The at-sea behaviour of the Manx shearwater

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Abstract

Seabirds are vulnerable to a wide range of impacts at sea and function as important indicators of ocean health. A detailed understanding of their movements and distributions at sea, as well as the types of behaviour in which they engage and the extent to which those activities make them vulnerable to different impacts is critical in effective conservation planning. But their elusive lifestyles and mobility have hampered studies of their at-sea behaviour. Using miniature data loggers deployed on Manx shearwaters *Puffinus puffinus* this thesis explores the movements, distribution and behaviour of a small-medium pelagic, procellariiform seabird during foraging trips at sea.

Foraging distributions were most variable during the pre-laying period when females departed the colony to build their egg. Females foraged close to the colony when local resources were adequate, but more typically foraged in distant shelf edge waters. Males returned frequently to the colony during this period and typically foraged close by, but also in shelf edge waters when local resources were poor.

During incubation and chick-rearing the foraging movements of birds tracked from up to four colonies showed considerable inter-annual variability, but were largely constrained to the Irish and Celtic Seas and the inshore waters of west Scotland. Birds from each of the colonies foraged in waters local to their own colony, but also in more distant locations, including the productive Western Irish Sea and Western Irish Sea Front where birds from multiple colonies co-foraged, presumably at high densities.

At-sea behaviour was organized into three principal activities representing: (1) sustained direct flight, (2) sitting on the sea surface, and (3) foraging, comprising tortuous flight interspersed with periods of immersion and diving in pursuit of prey. Foraging was highly constrained to daylight hours during which birds engaged in bouts of diving separated by periods of flight or rest on the surface. Most dives were up to 6 m deep, lasting up to 13 s, but some much deeper dives (maximum 55.5 m) were also made.

During chick-rearing the use of short and long duration trips may allow parents to control provisioning effort and their own body condition. However, reducing parents' requirement to provision their chick (by supplemental chick feeding) did not appear to alter the at-sea movements and behaviour of parents, suggesting that at-sea behaviour probably is controlled more by foraging conditions and prey distributions than by the nutritional demands of the chick.

Acknowledgements

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But it is people that make things happen, or not, and many people have helped realise this research. Firstly to Tim and Robin, for giving me this opportunity, for their support, enthusiasm in the project, and for their confidence in me, even when my own waned. Thank you both. Chris Perrins also supplied support, enthusiasm and sage advice throughout, all of which was much appreciated. Thank you Chris.

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Finally, though it hardly seems a commensurate means of acknowledgement, I dedicate this thesis to:

My parents, for a lifetime of love and support,

and to Hannah for everything.

At times I must admit to having felt great sympathy for Mr Barrington:

"We lay down to sleep, but it was a mockery, for as the night wore on, the noise became worse and at times awful. Unable to sleep, we determined to go out, and either frighten or kill some of the shearwaters. Armed with a stick each, we killed all we could carry – forty to fifty – in half-an-hour. Our midnight raid had no effect in quieting the birds, and we got no sleep until after two in the morning".

- R.M. Barrington, 1888

Contents

Author Contributions

All work in this thesis is primarily my own.

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

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

In all but one chapter, Holly Kirk participated in data collection in the field and contributed her ideas and feedback throughout the planning and data collection.

In chapters 3 and 5 Kerry Leonard participated in data collection in the field and contributed his ideas and feedback throughout the planning and data collection.

Annette Fayet participated in data collection in the field for all chapters and contributed her ideas and feedback throughout the planning and data collection, as well as contributing feedback to the preparation of the manuscript of chapter 5.

Richard Phillips contributed his ideas and feedback to the preparation of the manuscript of chapter 5.

Chapter 1

General Introduction

Why study the at-sea behaviour of seabirds?

Seabirds are long-lived, widespread, upper-trophic marine organisms with high adult survival and slow population growth (Rickleffs 1990). As such they are vulnerable to a wide range of impacts at sea including pollution, incidental mortality in fisheries, incidental mortality and habitat loss associated with marine developments, and changes in prey resources as a result of changes in fishery management, oceanic conditions and climate change (González-Solís & Shaffer 2009). Seabirds therefore function as important indicators of ocean health (Einoder 2009; Lewison *et al*. 2012), particularly in light of global climate change (Grémillet & Boulinier 2009) and our increasing use of the seas at industrial scales (Halpern *et al*. 2008).

While there is a long history of studying the breeding biology of seabirds at the nest, their elusive lifestyles and impressive mobility away from the nest have hampered studies of their at-sea behaviour. In particular, a lack of detailed knowledge on the movements and distributions of seabirds across species, colonies, sex, age classes and breeding status has presented a substantial challenge to seabird ecology (Lewison *et al*. 2012). An understanding of the movements of seabirds at-sea, as well as the extent of variability in those distributions and the environmental and ecological interactions that drive it is critically important in the identification and subsequent protection of important bird areas at sea (Garthe *et al*. 2009; Louzao *et al*. 2009). In addition, a detailed understanding of the types of behaviour seabirds engage in at sea and the extent to which those activities make them particularly vulnerable to a variety of impacts is critical to the effective management of those areas. Systematic ship-based surveys of seabird distributions (e.g. Stone *et al*. 1995) have provided valuable information on the large-scale at-sea distribution and abundance of multiple species of seabirds, highlighting the locations of the main foraging concentrations. However, it is not possible to determine the provenance (colony of origin), or the breeding status of birds recorded in this way. In addition, such surveys may not anticipate the full range of foraging movements and cannot provide

information on the spatial and temporal patterns of movement and behaviour of individual birds.

Opportunities and problems of using data loggers to study at sea behaviour

The majority of data presented in this thesis was collected by the deployment of data loggers to record the movements and behaviour of birds during foraging trips at sea. The development and miniaturisation of tracking and data logging technologies has transformed the study of seabirds and other elusive species (Burger & Shaffer 2008; Phillips *et al*. 2008; Rutz & Hays 2009; Bograd *et al*. 2010). Measurement of individual movement using miniature tracking devices, platform terminal-transmitters (PTTs) and increasingly Global Positioning System (GPS) loggers, has provided fine-scale data on the routes and destinations of foraging trips. In addition, the deployment of auxiliary data loggers (immersion loggers, stomach temperature loggers, time-depth recorders, or accelerometers) allows scientists to record multiple variables relating to the behaviour of free-ranging animals (Ropert-Coudert & Wilson 2005; Wilson & Vandenabeele 2012).

While the deployment of data loggers can provide large amounts of detailed data on the movements and behaviour of animals, there are several important problems that must be overcome. First the animal must be captured and subsequently recaptured in order to retrieve the data. Critical in this process is the minimisation of impacts associated not only with the animal carrying the devices (see below), but also with handling the animal during attachment and removal of the devices. In this respect, Manx shearwaters *Puffinus puffinus* provide a good model species: they are relatively robust to disturbance and easy to catch since they nest in burrows, (from which they can easily be taken) show a high degree of philopatry, and their colonies are relatively accessible. Second, most of the miniature data logging technologies deployed are relatively expensive, which in conjunction with a desire to minimise impacts at the colony or population level necessarily limits the number of individuals that can be studied. The

scale of tracking undertaken in this thesis was possible only through a combination of primary funding from Microsoft Research Cambridge and the use of relatively cheap consumer miniature GPS units (i-gotU, Mobile Action) that can be waterproofed and retro fitted with a range of battery sizes. Third, the abundance of serially non-independent time-series data that can be collected by these types of devices can be overwhelming, requiring a range of computational techniques to explore the patterns of behaviour therein.

Impacts of data loggers

The effects on birds carrying attached devices cannot be overlooked both for ethical reasons and because of the potential effects of the devices on the parameters being measured. All devices will have some effect on birds and those effects are likely to be highly dependent upon the mass, shape, position on the body, attachment method, duration of the deployment, and the amount of associated handling (Phillips *et al*. 2003; Burger & Shaffer 2008). The total mass of devices including attachment materials in the studies presented here varied between 15 and 19.5 g depending on the combination of devices and the size of battery. These comprise around 4.5% of body mass for most Manx shearwaters but vary between around 3.7 and 5.2% in the extremes. Previous studies of procellariiforms (Sæther *et al*. 1993; Phillips *et al*. 2003) have demonstrated negative impacts including nest desertion, increased trip duration and reduced meal sizes on a range of species carrying loads comprising 0.6–6.0% of body weight. In addition, it is likely that birds experience increased diving and flight costs and stress (Burger & Shaffer 2008), which probably are passed on to the offspring in the form of reduced incubation effort, provisioning rate and meal sizes (Sæther *et al*. 1993; Mauck & Grubb 1995).

Although the mass of our deployments was at the upper limit of previous studies, we took several important precautions. The shape and buoyancy of deployed devices and the attachment methods are at least as important as weight (within limits) and for this reason we used flat, streamlined packages, attached with temporary (failsafe) tesa tape that disintegrates

after about 14 days. In addition, most of our deployments were of shorter duration than many previous studies: median 8 days (interquartile range (IQR) 5-11) during incubation and 5 days (IQR 3-8) during chick rearing. Capture and handling of birds during deployment and removal of devices also provides an important impact on the welfare and behaviour of birds. With the exception of Lundy Island (where a lack of access to burrows necessitated the use of purse nets) we captured birds by carefully removing them from the burrow by hand. Birds were kept as calm and quiet as possible during the attachment and removal procedures, which were undertaken in cool, dark, quiet conditions, as close to the colony as possible. Where possible, we have monitored the impacts of our deployments on the breeding success of the birds. These suggest that the impacts of these deployments over the relatively short durations are minimal, but probably most significant during incubation. Following exodus, a similar proportion of females layed eggs as in untracked burrows although uncertainty in breeding status at this time of the season makes it difficult to assess. Those females departed for similar length trips as in previous studies and layed eggs of a similar mass, although perhaps slightly later. During incubation recorded trip duration was longer than in previous studies and the subsequent hatching success was slightly lower than for untracked parents. During chick-rearing, the mass growth rate of chicks was slightly (but not significantly) lower than for the chicks of untracked parents, while fledging success was identical. The data on the at-sea behaviour of Manx shearwaters presented in this thesis must therefore be interpreted with the caveat that these birds are carrying devices that may have affected their behaviour.

The Manx shearwater

At this stage a brief description of the Manx shearwater and what we already know about its biology and behaviour would be useful. Much of what I could say here about the Manx shearwater is already said more elegantly in the invaluable and detailed book on the species by Brooke (1990). Nevertheless, I shall endeavour to provide a succinct and informative sketch. The

Manx shearwater is a small-medium sized (400g) Procellariiform seabird of the genus *Puffinus,* which comprises 25 or so species of small to medium sized shearwaters ranging in size from the little shearwater *Puffinus assimilis* (220-260 g) to the great shearwater *Puffinus gravis* (715-950 g) (Onley & Schofield 2007). In common with other Procellariiforms, adult survival is high and many breeding birds live 20-30 years (although some may exceed 50 years) and do not start to breed until around 5-6 years old. The majority (approximately 90%) of the world population breeds in Britain and Ireland (Mitchell *et al*. 2004), predominantly in colonies at remote locations off the west coasts (figure 1). Of those colonies, two sites are of particular importance in terms of numbers (together accounting for over 90% of the UK breeding population): the colony on the Island of Rum (Inner Hebrides, Scotland) hosts an estimated 120,000 breeding pairs (Mitchell *et al*. 2004), while the colonies on the islands of Skomer, Skokholm and Middleholm (Pembrokeshire, Wales), host an estimated 316,000, 46,200 and 3,000 breeding pairs respectively, together accounting for approximately 365,000 pairs (Mitchell *et al*. 2004; Perrins *et al*. 2012). Birds are present on the colonies only during the hours of darkness, either returning to the sea at dawn, or remaining underground in their burrows during the day (figure 2).

This thesis is concerned with questions about the at-sea behaviour of the Manx shearwater during the breeding season, that is, from the pre-laying period until the fledging of chicks (figure 1). Nevertheless, in examining aspects of the breeding behaviour it is important to bear in mind that the breeding season precedes and follows a long trans-oceanic, trans-equatorial migration to the Patagonian shelf where they spend the winter (October-March) before returning to the breeding colonies in April (Guilford *et al*. 2009) (figure 1). There then follows a pre-breeding period during which breeding birds must reclaim, prepare and defend their nests; form (or reform) pair bonds; and engage in copulation (Brooke 1990). After copulation, females then embark on a prolonged (two-week) absence from the colony, during which they develop their single egg (Brooke 1990; Guilford *et al*. 2009). On return, females lay their egg in an

underground nest and during the incubation period, which lasts around 51 days, both parents alternate incubation stints of 5-8 days at the nest with long foraging trips (Guilford *et al*. 2008) on which they recover body condition. A short brood guard period of a few days typically follows hatching, after which both parents make repeated, shorter duration (1-4 days, but some longer) foraging trips to sea, returning at night to provision the chick (Gray & Hamer 2001). While foraging at sea, birds make long-distance movements travelling hundreds of kilometres (Guilford *et al*. 2008), plunge and pursuit diving for prey (King 1974; Jones 1975) using their wings and feet for propulsion (King 1974; Jones 1975; Brown *et al*. 1978). Much of their foraging behaviour occurs in large, dense flocks (King 1974; Jones 1975; Stone *et al*. 1994). The primary type of prey recorded from regurgitates, crop and gizzard contents are relatively undigested *Clupeid* fish, but also some squid (Brooke 1990; pers. obs.). Chick development is slow and nestlings accumulate large quantities of fat during the 60 or so days that parents continue to provision them; at their peak mass they far exceed the mass of their parents. Around ten days prior to fledging parents typically cease provisioning the chick, which undergoes a period of mass recession and final development, before fledging alone one night at around 70 days old.

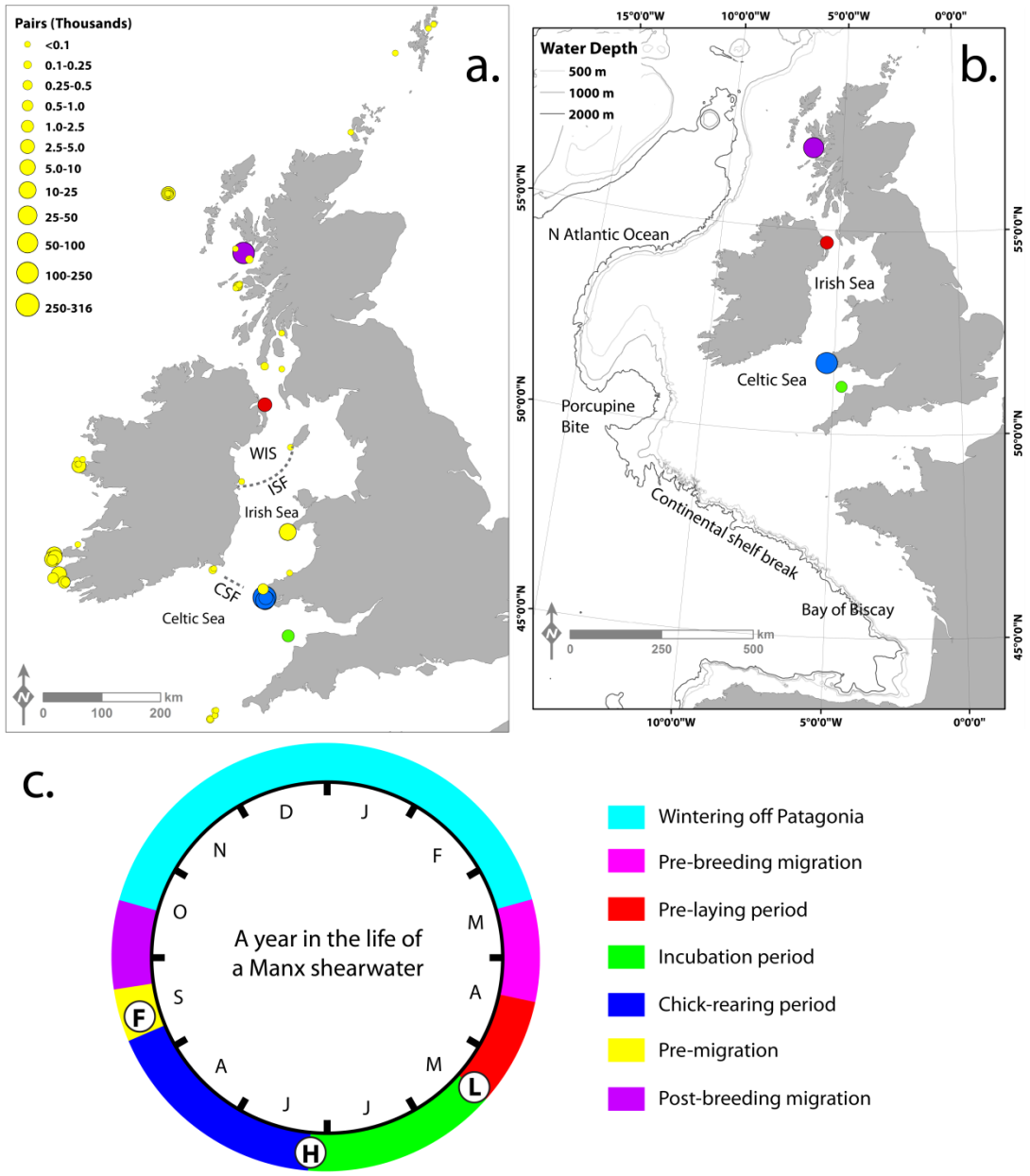

Figure 1. (a) The breeding distribution of Manx shearwaters in the UK and Ireland (from Mitchell *et al*. (2004). Colony locations (yellow) are shown scaled by estimated number of breeding pairs (in thousands) (Mitchel et al. 2004; Booker & Price 2010; Perrins *et al*. 2012). The colonies from which birds were tracked in this thesis were Rum (Purple), Lighthouse Island (Copeland) (Red), Skomer Island (Blue) and Lundy Island (Green). The Irish Sea, Western Irish Sea (WIS) and Celtic Seas are labelled along with the approximate positions of the Irish Sea Front (ISF) and Celtic Sea Front (CSF), which may be important areas for foraging Manx shearwaters. (b) The location of the colonies from which birds were tracked in relation to wider scale oceanic features. (c) Approximate phenology of an adult Manx shearwater breeding on Skomer Island, based on Brooke (1990) and Guilford *et al*. (2009); L = Laying, H = Hatching, F = fledging.

