiology (Elliott et al. 2012; Quillfeldt et al. 2012; Heggoy et al. 2015), and breeding success of animals (Massey et al. 1988; Beaulieu et al. 2010). Studies like (Igual et al. 2004; Ropert-Coudert et al. 2009; Agnew et al. 2013) showed that it is possible to minimise impacts to make their effect as negligible as possible. However these studies were all conducted in relatively large animals (> 400g), and lack of device effect remains to be shown in smaller species. In addition to minimising the impact of loggers, it is important to assess potential impact by monitoring as much as possible the performance of tagged animals for comparison with that of non-tagged individuals, using appropriate controls (Authier et al. 2013). Finally, it is crucial always to interpret the results from tracking studies with these potential limitations in mind.

It is therefore necessary to minimise disturbance as much as practicable and to reduce weight as much as possible (current UK recommendations advise the weight of the device not to exceed 3-5% of the animal’s body mass). It is also essential to consider the position of the logger and the drag it will create, especially in diving birds (Chiaradia et al. 2005; Vandenabeele et al. 2014). Finally, it is important to test for potential negative effects by using appropriate controls (Authier et al. 2013). Throughout this thesis, I tagged seabirds with geolocators or GPS loggers, in some cases for multiple years. I tried to minimise disturbance by taking a series of measures: (i) I restricted handling time to a minimum (limited to a single <10 min handling event per year for puffins); (ii) handling was immediately interrupted if birds showed any sign of distress (e.g. panting); (iii) the weight and drag of devices was minimised as much as possible (e.g. lightweight, shorter-lived geolocators were used on puffins) and GPS loggers were stripped out of their unnecessary casing and filed to decrease weight kept; (iv) human disturbance was limited as much as possible, for example all puffins catching events were spread across the chick-rearing season to limit disturbance induced by my presence on the colony to a minimum, and when possible an infra-red burrowscope was used to check for laying dates and breeding success; (v) extended observations of tagged and non-tagged birds at the colony were conducted to allow researchers to quickly detect any abnormal behaviour from a tagged individual; finally (v) all tagged birds were monitored until the end of the breeding season to measure breeding success, and compared to a subset of other birds which were not manipulated (apart from Chapter 4 where most of the data were collected by colleagues abroad and for which breeding success of tagged animals could not be monitored). There were no significant differences between the reproductive success of tagged and untagged birds for both shearwaters and puffins (apart from Chapter 4 where diminished breeding success in one treatment group was due to intentionally manipulated reproductive effort the previous year). However this does not mean that there was no impact at all – I may simply have failed to detect it. For example, despite having a similar breeding success, it is possible that the chicks reared by tagged birds were lighter, or fledged later, than control chicks. In our studies most comparisons are made between groups of tagged birds of similar size (e.g. males vs. females or immatures vs. adults). Paradoxically, increasing monitoring to assess potential disturbance effects can also create additional disturbance, and so we did not measure these variables consistently. In our studies most comparisons were made between groups of tagged birds of similar size (e.g. males vs. females or immatures vs. adults), therefore, while it is important to interpret results with caution, it is likely that the potential effect of tagging was similar among groups.

Behavioural classification

Identifying behaviour in tracking data and estimating activity budgets is a recurrent theme in this thesis. In every chapter, I used a combination of light and saltwater-immersion data from geolocators, or high-resolution GPS data, to measure and classify at-sea behaviour in different behavioural states. I used three different methods. The first and simplest, used in Chapters 2, 3, and 4, was to use 2 thresholds to classify all saltwater-immersion data in “mostly wet” (sitting on the water), “mostly dry” (sustained flight) and “intermediate” (foraging) states (similar methods were used in (Yamamoto et al. 2008; Lecomte et al. 2010; Dias et al. 2012; Shoji et al. 2015).

The second and third ones, more complex, relied on machine learning techniques used for pattern recognition (Bishop 2006). Briefly, given a number of states, *K*, they can identify the characteristics of these K states (e.g. different flight speeds and turning angles), calculate the probability of each data point being generated by each state, and classify all data points by their most probable states (Patterson et al. 2008; Jonsen et al. 2013). In Chapter 6 I used Gaussian Mixture Models to classify automatically high-resolution GPS data based on different patterns of speed and turning angle to classify, once again, 3 states: high speed and low turning angle (sustained flight), low speed and low turning angle (sitting on the water), low speed and high turning angle (foraging) (Gaffney and Smyth 1999). In Chapter 5 I used Hidden Markov Models to classify saltwater-immersion data, a method similar to Gaussian Mixture Models but which also account for temporal autocorrelation (Rabiner 1989). This time, the optimum number of states was 3 again during the non-breeding season but 6 during the breeding season (including days spent incubating in the burrows, and night visits to the colony).