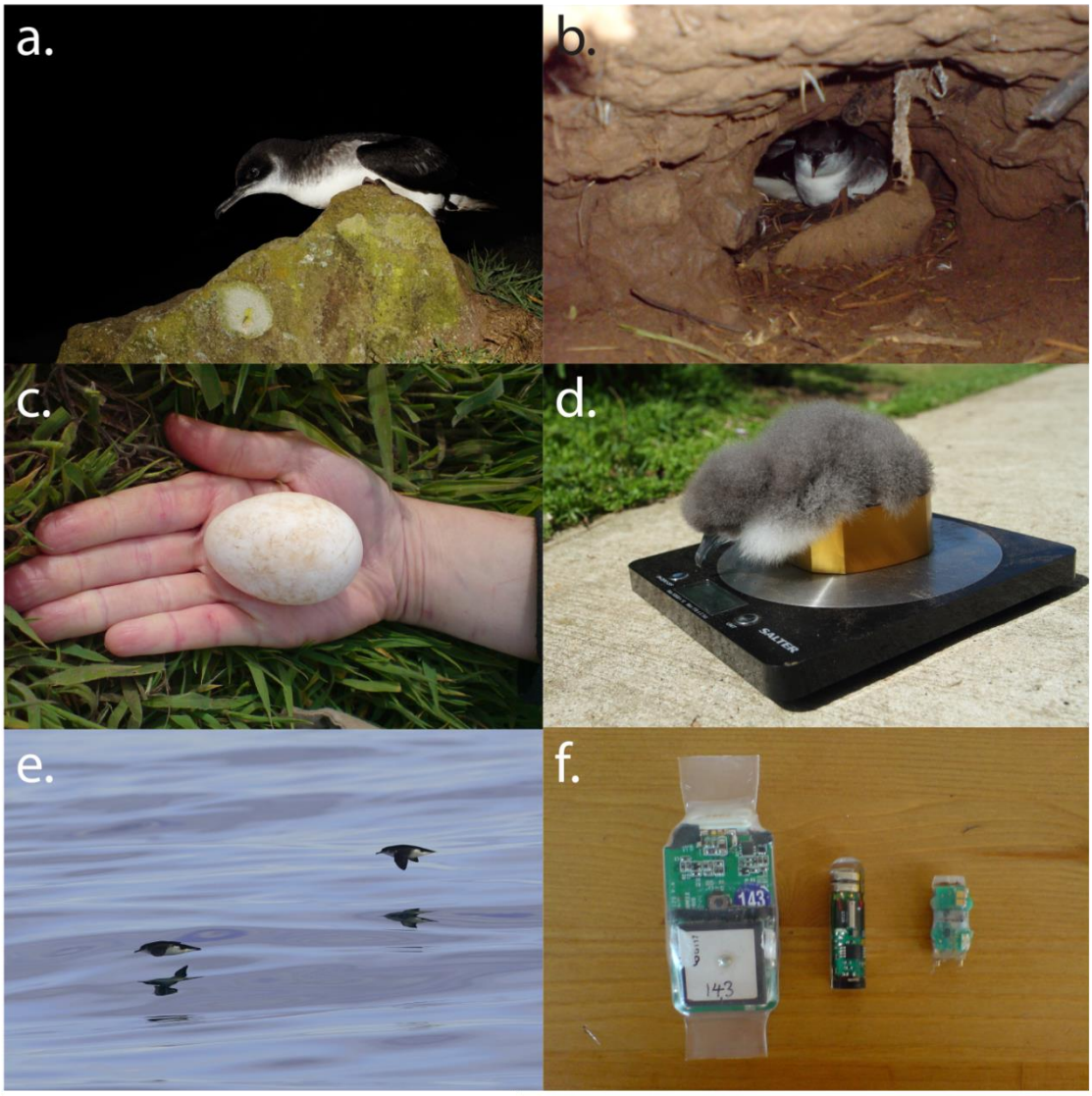

Figure 2. (a) Adult Manx shearwater on the surface of the colony at night, (b) breeding pair in their nesting burrow, (c) single large white egg laid by the Manx shearwater, (d) Manx shearwater chick at approximately 10-15 days old, (e) two Manx shearwaters at sea, (f) from left to right: waterproofed GPS logger, geolocator-immersion logger, and time-depth recorder.

Aims and structure of the thesis

Much of this thesis is exploratory in nature and my aim is to reveal new insights into the at-sea behaviour of the Manx shearwater (and indirectly other procellariiform seabirds) rather than testing a set of specific hypotheses. The nocturnal deployment and recovery of bird-borne data loggers over 3-4 years on four different colonies, and in parallel with the recording of

complimentary field data represents a huge investment of time and effort. Through experience, I learned that the best returns on time in the field, equipment and minimising disturbance to the birds were gained by pursuing several questions simultaneously. Some data therefore are used in multiple chapters to answer different questions about the behaviour of Manx shearwaters. The following chapters are presented as self-contained manuscripts, and each is intended to be able to be read independently. Seven other people collaborated in the work of one or more chapters: Tim Guilford, Robin Freeman, Chris Perrins, Holly Kirk, Kerry Leonard, Annette Fayet and Richard Phillips (see Author Contributions).

Chapter 2 examines the movements and at-sea behaviour of Manx shearwaters during the pre-laying absence, or exodus from the colony. This period is of particular interest since it is the part of the breeding season when males and females have the most starkly different objectives, and one for which very little detailed information exists on the at-sea behaviour of any procellariiform species. The process of egg formation places high energy and nutrient requirements on female birds (Nager 2006) and Procellariiform seabirds typically lay a single, large, energy rich egg, formed over a relatively long period (Warham 1983). In the Manx shearwater, the egg typically comprises approximately 15% of female body mass. As a result, in most species, this corresponds with an extended period of absence from the colony, during which pre-laying females may range widely to gather the nutrients necessary for egg production (Warham 1996). In the Manx shearwater, the males continue to visit the colony regularly during this period probably to defend the nest and possibly to engage in further copulations (Brooke 1990). As a result the foraging movements of males are likely to be much more constrained. We examine the movements and at-sea behaviour of males and females operating under these constraints across four pre-breeding periods in which oceanographic (and probably prey) conditions varied.

Chapter 3 explores large-scale patterns in the foraging distributions of birds breeding at multiple colonies across the UK range of the species. The identification of important bird areas at sea (Garthe *et al*. 2009; Louzao *et al*. 2009), an understanding of their variability and an understanding of the environmental and ecological interactions that drive it are critical questions in marine conservation (González-Solís & Shaffer 2009; Lewison *et al*. 2012). Advances in miniature telemetry and data logging systems have enabled a vast number of tracking studies on a wide range of species, providing insights into many aspects of seabird behaviour and ecology (Burger & Shaffer 2008; Wilson & Vandenabeele 2012). However, many studies necessarily follow only a small number of individuals, sometimes during a single stage of the breeding season, in a single year, from single colonies, or from multiple colonies asynchronously. The extent to which such studies can capture the range of variation in distribution and behaviour across populations and years, or examine interactions between birds from different colonies, independent of temporal variation in oceanographic conditions and prey distributions is likely to be limited (Holdo & Roach, 2012). We analyse a large three-year tracking dataset collected at two colonies simultaneously during incubation and up to four colonies simultaneously during chick-rearing. In particular, we examine the distribution of foraging activity with respect to colony location, the extent to which birds from different colonies might depend on the same resources, and the likely function of trips of different, duration, range and destination.

Chapter 4 examines the diving behaviour of Manx shearwaters. Although shearwaters of the genus *Puffinus* morphologically are well adapted for swimming under water (Wahram 1977; Brown, Bourne & Wahl 1978) and while species in this group have long been known to engage in pursuit plunging and pursuit diving, little detailed information exists on the diving behaviour and typical dive performance of these species. We deployed high sampling rate time-depth recorders alongside miniature Global Positioning System (GPS) loggers on a large sample of chick-rearing birds. These data provide the first insights into the diving behaviour and

performance of the Manx shearwater and the first large dataset providing detailed information on the diving behaviour of any *Puffinus* shearwater. By linking diving information with the co-deployed GPS loggers, we demonstrate the fine-scale spatial distribution of diving for two example birds, as well as the large scale distribution of diving activity across the Manx shearwaters' foraging range, and temporal patterns of diving activity through the day.

In ***Chapter 5*** we build a detailed picture of the at-sea behaviour of the Manx shearwater during the incubation and chick-rearing periods. While the use of miniature data loggers is rapidly increasing our understanding of the movements and habitat preferences of pelagic seabirds, objectively interpreting behavioural information from the large volumes of highly-detailed serially non-independent data collected by such devices can be challenging. Yet in many cases, an understanding of where and when birds undertake different activities may be critical to the planning of appropriate conservation action. We used a hidden Markov model (Rabiner 1989) to explore the discrete behavioural states (or activities) within data collected simultaneously by three bio-logging technologies - GPS, saltwater immersion and time-depth recorders.

In ***Chapter 6*** we experimentally manipulate the energetic demands placed on chick-rearing shearwaters to test the effects on their foraging behaviour at-sea. Procellariiform nestlings accumulate large quantities of fat during the nestling period (Warham 1990), but this accumulation appears to be regulated in many species, potentially allowing the fat reserves of chicks and parental provisioning to be optimized to maximise the survival of the chick up to and beyond fledging, and minimize foraging effort by the parents (Ricklefs & Schew 1994; Lorentsen 1996). Foraging trip duration and hence provisioning rate provides a potential mechanism by which parents may regulate provisioning effort (Weimerskirch *et al*. 1997). The parents of well-fed chicks have been shown make fewer nest visits and hence a greater proportion of longer duration (self-feeding) foraging trips (Hamer *et al*. 2005). However, the role of foraging ranges, destinations and at-sea foraging behaviour of parents in this flexible provisioning response is

unknown. We provided a high energy supplemental diet to Manx shearwater chicks, then monitored the provisioning behaviour and tracked the at-sea behaviour of their parents and the parents of control chicks.

A general discussion (***Chapter 7***) summarizes the key findings of this thesis and discusses some of the questions that remain for future investigation.

References to Supplementary Materials are made in some chapters, and these are provided as appendices at the back of those chapters. Chapter 3 includes some visualisations as mp4 movies and a large number of images which can be found on the accompanying disc.

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Chapter 2

Tracking the pre-laying exodus of male and female Manx shearwaters

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Abstract

The process of egg formation places high energy and nutrient demands on female birds. Procellariiform seabirds typically lay single, large eggs, which are formed over relatively long periods. In most species, this corresponds with an extended period of absence from the colony, during which pre-laying females may range widely to gather the nutrients necessary for egg production. In many species including the Manx shearwater *Puffinus puffinus*, males continue to visit the colony during this time, probably to defend the nest and possibly to obtain further mating opportunities. Males therefore are more constrained in their foraging opportunities during this period.

We used a combination of GPS and geolocator-immersion loggers to track the pre-laying exodus behaviour of male and female Manx shearwaters in four consecutive years. Some individuals were tracked in more than one year. Following copulation at the colony, females embarked on a pre-laying exodus lasting around 12-18 days, during which they completed the formation of their egg. The duration of exodus suggests that many females may initiate yolk development several days prior to departing the colony. The foraging destinations of females appeared to be flexible between years. In 2009, females remained within the Celtic Sea, approximately 150 km west of the colony and were strongly associated with patches of high productivity. In subsequent years, when primary productivity was lower, or less densely aggregated close to the colony, females ranged over 600 km, foraging primarily along the continental shelf slope to the west and southwest of the colony. Males showed a similar pattern, although they retained a strong association with the colony, which they continued to visit frequently. In 2009, males and females foraged in the same location. During subsequent years, when females foraged along the continental shelf slope, most males remained within the Irish and Celtic Seas less than 150 km from the colony, but several departed the colony for up to eight days in order forage further afield.

The behaviour of individuals was flexible, with birds of both sexes selecting different strategies in different years. Although in each year there was a clear majority decision. These data suggest individual decisions based on an interpretation of body condition and prevailing foraging conditions in each year. This study provides the first high spatial precision data on the movements and at-sea behaviour of the Manx shearwater (and perhaps any procellariiform) during the pre-laying exodus. The combination of flexible, wide-ranging movements, during a critical stage of the breeding season makes these data of high value in conservation planning.

Introduction

The process of egg formation places high energy and nutrient demands on female birds. They must collect specific nutrients (proteins, lipids, calcium) to meet the requirements of egg formation, often over short periods when food may not yet be abundant. Procellariiform seabirds share two important reproductive characteristics with respect to egg formation. First, females typically lay a single, large, energy rich egg (Warham 1983). In Manx shearwaters this comprises approximately 15% of the female's body mass (Brooke 1990). The egg is then incubated by the male for the first long shift, before a regular alternating pattern of incubation becomes established (Warham 1990; Warham 1996). Second, laying typically is preceded by an exodus (Marshall & Serventy 1956), or pre-laying absence (Imber 1976) from the colony (Warham 1990; Warham 1996). Although common throughout the order, the duration and nature of the pre-laying exodus differs widely between species. The duration of the absence from the colony varies from a few days for the Shy Albatross *Thalassarche cauta* (Abbott *et al*. 2006) to two months for female Grey-faced petrels *Pterodroma macroptera gouldi* (Imber 1976). In some species, such as the Short-tailed shearwater *Puffinus tenuirostris* (Serventy 1967) and Barau's petrel, *Pterodroma baraui* (Pinet *et al*. 2012) both males and females desert the colony for similar durations. In some, such as Northern fulmars *Fulmarus glacialis* (MacDonald 1977; Hatch 1990) and Grey-faced petrels (Imber 1976) both sexes depart, but the male's absence is

typically shorter than the female's. In others such as the Wandering albatross *Diomedea exulans* (Croxall *et al*. 1999) and the Balearic shearwater *Puffinus mauretanicus* (Guilford *et al*. 2012) only the female departs, while the male continues to visit the colony regularly.

After returning to the colony from their wintering areas, breeding birds must reclaim, prepare and defend their nests; form (or reform) pair bonds; and engage in copulation. These activities are likely to have high energetic costs and both sexes lose body mass during this period (Fitzherbert 1985; Brooke 1990; Mallory *et al.* 2008). Following this pre-breeding period, breeding birds may consequently lack the energy and nutrient reserves necessary to form an egg or undertake a long incubation stint. The main functional interpretation of the pre-laying exodus is therefore that it enables the female to gather the nutrients necessary for egg production, while the male gathers the fat reserves necessary to sustain him through the first incubation stint (Warham 1990; Mallory *et al*. 2008). Implicit in this interpretation is the notion that a prolonged absence from the colony is necessary because the required resources are not available close by and/or are spatially unpredictable: Warham (1990) suggested that a key factor in determining the nature and duration of pre-laying exodus would be the distance to suitable feeding grounds.