Although these techniques are only beginning to become widely used in behavioural studies, they have been successfully used in published literature. Gaussian Mixture Models, Hidden Markov Models and other similar hierarchical classification models have been used to classify behaviour in migrating and chick-rearing Manx shearwaters (Guilford et al. 2009; Freeman et al. 2010; Dean et al. 2012; Freeman et al. 2013) and many other species (Wakefield et al. 2009; Jonsen et al. 2013). The simple threshold-based technique used in Chapters 2 to 4 and similar derived techniques, more accessible and less computationally heavy, have also been used in multiple studies, mainly in procellariiformes (Weimerskirch, Wilson, et al. 1997; Daunt 2006; Yamamoto et al. 2008; Lecomte et al. 2010; Hedd et al. 2014). The idea behind the classification into 3 states is that while the “mostly dry” and “mostly wet” states are pretty self-explanatory, the intermediate state is associated with foraging because it represents short bouts of flights combined with short wet bouts corresponding to diving or looking for prey from the surface. In shearwaters, the “foraging” state identified from GPS data (low speed, high turning angle) was highly correlated with diving activity, with 96 % of diving activity occurring during this state (Dean et al. 2012). Automatic classification of saltwater-immersion data, trained with GPS data, lead to similar patterns of immersion in each of the 3 behavioural states to those found by the “threshold method” described above, however the accuracy was lower (validation with GPS data showed that 74 % of the saltwater-immersion data was correctly classified, Freeman et al. 2013). There is therefore a trade-off between the size of the devices deployed and the accuracy of behavioural classification. Saltwater-immersion data is less accurate at predicting behaviour than high-resolution GPS data but can be collected with small geolocators year-round, while larger GPS loggers lead to higher quality behavioural data but their size currently limits their use on small seabirds to short-term deployments.

In this thesis, we have applied these techniques to geolocator data collected from puffins. It was not possible to combine deployment of geolocators with dive and GPS loggers because of the small size and high sensitivity of puffins, therefore we could not directly validate the classification with other behavioural data. However, we believe this technique is appropriate for puffins for three reasons. First, in Chapter 2 and 3 we found that puffins which went on longer routes spent more time in the "mostly dry" state, which is therefore likely to be related to sustained flight. Furthermore, puffins which spent more time engaged in the "intermediate" state had a higher breeding success the following season. Foraging effort during the non-breeding season is likely to have a significant impact on breeding success, as it allows energy gain and improvement in body condition. Second, in Chapter 4 we found that the behaviour classified as "foraging" was positively correlated with net primary productivity, while "sitting on the water" and "sustained flight" were not. This relationship may reflect more frequent encounters with prey (however it is important to note that another study found a negative correlation between foraging and NPP in shearwaters on a migratory journey, perhaps because less effort was required to catch sufficient prey (Freeman et al. 2013)). In any case, the relationship of this intermediate state to water productivity, and the lack of relationship of the other two states, suggest that this state is, if not directly foraging, at least related to foraging. It may, for example, represent active area-restricted search (Kareiva and Odell 1987) associated with foraging behaviour (Weimerskirch et al. 2007; Hamer et al. 2009). Finally, tracking puffins with dive-loggers during the chick-rearing season showed that they spent a substantial amount of time alternating flying and diving (Shoji et al. 2015), and my personal observations of puffins near the colony support this finding. Even if diving occurs under water and therefore would not look different to sitting on the water in immersion data, birds undertaking diving and generally active behaviour while sitting on the water surface frequently tuck their leg up for short periods of time, which would be classified as intermediate behaviour. In our data longer leg-tucking periods only occur at night, and are immediately identifiable as long periods (several hours) of uninterrupted dryness, which are much longer than any flight bouts observed during the day, even on migration, and are also not associated with a change of location the following day.

We are therefore confident that the three methods of behavioural classification used in this thesis produce reasonable estimates of behaviour. However, it is important to remember that these are only estimates and therefore all the measures associated with them (activity budgets and energy expenditures) are not exact measures of behaviour. With the recent availability of small dive loggers, the next logical step would be to concurrently deploy geolocators with dive loggers on a subset of puffins for a short period during the breeding season, and use diving activity to validate or correct the classification of foraging behaviour from saltwater-immersion data. Alternatively, one could use feeding events at the colony (birds carrying sandeels to their burrow) to identify the preceding bouts of foraging in activity data, or link prey species (observed or obtained from stomach content) with the last diving event (Ito et al. 2010). Finally, some geolocators collecting finer scale immersion data (recording every single wet/dry transition instead of averaging it over 10min periods) are now small enough, and have a large enough memory, to be deployed on puffins and other small seabirds year-round.

Implications for conservation

Seabirds, as long-lived top marine predators, are good indicators of ocean health (Ainley et al. 1995; Einoder 2009; Grémillet and Charmantier 2010; Thompson et al. 2012; Lyday et al. 2015) and can be used to monitor oceans (Wilson et al. 2002). They are also vulnerable to a range of at-sea anthropogenic disturbance, including, but not restricted to, overfishing, interactions with increased human marine activity such as bycatch, fisheries, maritime traffic, and offshore energy developments (Frederiksen et al. 2004; Halpern et al. 2008; Furness et al. 2012), and to changes to the marine environment due to climate change (Gremillet and Boulinier 2009). Many appropriate conservation measures have been taken on land to protect seabirds from devastating terrestrial predators like rats (Jones and Kress 2012), although much remains to be done (Jones et al. 2008; Russell and Holmes 2015). However, conservation of seabirds at sea, especially during the non-breeding season, is challenging, from a scientific (identifying important areas to protect can be difficult) and political (many areas are in international waters, and important areas may overlap with intensive fishing activity) point of views (Yorio 2009; Lewison et al. 2012). This has resulted in fewer protected areas in the entire pelagic ocean than in any other ecosystem on the planet (Game et al. 2009).

Although the questions addressed in this thesis are not motivated by conservation, by answering questions about the behaviour and ecology of seabirds many of the results obtained can be valuable for seabird conservation (Ronconi et al. 2012). Chapter 4 in particular reveals the non-breeding distribution of Atlantic puffins across their entire breeding range, and identifies important “hotspots” where puffins from different colonies overlap. Furthermore, the apparent constraint of temperature on the latitudinal dispersal of puffins suggests that warming of sea waters may become a threat to puffins, which may be forced to winter at higher and higher latitudes. In Chapter 6, although the foraging distribution of breeding shearwaters is already well-known (Guilford et al. 2008; Dean et al. 2012: 20; Freeman et al. 2013; Dean et al. 2015), we reveal spatial segregation between adults and immatures foraging simultaneously around the colony. Very little data are currently available on the distribution of immature seabirds, because of the technical challenges involved in catching and recapturing birds which are not coming back to a nest. However their conservation is equally important: they are future recruits to the breeding population, they can represent a large proportion of a species’ population and are therefore important components of marine food webs (Brooke 2004), and their higher rates of dispersal may help population resilience to threats and act as buffers against climate change (Klomp and Furness 1992; Kokko and Lopez-Sepulcre 2006). Our results in chapter 6 not only bring important information regarding the distribution of immature shearwaters in British waters, but also reveal the potential segregation between breeding and immature individuals, and therefore highlight the need to track individuals across ages to obtain a good understanding of their population-wide distribution.

In addition, the methods we used throughout this thesis allowed the identification of foraging behaviour in breeding and non-breeding individuals throughout the year, which we found was positively correlated with productivity (Chapters 4 & 6) and reproductive success (Chapter 2 & 3). This could potentially be used to allow the identification of important foraging areas more accurately than by simply using the distribution obtained from tracking data, and would make it possible to precisely pinpoint areas critical for the survival of seabirds during the breeding as well as during the non-breeding season.

Concluding remarks

When I began working on my thesis, little was known about the non-breeding distribution and behaviour of puffins, and I hope this thesis has helped in filling the gaps in this area. Perhaps more importantly, most tracking studies were using data to investigate the at-sea distribution of seabirds. The work in this thesis highlights how identifying and investigating the underlying behaviour behind movement data can be a powerful tool to investigate drivers of distributions and migratory routes, but also study the causes affecting non-breeding behaviour, and how variations in behaviour can have important life-history consequences. Some of these techniques are currently coarse, but there is scope for improvement. The constant improvements in tracking technology and miniaturisation of devices, which will not only allow the collection of higher quality data but also the combining of devices, and the advances of lab-based techniques such as stable isotopes to study trophic levels, will allow researchers to obtain unprecedented insights into the life of seabirds at sea. It is an exciting time to be a seabird researcher.

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