Visual observations (e.g. Croxall *et al*. 1999), have revealed insights into the destinations of birds during this period of absence. But only since the advent, increasing miniaturisation and longevity of bird-borne tracking systems has the remote observation of long-distance movements over these extended periods of absence been possible. In particular, deployments of miniature geolocators or Global Location Sensors (e.g. Afanasyev, 2004) have provided year-round tracking of many Procellariiforms, including the pre-laying exodus (Phillips *et al*. 2006; Catry *et al*. 2009; Guilford *et al*. 2009; Pinet *et al*. 2012; Rayner *et al*. 2012). Although the spatial accuracy of these devices is poorer than that of satellite-transmitters (Phillips *et al*. 2004), or Global Positioning System (GPS) loggers, these studies have identified the general distribution of pre-laying activity.

In most of these examples (Phillips *et al*. 2006; Guilford *et al*. 2009; Pinet *et al*. 2012; Rayner *et al*. 2012), pre-laying excursions typically were of similar or greater extent than foraging trips made during incubation, and of much greater extent than the majority of foraging trips during chick-rearing. Two of these studies indicate clear differences in the distributions of males and females during their exodus. Tracking of Barau's petrel *Pterodroma baraui* (Pinet *et al*. 2012) and Chatham Petrel *Pterodroma axillaris* (Rayner *et al*. 2012) indicated that the maximum foraging range of males is significantly greater than that of females during the pre-laying period. Given the different reproductive roles and nutritional demands placed on males and females during and following the pre-laying exodus (egg formation versus fat reserves for incubation), it is not surprising perhaps that distinct foraging destinations are seen in some species.

We studied the pre-laying exodus behaviour of male and female Manx shearwaters *Puffinus puffinus*, a 400g procellariiform seabird that breeds predominantly in colonies at remote locations off the west coasts of Britain and Ireland. The species typically nests in burrows, appears to feed primarily (perhaps exclusively) diurnally (Dean *et al*. 2012, Chapter 4), and returns to the colony only during the hours of darkness (Brooke 1990). In the Manx shearwater, as well as several other procellariiforms (Pinder 1966; Tickell 1962; Croxall *et al*. 1999), there is an added complication to pre-laying behaviour: only the female undertakes an exodus, while the male continues to visit the colony regularly, even remaining in the burrow during the day (Brooke 1990). Two functional advantages of this behaviour have been suggested: First, continued visits by the male during the female's absence may serve to ensure that the pair retains ownership of their burrow. Breeding is largely asynchronous in this species and so late breeding pairs potentially could evict earlier birds during their absence (Brooke 1990). Second, continued visits by the male may afford the opportunity for extra-pair copulations (EPCs) with females that have not yet departed. EPCs have been recorded in several procellariiforms (Hatch 1987; Austin & Parkin 1996; Huyvaert *et al*. 2000; Jouventin *et al*. 2007) and evidence of extra-

pair paternity found in 10-25% of tested families in at least three species (Austin & Parkin 1996; Huyvaert *et al*. 2000; Jouventin *et al*. 2007).

Whatever the function of this behaviour, the consequence for the male is that he must forage at sea during the day to reach an adequate body condition for the first long incubation stint, but must continue to visit the colony and maintain a presence at the burrow. Males would therefore be predicted to remain close to the colony as long as sufficient prey is available close by. But if local resources are not sufficient, males must choose to forage under poor local conditions, potentially failing to reach adequate condition for incubation, or forage further afield, paying higher commuting costs, risking losing the burrow to a competitor, and/or missing opportunities for EPC. Females would also be expected to remain close to the colony as long as sufficient prey (or suitable nutrient resources) is available close by. However, because they rarely return to the colony during this period (Brooke 1990) they may forage elsewhere (even long distances from the colony) if sufficient resources are not available close by. Using geolocators, Guilford *et al*. (2009) demonstrated that (in one pre-laying period) most males (5/6) and a few females (2/6) remained close to the colony, while most females (4/6) and one male undertook excursions of around two weeks, some travelling as far as the continental shelf-break and slope, southwest of Ireland. This suggests that the resources necessary for forming an egg were not available locally, and that either: (i) local resources were nevertheless adequate for males to gain condition, or (ii) males were foraging under relatively poor conditions and potentially losing mass. In order to better understand the conditions that affect the foraging decisions of the Manx shearwater during the pre-laying exodus, we tracked the movements of pairs of birds using a combination of GPS and geolocator-immersion loggers. We then examined the movements and behaviour of birds in relation to changes in body mass over the period and the prevailing oceanographic conditions in four consecutive years.

Materials and Methods

Data loggers

In four consecutive years (2009-2012) between 1 and 25 April, we monitored the pre-breeding season attendance of Manx shearwaters in study nests on Skomer Island, Wales (Southern Irish Sea: 51°44′N, 5°17′W). Using purpose built inspection hatches we checked nests during the day and night and recorded the identity (metal leg ring) of any birds present. Between 25 April and 10 May of each year we continued to check nests with the aim of finding pairs in the nest together for the first time; these were likely to be pairs copulating prior to the female pre-laying exodus (Brooke 1990). When we found likely pairs, both birds were removed one at a time from the burrow. Birds were weighed, tracking devices deployed and birds returned to the burrow within 15 minutes. Birds were sexed later in the season (or subsequent seasons) either by cloacal inspection immediately following laying (females cloacae appear bruised and swollen), or by feeling an egg inside returning birds.

We tracked the movements of 7 pairs in 2009, 7 pairs in 2010, 9 pairs in 2011 and 11 pairs in 2012. Some individuals were tracked in multiple years. Males: two individuals tracked in three years and two tracked in two years; Females: one individual tracked in all four years, one tracked in three years and three tracked in two years. Birds were fitted with a global positioning system (GPS) logger (modified i-gotU GT-120: Mobile Action). During 2009, 2011 and 2012, birds were also fitted with a British Antarctic Survey geolocator-immersion logger. GPS loggers were configured to record location once every 60 minutes (90 minutes for females in 2009). GPS were sealed in heat-shrink plastic and attached dorsally using thin strips of tesa marine cloth tape underlying a small number of contour feathers (Guilford *et al.* 2008; Dean *et al.* 2012). Geolocator-immersion loggers test for saltwater immersion every 3 seconds and record the number of samples immersed at the end of each 10-minute interval. Immersion loggers were attached by two lightweight cable ties to a leg ring so as to be immersed when the bird was

sitting on the sea surface or diving. GPS weighed approximately 10.5 g for females and 15g for males. Geolocator-immersion loggers weighed approximately 1.5g. The total mass of devices was approximately 13.5-15.5 g for females and 18-19.5 g for males. All deployments were made between the 27 April and 7 May. On return, birds were recaptured from the burrow, reweighed, devices removed, and birds returned to the burrow within 10 minutes. Throughout the tracking period and following device retrieval we continued to monitor attendance at the nest until the females had returned and laid their egg. Once laid and discovered, eggs were weighed and replaced.

Analysis of GPS and saltwater-immersion data

GPS tracks (which may contain multiple trips away from the colony) were segmented into individual trips based on the bird returning to within 1km of the colony between 20:00 and 03:00. Any trips that were incorrectly segmented using this method (usually where birds came close to the colony at night, but did not make landfall) were subsequently corrected manually. For each trip, the maximum range and distance travelled per day were calculated. To visualise the main areas used by shearwaters during the pre-laying exodus period, we calculated kernel density distributions (for each sex in each year of tracking) over a grid of 1 km^2 cells in ArcGIS. A kernel bandwidth (smoothing parameter *h*) of 26.6 km was chosen as the mean of optimal bandwidths calculated for each year using Least-squares cross-validation (Worton 1995). We analysed the saltwater-immersion data from the geolocator-immersion loggers co-deployed on birds in 2009, 2011 and 2012. For each bird we calculated the total proportion of daylight hours at-sea spent immersed (on or under water, as opposed to in-flight). To examine the timing of behaviour, we also calculated the proportion of each hour each bird spent on or under the water.

Analysis of oceanographic data

We investigated how the distribution of birds in each year was related to prevailing oceanographic conditions (bathymetry, chlorophyll concentration and SST). Bathymetry data were downloaded from the General Bathymetric Chart of the Oceans website (http://www.gebco.net) as a 30 arc-second grid. Remotely sensed (by the MODIS Aqua satellite) chlorophyll concentrations (mg m^{-3}) and daytime sea-surface temperatures (SST) (˚C at 11µ) were obtained as 32-day composites corresponding to each tracking period (23 April – 24 May) at 4 km^2 grid resolution. Data were downloaded from the Ocean Color website (http://oceancolor.gsfc.nasa.gov) as Standard Mapped Images (SMI) in Hierarchical Data Format (HDF), converted into ASCII format and then into raster grid datasets in ArcGIS. Contemporary water depth, chlorophyll concentration and SST values were extracted from the above datasets for each recorded bird location in ArcGIS. To test whether recorded bird locations were more strongly associated with specific ranges of water depth, chlorophyll concentration and SST than expected by chance, we created corresponding random distributions of locations for each bird tracked. We created a grid of null locations spaced 1 km apart over the full extent of all recoded pre-laying movements (Supplementary Material figure S1). For each tracked bird we randomly selected a number of points from the null locations equal to the number of locations recorded for that bird and extracted water depth, chlorophyll concentration and SST values for those random locations.

Results

Bird masses and logger deployments

The mean mass of males at deployment was slightly heavier (412.4 ± 34.0 g) than the mass of females (403.7 ± 31.3 g), but not significantly: t-test t (52) = 1.63, p = 0.11. Devices for males were 18-19.5 g comprising approximately 4.2-4.9% of body weight. Devices for females were 13.5-15.5 g comprising approximately 3.5-4.1% of body weight. Males carried the devices for a

median of 8 days (interquartile range (IQR) 7-12), while females carried the devices for 14.5 days (IQR 9-18). In half (30/60) of the successful deployments, the GPS stopped logging before the bird returned to the colony (or before we recovered the device in the case of males) (table 2), either because the battery, or the GPS failed. The recording durations of GPS were significantly shorter for males than females in 2009, but were not significantly different between the sexes in each other year (table 2) and for each sex, were not significantly different across years: Kruskal-Wallis (males) χ^2 (3,22) = 1.71, p=0.64, (females) χ^2 (3,24) = 4.00, p=0.26. Because females on exodus tended to be absent from the colony for longer than males and because they carried smaller batteries, their GPS tended to fail more days prior to their return, although this difference was only significant in 2011 and 2012 (Table 2). The number of days prior to return (or recovery for males) that the GPS failed, differed between years for males, but not for females: Kruskal-Wallis (males) χ^2 (3,22) = 14.06, p=0.003, (females) χ^2 (3,24) = 0.64, p=0.89.

Laying success

The numbers of pairs tracked in each year, the number of successful deployments and the number of females laying an egg are given in table 1. Overall 47% of tracked pairs laid eggs either just after the tracking period (egg discovered in the nest within two days of return), or within the following month, after further foraging trips. This compares to 55.5% laying in all other burrows we monitored throughout the four breeding seasons. In 2010 only two out of seven tracked pairs laid (2 – 4 weeks later). This was a late season with low breeding success among our study burrows. Because the season was late, with low breeding success our tracking did not appear to record pre-laying exodus behaviour. Excluding 2010, 74% of the tracked pairs laid eggs, compared to 56.1% in all other burrows. One pair tracked in 2009 was evicted during the exodus period and may not have been a breeding pair. It is also likely that some of the other pairs we tracked may not have been pre-breeding pairs, and so should not have been expected to lay. The median lay dates for tracked birds (18 May 2009, 26 May 2010, 15 May 2011, and 16

May 2012) were later than the median lay dates for all other study burrows in each year (09 May 2009, 17 May 2010, 13 May 2011, and 12 May 2012).

Table 1. Number of GPS deployments made on male, female and unsexed birds in each year, as well as the number of tracked females that laid following the tracking period, or after subsequent trips to sea.

	2009	2010	2011	2012	Totals
Pairs tracked	7	7	9	11	34
Males, GPS recovered	7	4	8	7	26
Females, GPS recovered	6	5	9	8	28
GPS recovered, sex unknown	0	1	0	5	6
N females laying egg on return	5[1]	0	6	5	16
N females laying after subsequent (untracked) trips	0	2	2	2	6

Foraging destinations

We recorded 154 foraging trips: 96 made by males, 43 by females and 15 by birds that we could not sex. The number of trips recorded and duration, range (maximum recorded distance from colony) and km travelled per day are given for males and females in each year in table 2. All recorded GPS tracks are shown in figure 1, grouped by sex and year. Kernel density distributions, showing the main areas of usage by males and females in each year are given in figure 2. Because half of the GPS loggers failed before the bird's return to the colony (table 2), the recorded extent of trips may be more restricted than the actual movements of the birds over the entire deployment. However, we conducted a supplementary analysis of the daylight-location data from the geolocator-immersion loggers co-deployed with GPS in 2009, 2011 and

[1] One pair was evicted during exodus 2009 and may not have been a breeding pair.

2012 (Supplementary Material figure S2). These loggers offer low precision (location estimates ±186 km, Phillips *et al*. 2004), but the loggers lasted for the entire duration of each deployment. This supplementary analysis supports the general distribution patterns shown by the GPS data.

During 2009 and 2010 males and females were recorded in similar locations, within 150 km west of Skomer, in the Celtic Sea. In 2010 we recorded only two birds heading to the area of the continental shelf slope, beyond the shelf-break (particularly the Porcupine Bight), one female and one unsexed bird. For most birds tracked in 2010, we probably recorded pre-breeding movements, rather than pre-laying exodus. In 2011 the distributions of males and females differed, with most male birds foraging within the same area of the Celtic Sea as in 2009 and 2010, but also in the Irish Sea north of Skomer. Only one (1/8) male headed to the area of the continental shelf slope and the Porcupine Bight. In contrast, only two females (2/9) remained close to the colony in the Celtic Sea, while the rest (7/9) headed to the continental shelf slope and the Porcupine Bight. In 2012, most (5/7) males foraged in the same area west of Skomer as in previous years, although two of those ventured further west along the southern Irish coast. Only two (2/7) males headed to the area of the continental shelf slope and the Porcupine Bight. In contrast, only two females (2/8) remained close to the colony, one in the Celtic Sea west of Skomer, the other venturing into the Irish Sea north of Skomer. The rest (6/8) headed to the continental shelf slope and deeper waters beyond. In 2012 we also successfully tracked five birds that we could not sex (2 pairs plus 1). Two of these remained in the Irish and Celtic Seas, one ventured west along the southern Irish coast and two (probably a pair) headed to the continental shelf slope and the Porcupine Bight. The routes of birds travelling to and from the continental shelf were remarkably consistent and direct (approximately 40 km h^{-1}), with most birds heading directly towards the Porcupine Bight area, and then exploring the continental shelf edge.

Individual variability

Among the four males and five females tracked during more than one year, there was both individual consistency and variability in their destinations (figures 3 and 4). Males typically foraged close to the colony, only making longer trips to the continental shelf slope and Porcupine Bight during 2012 (figure 3). One female (figure 4a) remained close to the colony in both years she was tracked. One female tracked in all four years (figure 4b), remained close to the colony during the first three and ventured to the shelf slope only in 2012. Another, tracked in three years (figure 4c) remained close to the colony during 2009, but travelled out to the shelf slope during 2011 and 2012. The last two females tracked during 2011 and 2012 (figure 4 d & e) travelled out to the shelf slope in both years.

Table 2. Deployment metrics: total number of trips recorded; date of the first and last locations recorded; median (+interquartile range) GPS duration; median number of days that the GPS stopped recording before the bird returned; number of trips recorded per deployment for each sex in each year. Median trip metrics: trip duration, maximum range and km travelled per day. Significant differences between sexes are highlighted in ***bold italics*** and indicated by *<0.05 and ** <0.01, with (numbered) test statistics given below.

Year	Sex	N trips recorded	First GPS data dd/mm	Last GPS data dd/mm	GPS. dur. (days)	GPS failure prior to return (days)	Trips per deploy. -1	Trip duration (days)	Max. range (km)	Km day-1
2009	**M**	24	28/04	15/05	***7 (3-8)*[1]***	2 (1-7)	2 (1-5)	***2 (1.5-3.5) *[6]***	103.1 (76-114)	107.1 (93-173)[21]
	F	10	29/04	12/05	***11.5 (11-15)*[1]***	3.5 (1-8)	1.5 (1-2)	***11.5 (6-18) *[6]***	116.0 (109-119)	81.4 (69-108)[21]
2010	**M**	16	29/04	12/05	7.5 (6-11.5)	0 (0-0.5)	4.5 (2-7)	2.3 (1.8-3.8)	110.1 (103-1184)	120.6 (106-154)[22]
	F	12	29/4	13/05	9 (3.8-11)	1 (0-7)	2 (2-3)	3 (1.8-5.5)	109.1 (103-256)	171.9 (124-176)[22]
2011	**M**	37	25/04	10/05	9 (5.8-13.8)	***0 (0-0) *[2]***	***4 (3.5-6)**[4]***	***1.63 (1.3-5.1)**[7]***	***127.3 (106-152)**[9]***	150.0 (121-199)[23]
	F	13	25/04	17/05	9 (7.75-13)	***5 (0-8) *[2]***	***1 (1-1.3)**[4]***	***14 (5.5-15.8)**[7]***	***658.1 (424-727)**[9]***	171.9 (168-204)[23]
2011	**M**	19	26/04	10/5	7 (7-9.5)	***0 (0-0) *[3]***	***2 (1.3-4.3)*[5]***	***3.5 (2.1-6.1)**[8]***	***241.5 (116-438)*[10]***	176.4 (145-246)[24]
	F	8	26/04	10/5	10 (8-10)	***4.5 (0-8)*[3]***	***1 (1-1)*[5]***	***12 (8-15.5)**[8]***	***691.3 (429-721) *[10]***	245.7 (165-282)[24]

[1] rs(11)=56, p=0.045; [2] rs(15)=51, p=0.43; [3] rs(13)=38.5, p=0.37; [4] rs(15)=100, p=0.004; [5] rs(13)=76, p=0.014; [6] rs(11)=58, p=0.020; [7] rs(15)=43.5, p=0.004; [8] rs(13)=31.5, p=0.003; [9] rs(15)=42, p=0.003; [10] rs(13)=36, p=0.021

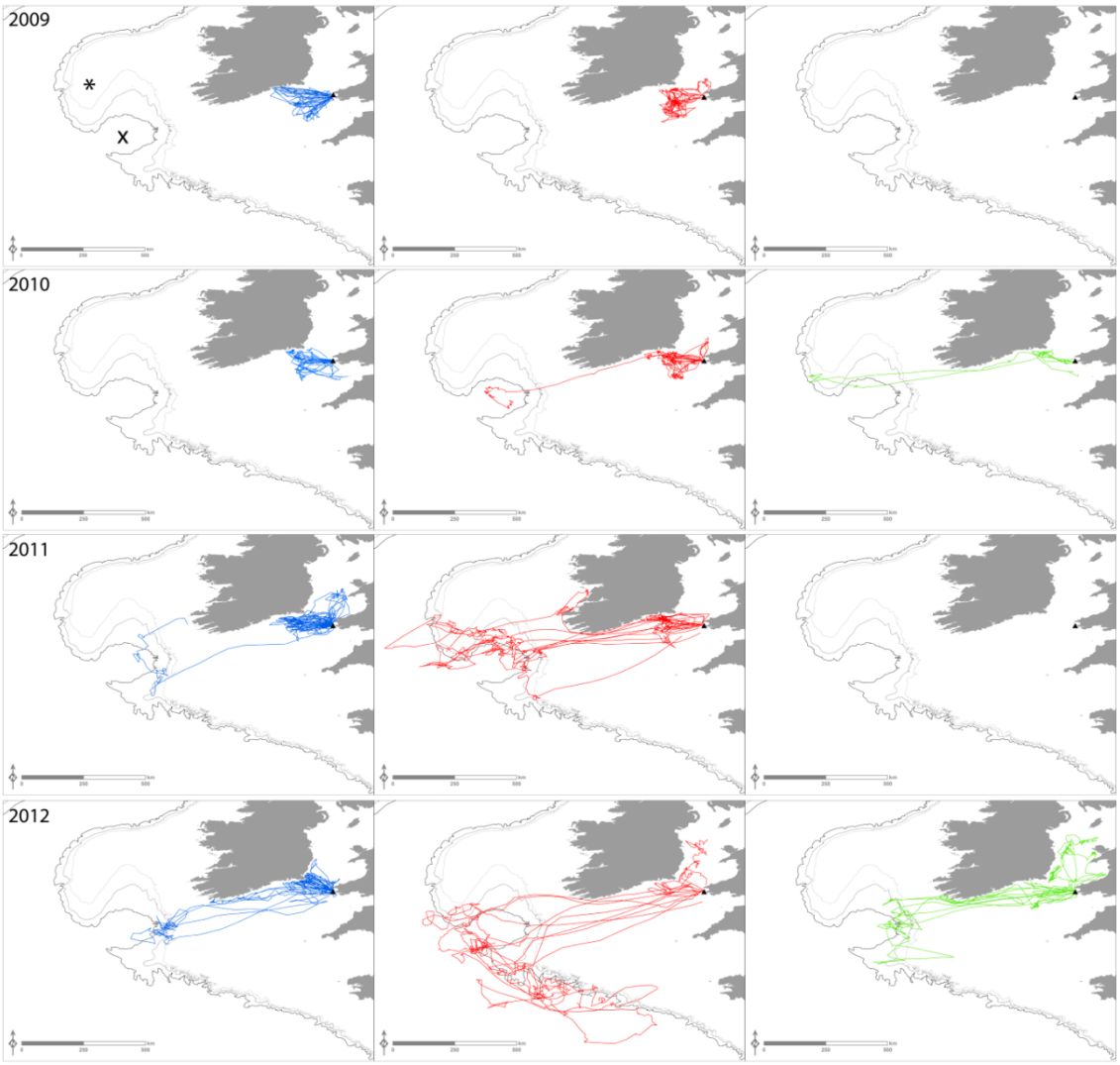

Figure 1. GPS tracks of foraging trips made by all males (blue), all females (red) and all birds of unknown sex (green) during the pre-laying exodus period (approximately 25 April – 15 May) in 2009, 2010, 2011, and 2012. The location of the colony on Skomer Island is indicated by a black triangle. The position of the steep continental shelf slope is indicated by the 500, 1000 and 2000 m depth contours (light-dark grey lines). The Porcupine Bight is indicated by X and the Porcupine Bank by * in the top left panel.

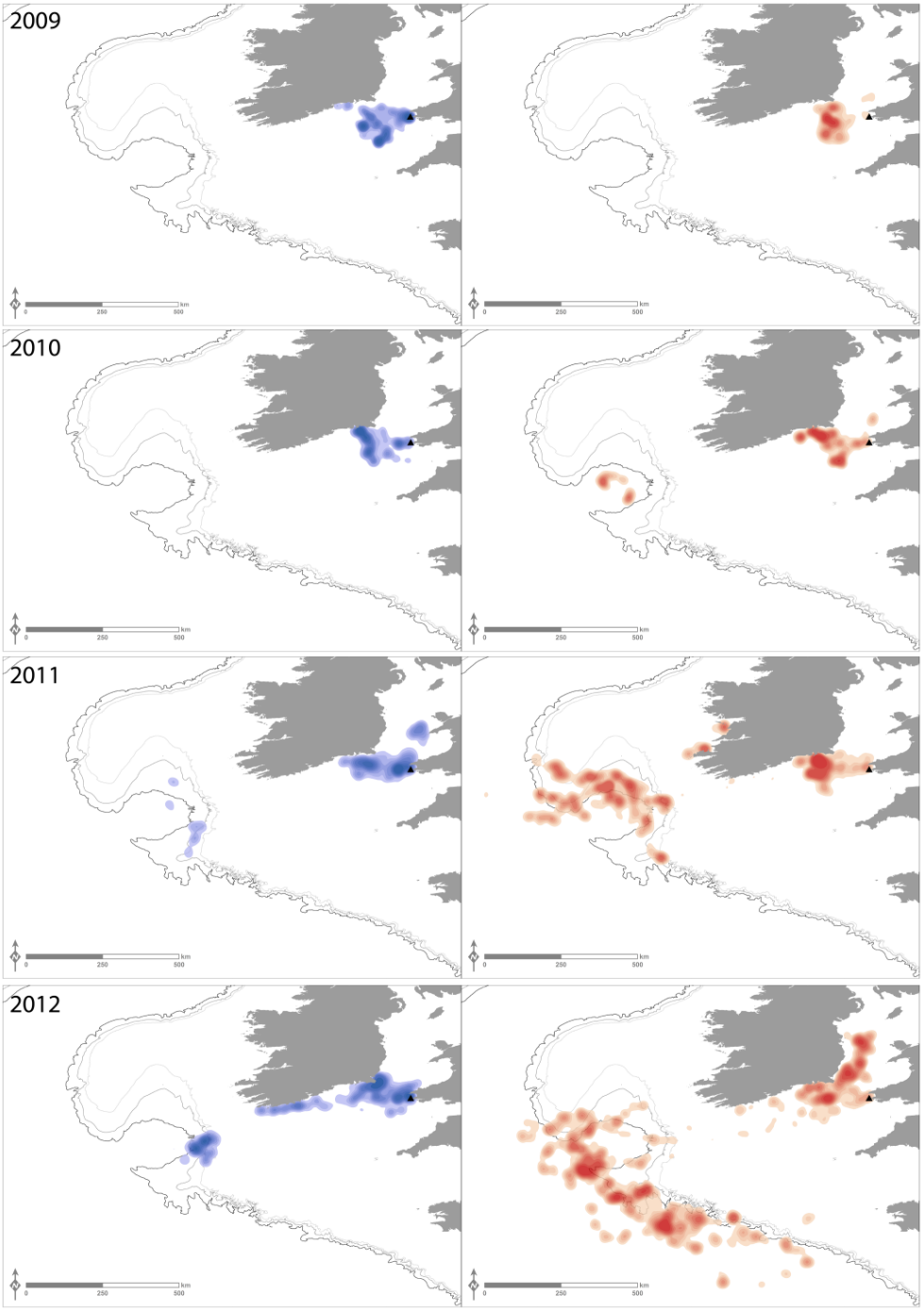

Figure 2. Kernel density contours calculated using all male (blue) and female (red) GPS locations, recorded during the pre-laying exodus period (approximately 25 April – 15 May) in 2009, 2010, 2011, and 2012. Data for birds of unknown sex are omitted. Density percentiles are indicated by colour density (95% lightest – 10% darkest). The location of the colony on Skomer Island is indicated by a black triangle. The position of the steep continental shelf slope is indicated by the 500, 1000 and 2000 m depth contours (light-dark grey lines).

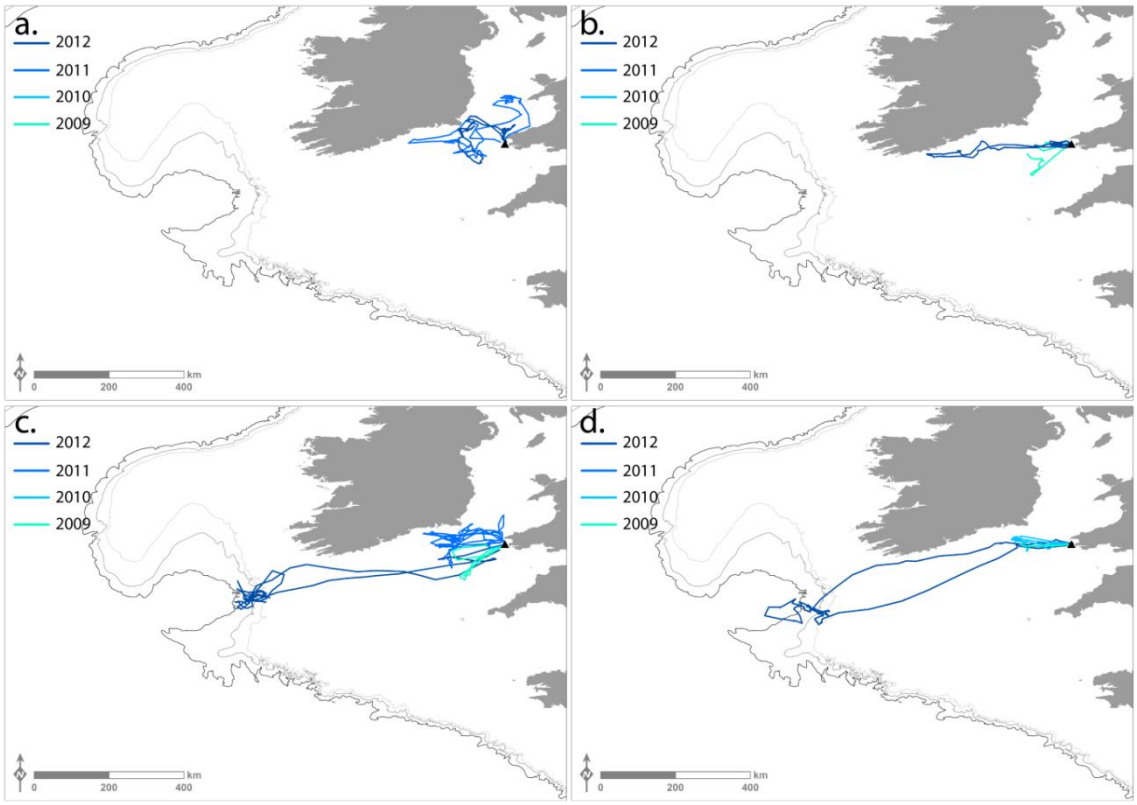

Figure 3. The GPS tracks of foraging trips made by four males that were tracked during more than one year. For each individual, tracks are coloured by year.

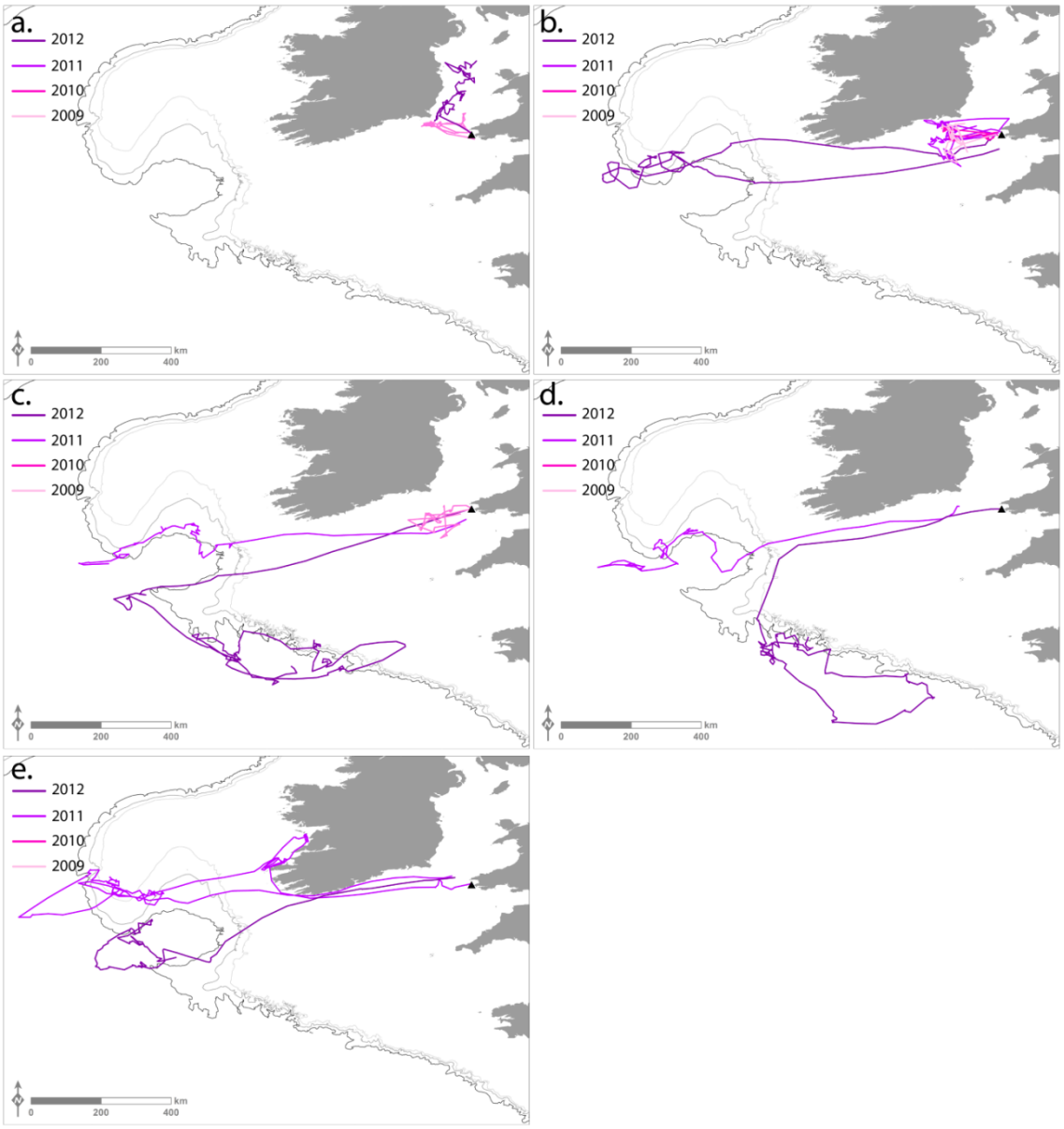

Figure 4. The GPS tracks of foraging trips made by five females that were tracked during more than one year. For each individual, tracks are coloured by year.

Trip range, duration and laying success

In 2009, the maximum recorded range of trips by males and females was similar (table 1) p = 0.18, but the duration of trips made by females was significantly longer (table 1) p = 0.02 (figure 5). In 2010, males and females made trips of similar range and duration (table 1) p = 0.904 and 0.73 respectively. Since none of the females laid following the tracking period it seems likely that none undertook their pre-laying exodus during the tracking period (figure 5). In 2011 females undertook significantly longer duration trips (table 1) p = 0.004, of greater range than males (table 1) p = 0.003 (figure 5). The same pattern was evident in 2012 (table 1) p = 0.003 and p = 0.021 (figure 5). The duration of trips (excluding 2010) was not different between years for either sex: Kruskal-Wallis (males) χ^2 (2,22) = 1.63, p=0.44, (females) χ^2 (2,20) = 0.012, p=0.99. The range of trips (excluding 2010) was different between years, increasing each year for both sexes: Kruskal-Wallis (males) χ^2 (2,22) = 5.82, p=0.054, (females) χ^2 (2,20) = 11.77, p=0.003.

In 2009 five of six successfully tracked females laid an egg following the tracking period. In 2010 none of five laid following the tracking period. In 2011 six of nine laid and in 2012 five of eight laid after the tracking period. Some individual females made both short duration, short-range trips and trips of longer duration and range – typically one or two short trips followed by one long trip. Others embarked on a single long trip immediately after logger deployment. The majority (15/16) of eggs were laid following a trip of at least 12 days. In 2009 all exodus trips by females that were followed by laying were short-range trips in the Celtic Sea. In 2011 and 2012 the majority (10/11) were to the area of the continental shelf slope and the Porcupine Bight. The tracks of all females coloured by laying success (and males coloured by their partners laying success) are shown in figure 6.

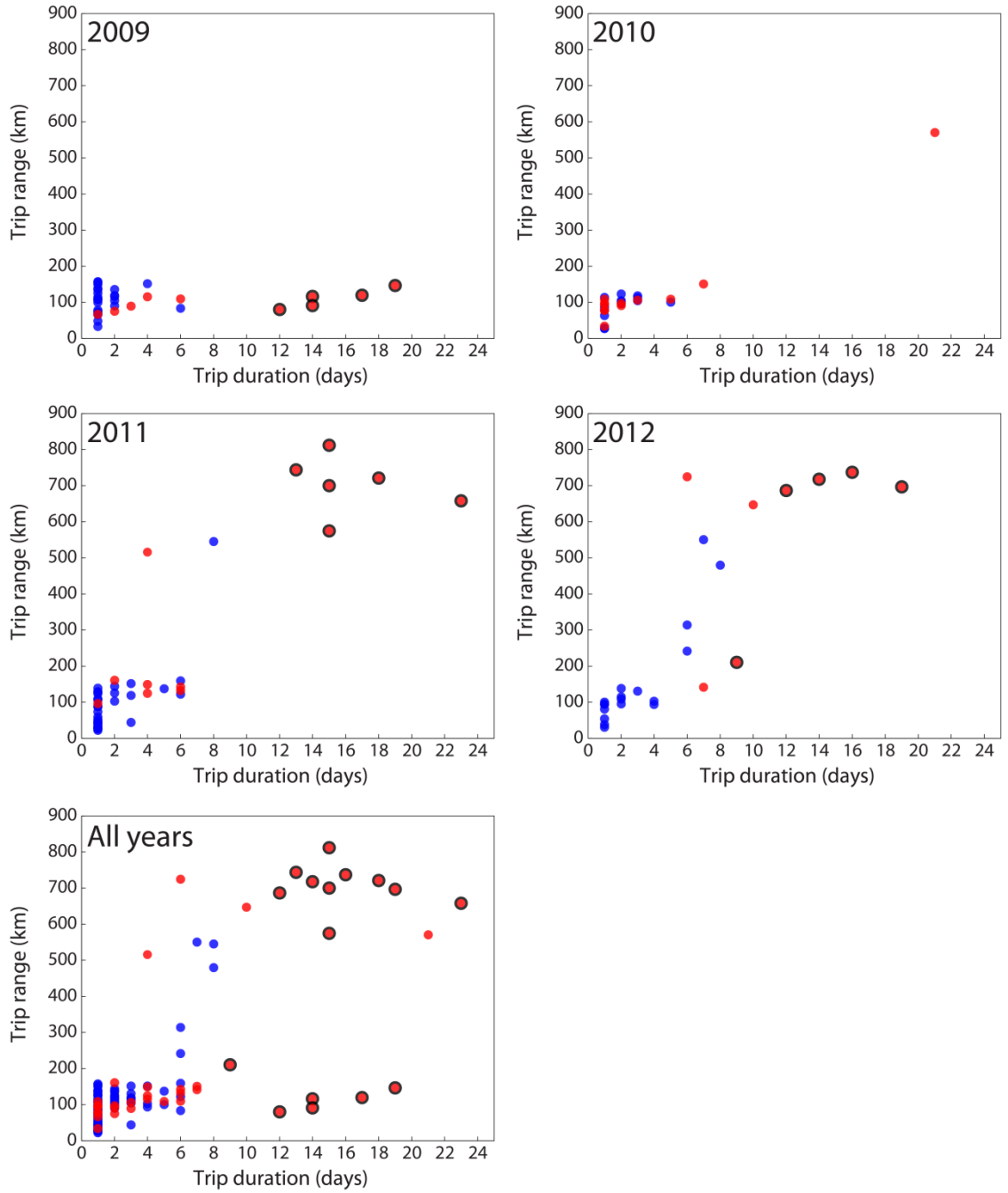

Figure 5. The relationship between trip duration (days) and trip range (maximum recorded distance from colony km) for males (blue) and females (red) in each year and all years combined (multiple trips for some birds in each year). Female trips after which eggs were laid are circled in black. Duration is known from nest monitoring, but the maximum recorded range may be shorter than actual range due to failure of half the tags prior to the birds' return.

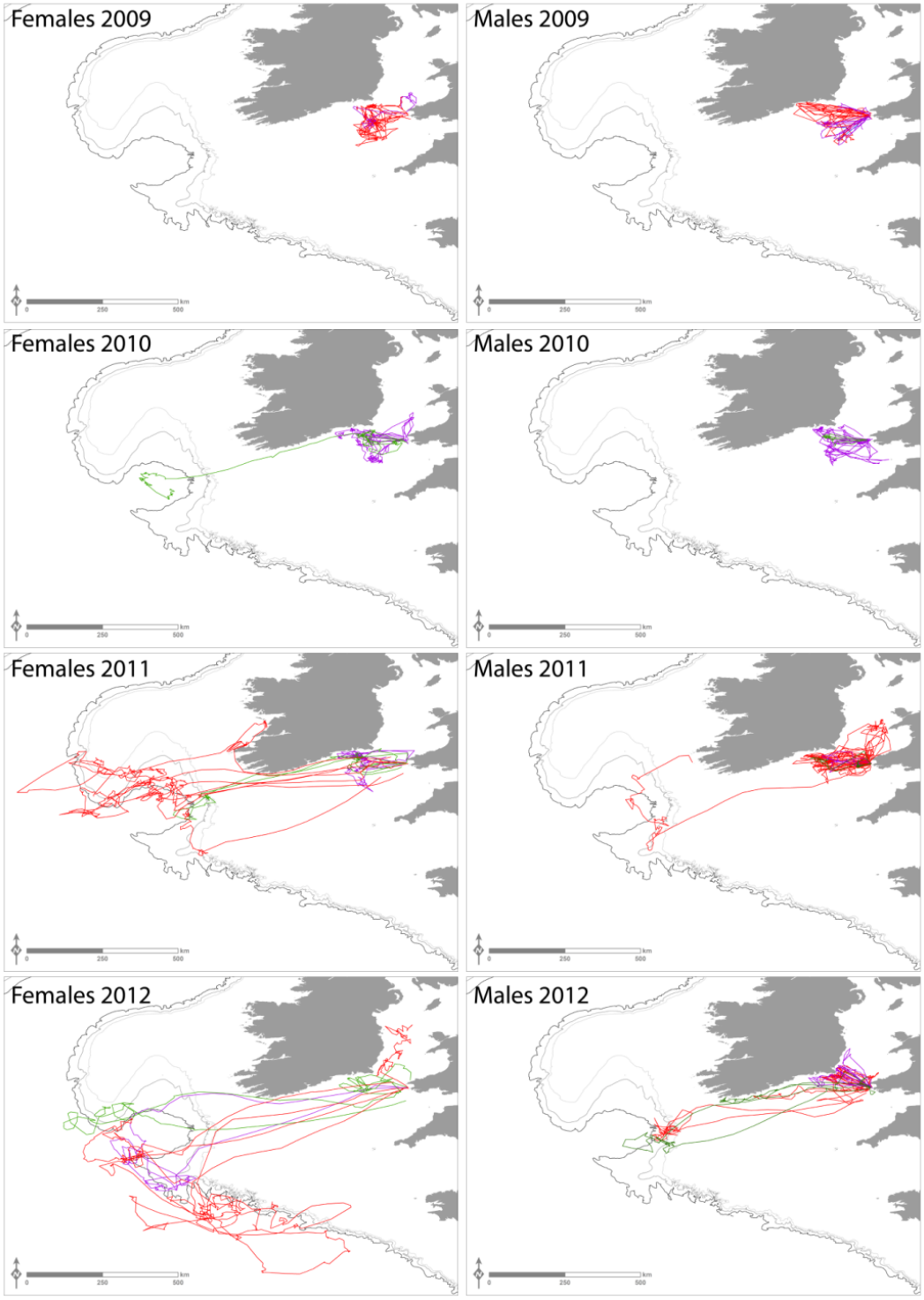

Figure 6. Pre-laying foraging trips and subsequent laying success. The tracks of females who laid at the end of the deployment are shown in red, females who laid later in the season are shown in green, and females who did not lay (or were not recorded laying) are shown in purple. Male tracks are similarly coloured according to whether their partner laid.

Activity at sea during the pre-laying period

The distance travelled per day (excluding 2010 when we were probably too early to record exodus) was not different between years for males: Kruskal-Wallis χ^2 (2,22) = 2.45, p = 0.29, but increased each year for females χ^2 (2,20) = 12.77, p = 0.002 (Table 2). The median proportion of daylight hours spent on or in the water was not significantly different for males (0.56 IQR 0.46-0.64) and females (0.54 IQR 0.42-0.65) over all years (excluding 2010, when no activity loggers were deployed): Wilcoxon rank-sum *z* (32) = 0.33, p = 0.74. However, the timing of activity was different between the sexes and between birds foraging in different locations (figure 7). Females spent most of the night on the water (particularly in 2011 and 2012), commencing airborne activity an hour or two prior to sunrise and ceasing activity around sunset (Figure 7). Females remaining close to the colony in 2009 and 2011 spent less time on the water during the night, which may indicate that although we did not detect them at the burrow, they did in fact visit the colony on a few nights. In 2012, females travelling to the continental shelf edge and beyond spent more of the daylight hours airborne than those remaining close to the colony. Males spent less time than females on the water during the night since most made frequent nocturnal visits to the colony. There was a consistent peak in time spent on the water just prior to sunrise followed by a peak in time spent airborne. There was also an evening peak in time spent airborne, followed by a peak in time spent on the water at sunset probably indicating roosting on the sea surface prior to and following visiting the colony. Two males that made trips to the continental shelf slope in 2012 remained on the water for most of the night (figure 7) and showed a peak of immersion around midday.

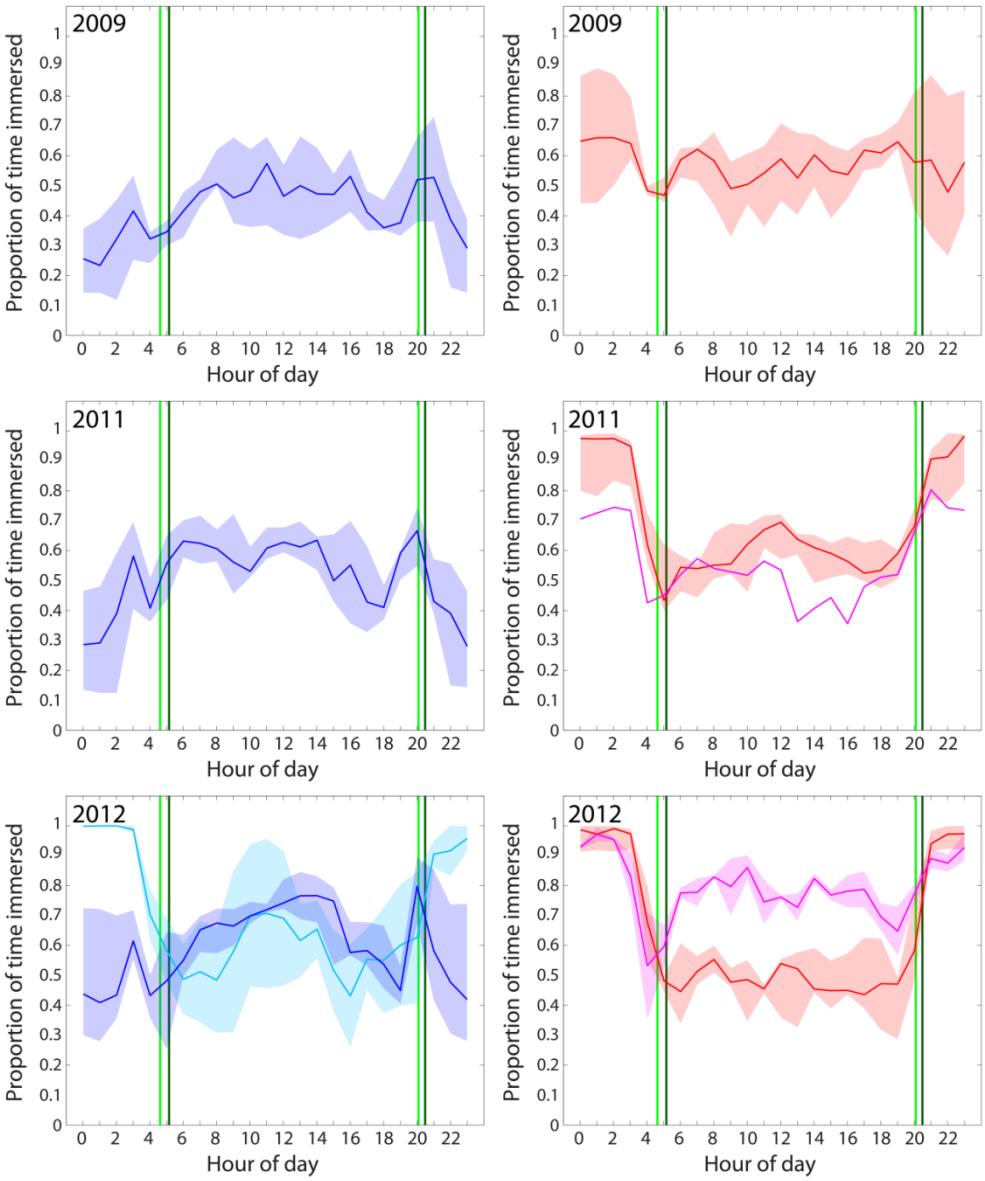

Figure 7. The proportion of time on the water through the day for males (blue/cyan) and females (red/magenta) during the exodus period. Lines indicate the median proportion of each hour spent on (or under) water, as opposed to in-flight or on the colony. Shaded areas represent the inter-quartile range. For males, dark blue indicates birds that remained close to the colony; cyan indicates males that visited the continental shelf area. For females, red indicates birds that visited the continental shelf area during their exodus; magenta indicates females that remained close to the colony. Green vertical lines indicate the timing of sunrise and sunset in (light green) the Celtic Sea, just west of Skomer (approx. 51.7˚N, 6.2˚W) and (dark green) in the centre of the Porcupine Bight (approx. 50.6˚N, 12.5˚W). Sample sizes are: 2009 males = 4, females = 6; 2011 males =4, females = 6; 2012 males = 6, females = 8.

Mass changes over the pre-laying period

In calculating mass changes during exodus we have excluded data from 2010 because our tracking did not appear to record exodus behaviour. Because we cannot be certain of their status during the tracking period, we also have excluded females that did not lay at the end of tracking, but did subsequently lay after further trips to sea. During the period of our GPS deployments, males gained mass at a mean rate of 1.95 ± 4.0 g day^{-1}, while those females that did not subsequently lay an egg gained mass at a mean rate of 5.21 ± 5.4 g day^{-1}, not significantly different to males: Wilcoxon rank-sum z (23) = 1.05, p = 0.30. Those females that did subsequently lay an egg lost mass (mass of the egg subtracted) at a rate of -1.45 ± 1.3 g day^{-1}, significantly different to males (Wilcoxon rank-sum z (36) = 3.62, $p < 0.001$) and females that did not lay (rank-sum(17) = 54, p = 0.002). This pattern was fairly consistent between years (figure 8): males gained mass at a similar rate in all three years: Kruskal Wallis χ^2 (2,19) = 1.72, p = 0.42; but laying females lost slightly more mass during 2012, although the difference was not significant: Kruskal Wallis χ^2 (2,13) = 5.4, p = 0.067. The mean mass of eggs laid by tracked females was 57.13 ± 2.82 g compared to 57.69 ± 4.47 g for all other study nests two-sample t-test t (218) = 0.51, p = 0.61. We calculated the rate of egg growth for those females that we could be certain left the colony and did not visit again until they returned to lay (n=14), assuming that egg development commenced following copulation the night they left. The mean rate of egg growth was 3.47 ± 0.56 g day^{-1}. This estimated growth rate was highly consistent between years: 2009, 3.24 ± 0.24 g day^{-1}; 2011, 3.68 ± 0.71 g day^{-1}; and 2012, 3.47 ± 0.56 g day^{-1}: Kruskal Wallis χ^2 (2,11) = 2.01, p = 0.35 (figure 8).

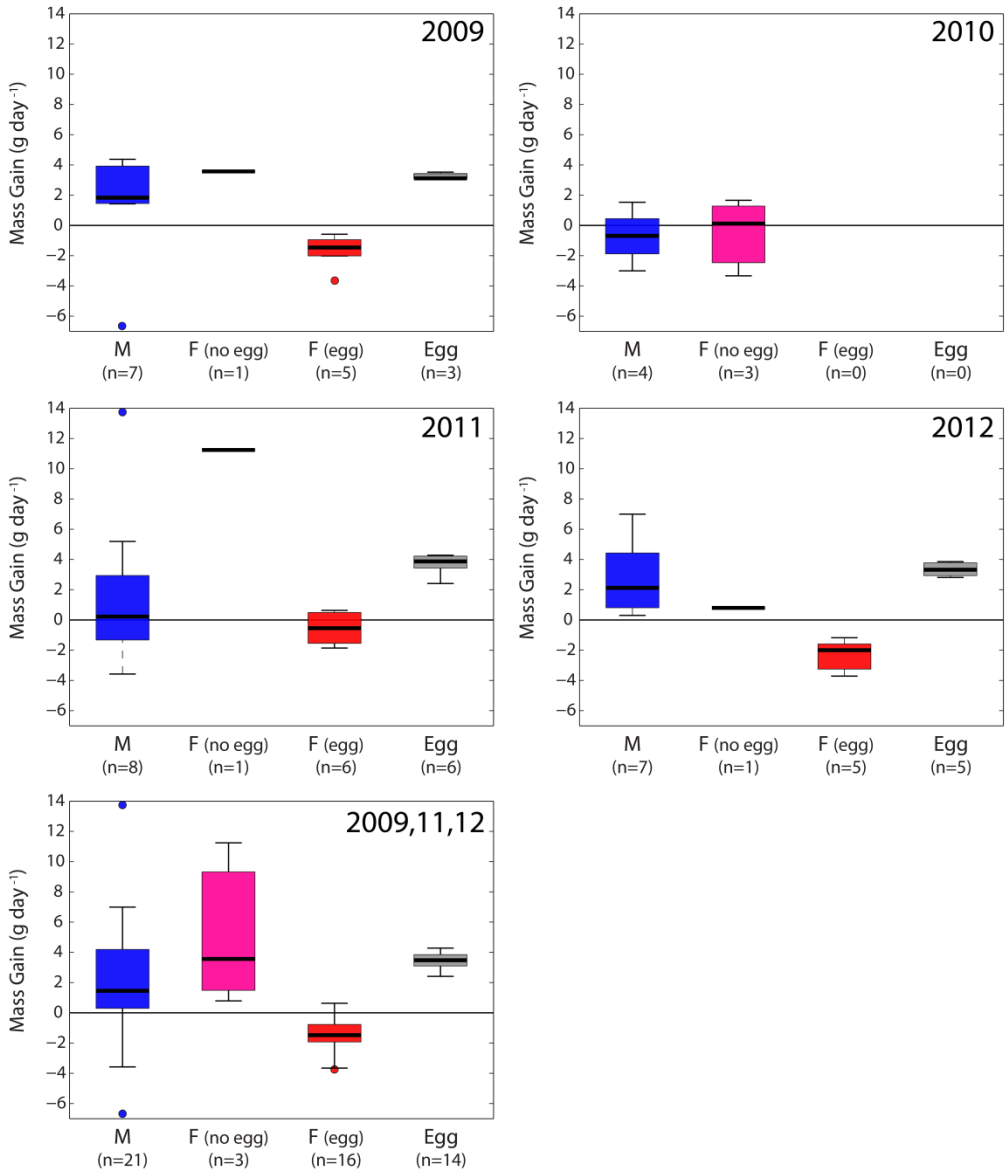

Figure 8. Changes in mass during each tracking period and for 2009, 2011 and 2012 combined. Males (blue) and females that did not subsequently lay an egg (pink) tended to gain mass, while females that did subsequently lay an egg tended to lose mass (once the mass of the egg was subtracted). The exception was 2010, where we probably tracked too early to record exodus. The rate that egg mass accrued was fairly consistent between years. Females that laid an egg after further (untracked) trips to sea are excluded, due to the uncertainty surrounding their status during the tracking period. Boxes show median and interquartile range, bars show range excluding outliers (indicated by points).

Oceanographic conditions during the pre-laying period

The water depth of the areas exploited by Manx shearwaters during the pre-laying exodus varied widely. The continental shelf ranges from zero to approximately 200 m deep at the shelf-break, while at the steep shelf slope, water depth increases rapidly from around 200 m to below 3,000 m. Approximately 100 km south-west of Ireland there is a large bight in the continental shelf (the Porcupine Bight) where the shelf slope is less steep (figure 9). Sea surface temperature (SST) and chlorophyll concentration varied spatially in each year and between years. Chlorophyll concentrations were typically higher in inshore waters (and along parts of the shelf-break), decreasing further offshore. SSTs in the Irish and Celtic Sea were typically <11˚C, increasing offshore to >12 - 13˚C beyond the continental shelf (figure 9 a-d). Distinct patches of higher chlorophyll concentration were apparent in the cool waters (<11˚C) approximately 50-75 km west of Skomer in 2009 and 2010 (figure 9 a-b), possibly indicating well established tidal mixing fronts. These patches appear to correspond temporally and spatially to the activity of birds in these two years (figures 10 and 11). In 2011 there was a less distinct patch of higher chlorophyll concentration to the west of Skomer. In 2012 the Irish and Celtic Seas were cooler than in previous years and no distinct patches of high chlorophyll concentration were apparent within the Irish and Celtic Seas (figure 9 c-d). Chlorophyll and SST values for the randomly selected null locations varied significantly between years: Kruskal Wallis χ^2 (3,56) = 47.94, $p < 0.001$ (chlorophyll) and χ^2 (3,56) = 51.58, $p < 0.001$ (SST).

Comparison of the oceanographic parameters associated with recorded bird locations and those for the sets of randomly selected null locations shows that birds were recorded in areas that differed in respect of chlorophyll, SST and water depth to that expected by chance (figure 12 and Supplementary Material table 1). The areas in which males were recorded differed in respect of chlorophyll and SST between years: Kruskal Wallis χ^2 (3,22) = 14.11, $p = 0.0028$ (chlorophyll) and χ^2 (3,22) = 11.66, $p = 0.009$ (SST). As most males remained on the continental shelf in the Celtic

Sea, the depth of water in which they were recorded did not differ between years χ^2 (3,22) = 1.27, p = 0.73. The areas in which females were recorded differed more strongly in respect of chlorophyll and SST between years: Kruskal Wallis χ^2 (3,24) = 18.16, p < 0.001 (chlorophyll) and χ^2 (3,24) = 12.56, p = 0.006 (SST). The depth of water in which females were recorded differed between years, but because some females always remained in shallower shelf waters, the difference was not significant χ^2 (3,24) = 6.69, p = 0.082. The association of shearwater activity (50% occupancy kernels) with patches of elevated primary productivity in each year are shown for males (figure 10) and females (figure 11) in each year of tracking.

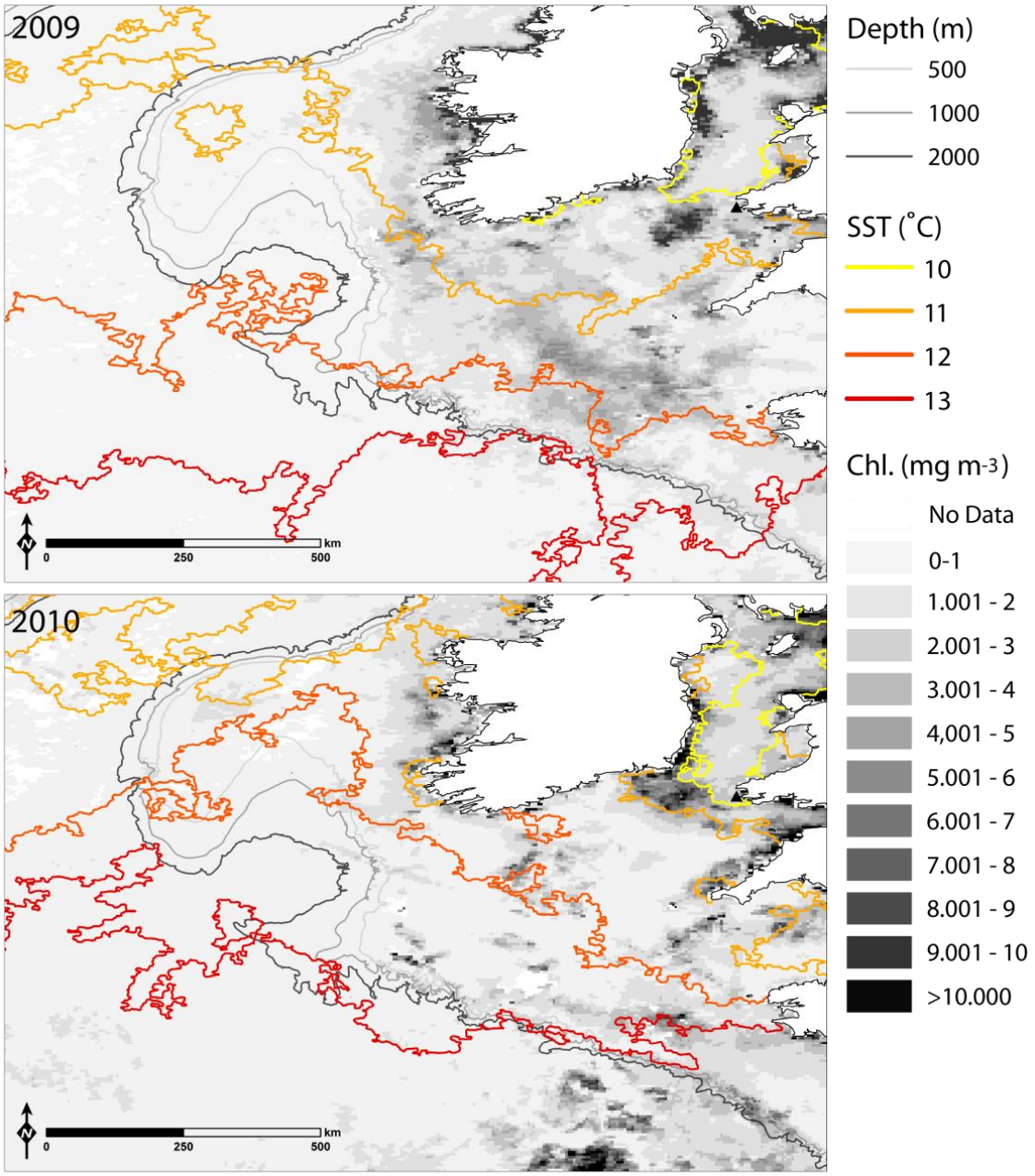

Figure 9 a & b. Oceanographic conditions in the area of sea exploited by Manx shearwaters during the pre-laying exodus in 2009 and 2010. The position of the continental shelf-break and slope is indicated by the 500, 1000 and 2000 m depth contours. Sea surface temperature is shown as a series of isotherms (10-13˚C). Chlorophyll concentration (mg m^{-3}) is shown as a greyscale grid with lighter colours indicating low concentrations and darker colours indicating higher concentrations.

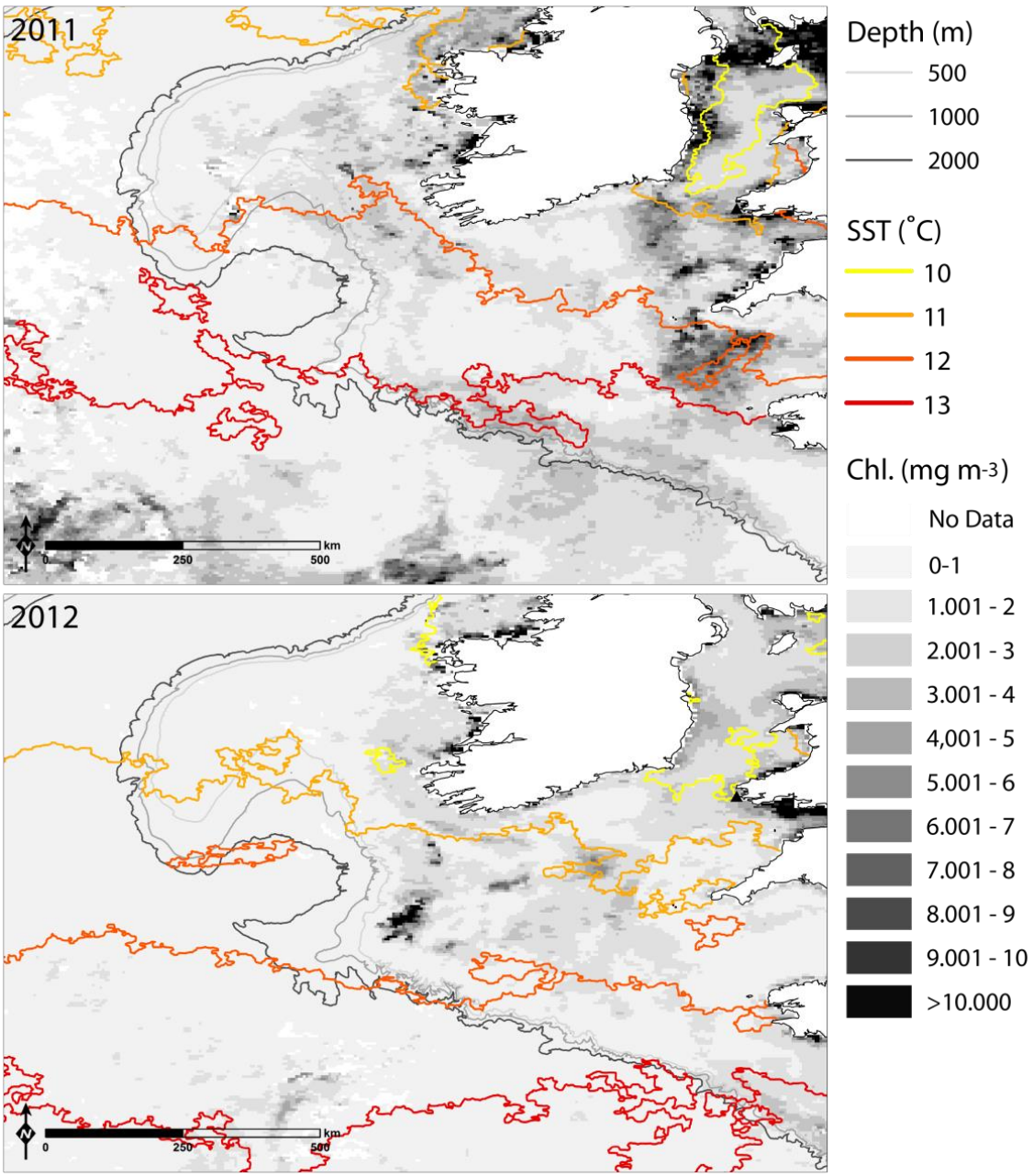

Figure 9 c & d. Oceanographic conditions in the area of sea exploited by Manx shearwaters during the pre-laying exodus in 2011 and 2012. The position of the continental shelf-break and slope is indicated by the 500, 1000 and 2000 m depth contours. Sea surface temperature is shown as a series of isotherms (10-13˚C). Chlorophyll concentration (mg m^{-3}) is shown as a greyscale grid with lighter colours indicating low concentrations and darker colours indicating higher concentrations.

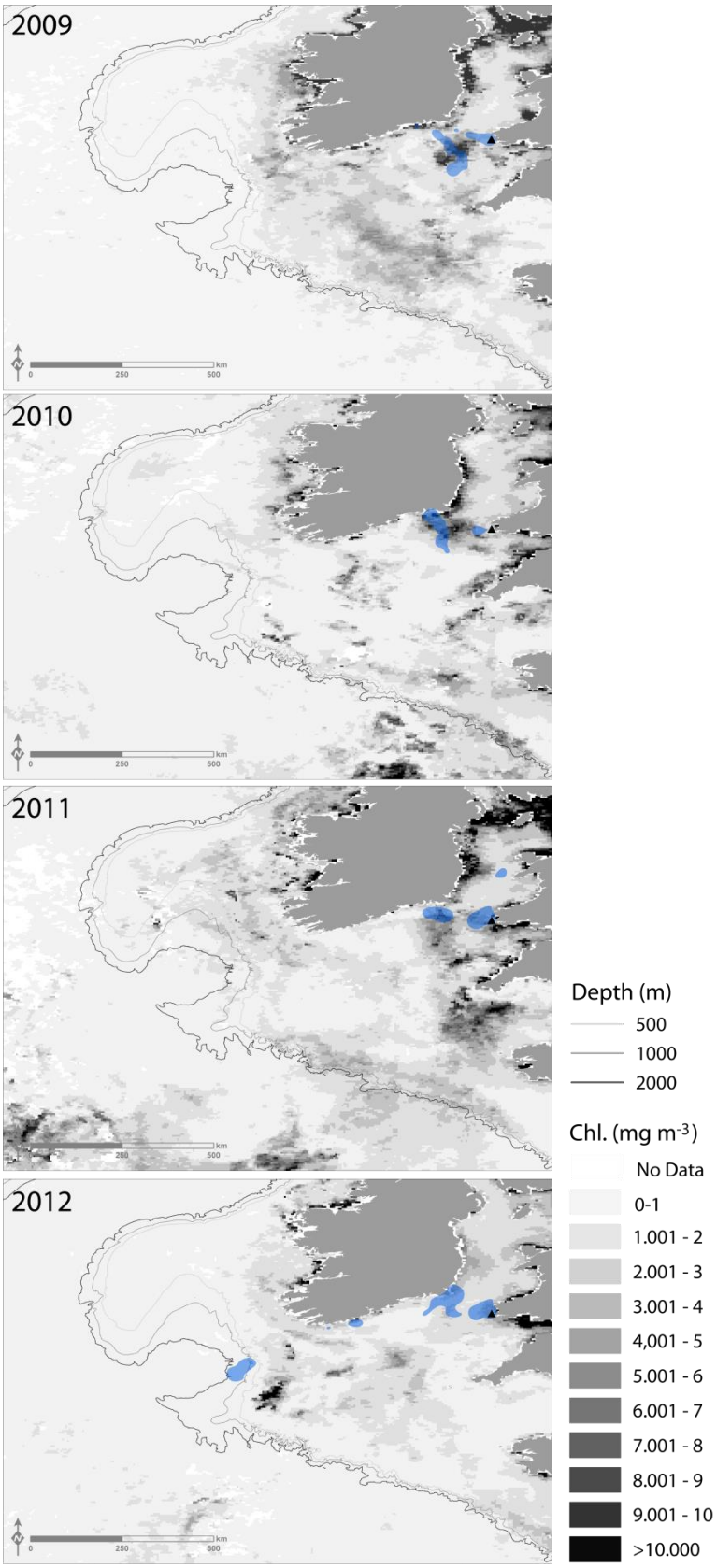

Figure 10. Chlorophyll concentration data overlaid with 50% occupancy contours for males tracked during the pre-laying exodus of each year.

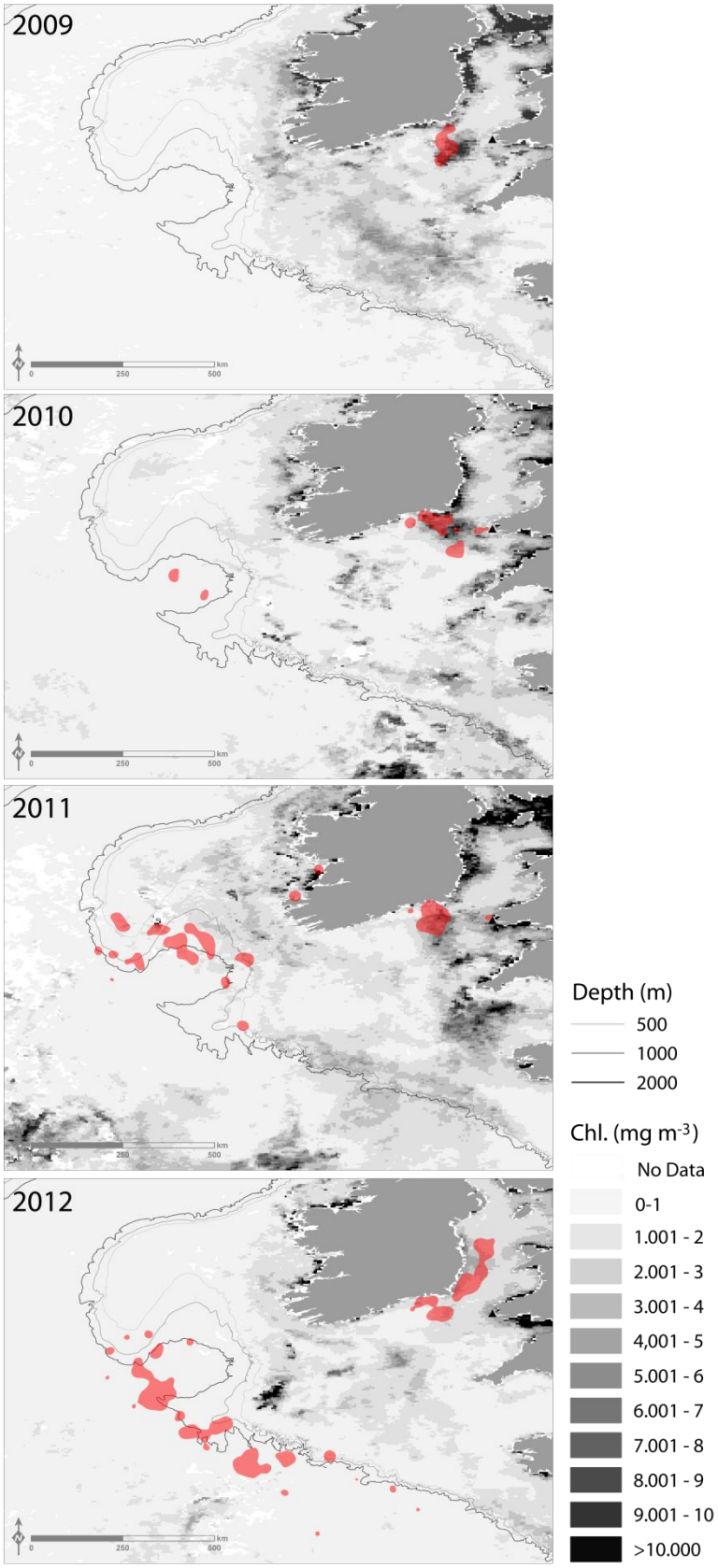

Figure 11. Chlorophyll concentration data overlaid with 50% occupancy contours for females tracked during the pre-laying exodus of each year.

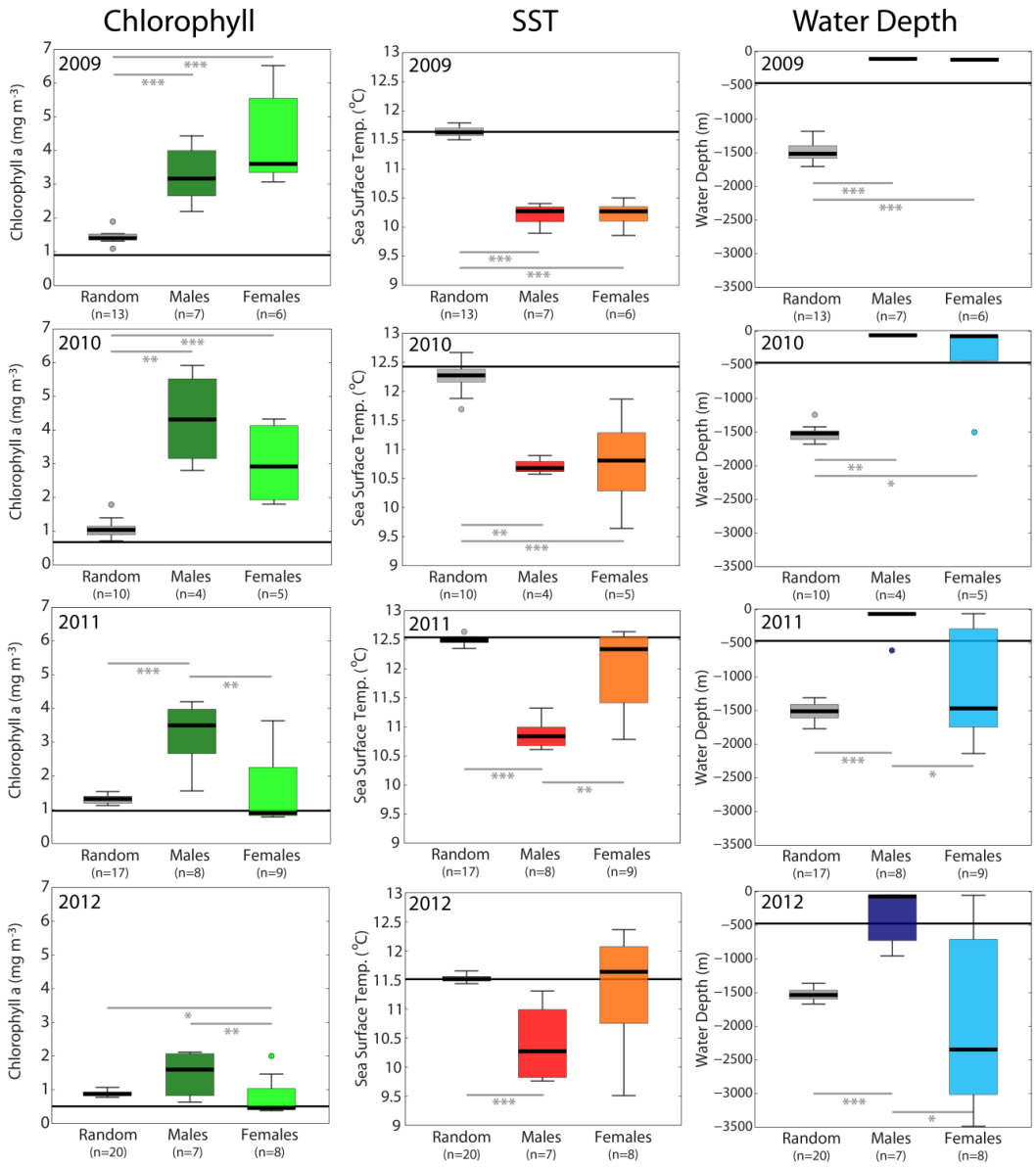

Figure 12. Comparison of oceanographic parameters associated with recorded GPS locations for male (dark colours) and female (light colours) birds, and for sets of random locations (grey). Comparisons are shown for chlorophyll concentration (left hand column in green), SST (centre column in red/orange) and water depth (right hand column in blue) in each year of tracking. A line is drawn through the overall median value within the entire area used by birds (Supplementary Material figure S1). Significant differences between groups (Wilcoxon rank-sum tests) are indicated by grey lines: $p<0.05$ *, $p<0.01$ **, $p<0.001$ *** (test statistics are given in Supplementary Material table S1). Boxes show median and interquartile range, bars show range excluding outliers (indicated by points).

Discussion

Impacts and success of tracking

This study provides the first high spatial precision data on the movements and at sea activity of the Manx shearwater (and perhaps any procellariiform) during the prey-laying exodus. This allowed us to build a detailed picture of the birds' behaviour during this important stage of the breeding season. Device loads comprised approximately 4.2-4.9% of male body mass and 3.5-4.1% of female body mass. Previous studies of procellariiforms carrying loads comprising 0.6–6.0% of body weight later in the breeding season (Sæther *et al*. 1993; Phillips *et al*. 2003) have demonstrated negative impacts including nest desertion, increased trip duration and reduced meal sizes. In addition, it is likely that tagged birds experience increased diving and flight costs and stress (Burger & Scaffer 2008). In this study, males visited the colony frequently: their trip durations (median = 2.25 overall) were consistent with the visit frequencies (at least every third night) recorded by Brooke (1990). They also gained mass at a mean rate of 1.95 ± 4.0 g day^{-1}. Because we were sensitive to the potential for device loads to impact on the ability of females to form and carry an egg, they were fitted with smaller devices. The median duration of trips to sea by females was 11 days overall, or 15 days for those birds that subsequently laid. This is consistent with the absence of around 15 days suggested by Brooke (1990). Our mean duration for laying females was 17 days, which is consistent with the mean of 20 days reported by Guilford *et al*. (2009). The mean mass of eggs laid by tracked females was identical to those laid in all other study nests. Those females that did not subsequently lay an egg gained mass at a mean rate of 5.21 ± 5.4 g day^{-1}. The median lay dates for tracked birds were 2-9 days later than the median lay dates for all other study burrows. However, this is unlikely to indicate a significant impact of the tracking, since our recorded exodus durations were consistent with previous estimates (Brooke 1990: Guilford *et al*. 2009). It is more likely that we biased the timing of breeding in our sample because we selected pairs who looked likely to embark on exodus between 25 April and 10 May. In addition, the pattern of movements seen in 2011 and 2012

were highly similar to those indicated by previous tracking using 2.5 g geolocator loggers (Guilford *et al*. 2009). However, the data on the at-sea behaviour of Manx shearwaters presented here must be interpreted with the caveat that these birds are carrying devices that may have affected their behaviour.

Overall 47% of tracked females laid eggs either just after the tracking period, or within the following month after further foraging trips (table 1). This compared to 55.5% laying in all other burrows we monitored throughout the four breeding seasons. In 2010 only two out of seven tracked pairs laid (2 – 4 weeks later). This was a late season with low breeding success among our study burrows and we probably started tracking too early to record the exodus. Excluding 2010, 74% of the tracked pairs laid eggs, compared to 56.1% in all other burrows. These estimates may underestimate the laying success in other burrows, since we cannot be certain breeding pairs ever 'intended' to breed in these, but the same also may be true of the tracked burrows. In addition, some of the pairs we tracked may not have been breeding pairs and may never have been expected to lay. The presence of two birds together in a burrow during the pre-breeding season does not guarantee this. For example, one pair tracked in 2009 was evicted during the exodus period and may never have been a breeding pair. Without definitive information on the history and breeding status of all the birds we tracked, we necessarily had to make educated guesses. Given this limitation, our attempt to capture exodus excursions was successful in 3 out of 4 years.

Egg formation

Procellariiforms typically lay a single, large, energy rich egg (Warham 1983). Egg formation therefore is a demanding process in terms of energy and nutrient requirements, requiring rapid transfer of lipid, protein and other nutrients to the developing egg from dietary sources or body tissues (Astheimer & Grau 1989; Nager 2006). After returning to the colony from their wintering areas, breeding Manx shearwaters engage in energetically expensive pre-breeding activities. The

mass of females declines steadily during this period (Fitzherbert 1985; Brooke 1990; Mallory *et al.* 2008) such that post-copulation, females are likely to lack the nutrients necessary for egg formation. The main functional interpretation of the pre-laying exodus is therefore that it enables the female to gather those nutrients, from distant, spatially unpredictable resources if necessary, without the energetic demands of visiting the colony.

The egg is comprised of three primary components: yolk, albumen and shell, each of which develops separately. The yolk is the main source of energy and nutrients available to the growing embryo and as such represents the greatest caloric investment by the female (Astheimer & Grau 1989; Nager 2006). The main components of the albumen are water and the protein albumin, which provides protein reserves for the developing embryo. The availability of albumin may directly affect hatchling size (Saino *et al*. 2010). The shell protects the embryo and is the main source of calcium during its development (Nager 2006). Based on the calculations in Warham (1983), a 57.13 g shearwater egg should comprise approximately: 20 g yolk; 33 g albumen; 4.5 g shell. In Procellariiforms, follicles in the ovary slowly increase in size prior to breeding. When breeding starts, a single follicle begins to grow quickly as yolk is deposited; a process known as rapid yolk deposition (RYD) (Astheimer & Grau 1989). Once RYD is complete, the ovum is released from the ovary into the oviduct and if sperm are present, the ovum may be fertilized (Bakst *et al*. 1998). Dye-feeding experiments on pre-laying females indicated that in four procellariiform species (Buller's shearwater *Pufinus bulleri*, Northern fulmar *Fulmarus glacialis*, and Fairy prion *Pachyptila turtur*) initiation of RYD does not begin until after females depart for their pre-laying exodus and that egg formation takes place wholly at sea (Fry *et al*. 1986; Astheimer & Grau 1989). In other species (Common diving petrel *Pelecanoides urinatrix*, Black-browed albatross *Diomedea melanophris*, and Grey-headed Albatross *D. chrysostoma*) RYD already may be as much as one third complete when females depart for their pre-laying exodus (Astheimer *et al*. 1985; Astheimer & Grau 1989). In both scenarios, fertilization of the ovum must occur at sea, requiring females to use sperm stored from copulations on the colony

prior to exodus for later use once RYD is completed at sea (Marshall & Serventy 1956; Hatch 1983; Fitzherbert 1985; Hatch 1987; Austin & Parkin 1996; Bakst *et al*. 1998; Abbott *et al*. 2006; Holt & Lloyd 2010). The ovum then traverses the oviduct, where albumen is secreted in the magnum, the shell membrane in the isthmus, and the shell in the uterus.

Regardless of destination or range, the median duration of exodus trips after which females laid was 15 days, with the majority of trips lasting 12-17 days (figure 5). This was consistent with the interpretation of the pre-laying exodus as enabling the female to gather the nutrients required for egg formation. However, RYD has been estimated to take 18 days for two other *Puffinus* shearwaters with body and egg masses similar to the Manx shearwater: Buller's shearwater *P. bulleri* (Astheimer & Grau 1989) and the Wedge-tailed shearwater *P. pacificus* (Fry *et al*. 1986). In addition, subsequent albumen synthesis appears to extend for a further two days, while deposition of the shell membranes and shell may take most of the final 24 hours prior to oviposition (Astheimer & Grau 1989). This suggests that Manx shearwaters breeding on Skomer Island may initiate RYD a few days prior to departing on exodus. In most procellariiforms RYD initially proceeds at a slow rate for the first 1-5 days, accelerating almost exponentially towards completion (Astheimer & Grau 1989). Female Manx shearwaters therefore may be capable of supplying the slow initial rate of RYD at the colony by mobilising endogenous nutrient reserves, stored perhaps during foraging stopovers on the pre-breeding migration (Guilford *et al*. 2009), or exogenous resources gathered on short trips during the pre-breeding period. But they must quickly depart on exodus in order to locate suitable prey resources to sustain the later rapid development. The minimum duration of exodus was about 12 days in this study, with most eggs being laid the following day, which suggests that females may be capable of sustaining no more than around five days of RYD before departing. Dye-feeding studies (e.g. Fry *et al*. 1986; Astheimer & Grau 1989) would be needed to clarify the timing of egg development in Manx shearwaters.

Even during exodus, females may rely both on endogenous and exogenous nutrient resources. For example, significant reductions in muscle mass during egg formation, caused by protein loss (Jones 1991) transferred to the egg (Houston *et al*. 1995a), have been recorded in many species (Kendal *et al*. 1973; Houston *et al*. 1995b). However, the daily investment of protein in laying gulls and terns may represent 232% of the daily requirement of a non-laying female (Robbins 1981) and cannot be met by endogenous reserves alone: most species must continue to forage to meet the total energy and protein requirements (Meijer & Drent 1999). Similarly, females have a high demand for calcium, primarily for the formation of the eggshell (Reynolds & Perrins 2010). Mobilisation of skeletal calcium may sometimes occur, but calcium is not stored to any great extent by birds during the pre-laying period (Pahl *et al*. 1997) so an adequate supply of dietary calcium is fundamental to successful egg formation. The use of some endogenous resources by female Manx shearwaters, regardless of foraging conditions, is suggested by the fairly consistent daily rate of mass loss by laying females (-1.45 ± 1.3 g day^{-1} figure 8) (although some of this may be a direct result of carrying a GPS). Post-laying, females subsequently require a second extended period at sea to recover sufficient condition for incubation duties (Brooke 1990). Those females that embarked on exodus, but did not subsequently lay, gained approximately 5.21 g day^{-1}, suggesting a similar potential intake of exogenous resources for laying females. Based on the 14 females that we could be certain left the colony on exodus and did not visit again until they returned to lay, we estimated that they formed an egg (all components) at a rate of approximately 3.5 g day^{-1} (figure 8). This estimate was highly consistent between years, but is likely to be slightly high if RYD had already progressed to some extent prior to departure. As there is little variability in the time required for individuals of a given species to form a yolk (Astheimer & Grau 1989), the variation in exodus trip duration for Manx shearwaters is likely to represent either individual variation in locating suitable resources at sea, or the extent to which individuals initiate RYD prior to departure on exodus.

Patterns of distribution and activity

It is likely that we started tracking too early in 2010 and did not record the exodus period of most birds. For this reason we exclude 2010 and focus on 2009, 2011 and 2012 in discussing the movements of birds during exodus. We were unable to sex six individuals and we exclude their movements because we cannot relate these to expected gender specific behaviour. The distribution of Manx shearwaters during exodus as recorded by GPS differed between years (figures 1 and 2). The most striking feature was that in 2009, males and females both remained close to the colony during the exodus. This differed to at least one previous year (2007 in Guilford *et al*. 2009) and the two following years in which we definitely recorded exodus (2011 and 2012). The difference could have resulted from incomplete recording of exodus movements using GPS. However, this is unlikely since the pattern was supported by a supplemental analysis of the corresponding geolocator location data: male and female distributions were similar in 2009, with no obvious westward movements to the continental shelf slope (Supplementary Material figure S2).

We investigated how the distribution of birds in each year was related to prevailing oceanographic conditions (bathymetry, chlorophyll concentration and SST). Chlorophyll concentration was included as a potential indicator of productive areas that might in turn indicate an abundance of prey. This interpretation rests on the assumption that (remotely sensed) patches of high productivity (in surface waters) were associated with aggregations of suitable and accessible prey. Several studies indicate that many species of seabirds do exploit areas of high primary productivity, signalled by elevated chlorophyll concentrations (e.g. Ainley *et al*. 2005; Gremillet *et al*. 2008). However, spatial and temporal mismatches may occur across the intervening trophic levels (zooplankton and fish), such that there often may be large temporal or spatial mismatches between areas of high primary productivity, areas of high prey density, and areas of high seabird foraging density (Gremillet *et al*. 2008). In addition, the

strength of associations between seabirds and indicators of productivity or prey may depend strongly on the temporal and spatial scales of the investigation (Fauchald *et al*. 2011). The use of data on the distribution and abundance of resources at higher trophic levels, such as copepods (Votier *et al* 2010; Fauchald *et al*. 2011; Fort *et al*. 2012), or prey-fish themselves (Karpouzi *et al*. 2007; Fauchald *et al*. 2011), should reduce the effects of such mismatches, providing a more direct link to the foraging distributions of seabirds. However, such data currently do not exist at the large spatio-temporal extents and high resolutions (temporal and spatial) of remotely sensed chlorophyll data. Where data are available, associations between seabirds and prey-fish still may be weak due variable detection and accessibility of prey patches (Fauchald *et al*. 2011).

To create a null model of oceanic conditions within the areas available to Manx shearwaters during exodus we sampled conditions at randomly selected locations within a polygon describing the full extent of recorded exodus trips (Supplementary Material figure S1). This approach has two major shortcomings. First, because of the birds' association with the colony and the energetic costs of movement, not all regions within this area were equally available to foraging shearwaters. Accessibility (and hence availability) is likely to vary inversely with distance from the colony (Orians & Pearson 1979; Wakefield *et al*. 2009). Second, random movement within an area is not a realistic representation of animal movement. The foraging movements of shearwaters must originate from, and terminate at, the colony. Between these points, movement typically comprises a series of small movements within restricted areas, separated by larger movements between areas of interest. A more biologically realistic null model of habitat availability then, would have been one in which the probability of selecting a null location decreased with distance from the colony (e.g. Wakefield *et al.* 2011), or one based on a model (e.g. random walks [Codling *et al*. 2008], correlated random walks [Byers 2001; Codling *et al*. 2008], or Lévy walks [Shlesinger & Klafter 1986]) that attempted to replicate realistic animal paths based on the distributions of movement distances and directions recorded by GPS. During the pre-laying exodus, the use of a null model in which habitat availability /

accessibility varies inversely with distance from the colony is likely to be more critical for males (which retain a strong attraction to the colony) than for females (which do not). A similar problem exists for the use of complex movement models, since different models of movement would be appropriate for males (which tend to return frequently) and females (which tend to range far and return infrequently). In addition the choice of an appropriate movement model is complex (Plank & Coding 2009; Reynolds 2012). To allow comparison of both males and females with the same null model, we used a basic random selection of locations within the maximum recorded foraging range, despite the above shortcomings of this method.

In 2009, males and females visited the same area, approximately 150 km west of the colony, concentrated in the north east Celtic Sea (figures 1 and 2). Comparison of bird locations with randomly generated locations suggest that in 2009 males and females were recorded in areas that were shallower, cooler and with higher chlorophyll concentrations than would be expected by chance (figure 12). Males and females spent similar proportions of daylight hours on the water or in flight, travelling similar distances per day during foraging, although males spent less time on the water at night and travelled slightly further per day, probably reflecting their frequent nocturnal visits to the colony (figure 7, table 2). Manx shearwaters forage primarily (perhaps exclusively) during daylight hours (Chapter 4) and nights away from the colony are predominantly spent roosting on the surface (Dean *et al*. 2012). The relatively low levels of nocturnal immersion seen for females in 2009 indicate that some spent significant periods of the night off the water. Although we did not detect them in their burrows some may have visited the colony at large.

During 2011, all but one male remained within approximately 150 km of the colony, concentrated either in the north east Celtic Sea or the southern half of the Irish Sea. One male left the colony for eight days and travelled 550 km west to the region of the continental shelf slope known as the Porcupine Bight. Two females remained in the same area of the north east

Celtic Sea as the majority of males, but the majority of females travelled at least 600 km west to forage along the continental shelf slope, especially within the Porcupine Bight. As in 2009, males were recorded in areas that were shallower, cooler and with higher chlorophyll concentrations than expected by chance. Females foraging at the shelf slope were recorded in areas that were similar in depth, SST and chlorophyll concentration to that expected by chance. Females were recorded in warmer, deeper waters, with lower chlorophyll concentrations than males. Both sexes spent similar proportions of daylight hours on the water or in flight, travelling similar distances per day, although females travelled slightly further per day probably reflecting the additional commuting to and from the shelf-break.

Again, in 2012, males typically remained within approximately 150 km of the colony, concentrated in the north east Celtic Sea, although two also made six-day trips along the south Irish coast. Two males left the colony for seven and eight days, travelling west to the Porcupine Bight. Two females remained close to the colony, one staying in the north east Celtic Sea, the other remaining in the Irish Sea. The majority of females travelled at least 600 km west to the continental shelf slope. Unlike 2011, few remained in the Porcupine Bight area, most explored the shelf slope to the south and deeper waters further offshore. Males were recorded in waters that were shallower and cooler than expected by chance, but with chlorophyll concentrations similar to that expected by chance; probably because there were no dense concentrations of chlorophyll close to the colony. Females foraging at the shelf slope were recorded in waters that were similar in depth and SST similar to that expected by chance, but with significantly lower chlorophyll concentrations. Females were recorded in warmer, deeper waters, with lower chlorophyll concentrations than males. Females travelling to shelf slope spent more time in flight and travelled greater distances per day than birds (males and females) that stayed near the colony. Some of that increased flight time is likely to be due to commuting, but it may also reflect females foraging in very different conditions: in 2012, foraging along the slope and in the deeper waters beyond appears to have been highly mobile and dispersive.

Overall chlorophyll concentrations varied between years and perhaps more importantly, the distribution of patches of high concentration varied spatially between years. It seems that when local productivity was high and (perhaps more importantly) aggregated in cool, shallow inshore waters, birds of both sexes were able to meet their differing nutritional demands without travelling large distances and males are able to visit the colony frequently. During the chick-rearing period Manx shearwaters from Skomer typically forage in the Irish and Celtic Seas (Chapter 3, Dean *et al*. 2012), diving to capture prey (Chapter 4), primarily catch small (ca. 15 cm) Clupeid fish and some squid (Brooke 1990). We don't know what birds were foraging on during exodus, although it seems likely that Clupeid fish attracted to zooplankton in areas of elevated primary productivity (coastal and tidal mixing fronts), would have dominated the diet of those birds foraging in the Irish and Celtic Seas during the pre-laying and exodus periods (Whitehead 1986). But when local productivity was diminished and/or less aggregated, most females foraged instead in the warmer, deeper and less productive waters along the shelf slope. Under increasingly poor conditions, males also may have been required to forage further afield to meet their nutritional demands. This pattern raises the question of why birds would travel 550 km or more to forage along the continental shelf slope and beyond, in areas that, based on remotely sensed chlorophyll maps suggest relatively low productivity. Shelf-breaks are often associated with strong vertical mixing of the water column (upwellings), creating areas of high productivity and bringing prey closer to the surface (Sharples *et al*. 2009) where they may be exploited by surface feeders and shallow diving seabirds. Prey may also become aggregated within cyclonic eddies generated over shelf-break canyons (Allen *et al*. 2001). Consequently, many studies have found shelf-breaks to be important for foraging procellariiforms (Catard *et al*. 2000; Ainley *et al*. 2005; Hyrenbach *et al*. 2006; Phillips *et al*. 2006; Piatt *et al*. 2006; Freeman *et al*. 2010), which may be capable of detecting such opportunities over large distances using olfaction (Nevitt 2000; Nevitt & Bonadonna 2005). The areas in which most females foraged in 2011 were typically beyond the shelf break and may have been associated with upwelling

activity within the Porcupine Bight, but spatially mismatched through interaction between the intervening trophic levels (Gremillet *et al*. 2008). However, the areas in which most females foraged in 2012 appear to have been deeper waters with very low productivity and no obvious upwellings. A few possibilities may account for this larger mismatch. First, satellite-based sensors only assess chlorophyll concentrations within the top few metres of the water column and deeper undetected chlorophyll maxima may have been present (Barlow *et al*. 2002), perhaps with associated aggregations of prey. Second the use of a 32-day composite of chlorophyll data may have hidden ephemeral but highly productive upwellings. Third, birds may have been foraging on prey that were not strongly associated with areas of high productivity, relying perhaps on ephemeral aggregations of prey formed by the foraging activities of other pelagic predators (Evans 1982; Pierotti 1988). Indeed, the highly dispersed distribution of females in 2012 and the large daily travel distances suggest that birds were foraging on sparsely distributed, ephemeral resources that were difficult to locate. This may have resulted in slightly greater mass losses for laying females in 2012, either through greater energetic demands of foraging, or through greater dependence on endogenous reserves for egg formation.

The routes and durations of trips were consistent with the interpretation of the pre-laying exodus as enabling the female to gather the nutrients required for egg formation from distant, spatially unpredictable resources. Similarly, the distributions and trip durations of males were consistent with the need to maintain or increase body condition by foraging under a continued strong association with the colony. Whether this behaviour functions to enable the defence and retention of the nest, to provide the opportunity for EPCs, or both, when local productivity is poor males must balance the benefits of remaining at the colony against the costs of foraging under suboptimal local conditions. Plotting the movements of individual males and females tracked in multiple years indicates that the exodus behaviour of individuals was flexible, with birds of both sexes selecting different strategies in different years (figures 3 and 4). Although in each year there was a clear majority decision. Taken together, these data suggest individual

decisions based on an interpretation of body condition and prevailing foraging conditions in each year. Males and females may both be capable of comparing current local conditions with a memory of conditions at the shelf slope, possibly obtained on return from their migration between 10 (most females) and 20 (most males) days earlier (Guilford *et al*. 2009).

The routes of birds travelling to and from the continental shelf were remarkably consistent and direct, with most birds heading directly towards the Porcupine Bight area, and then exploring the continental shelf edge. The direct nature and consistency of these routes suggest that they were informed by previous experience (previous exodus excursions, or return routes from migration) and imply an important role for learning and the building of a large-scale memorised map of foraging areas. The nature of the cues, or representations involved in navigation and map learning have yet to be investigated.

Conclusions

Female Manx shearwaters probably initiated RYD several days prior to departing the colony, possibly mobilising endogenous nutrient reserves to do so. As in other species (e.g. Hobson 2006), studies of stable isotopes, would be effective in determining the relative contribution of endogenous and exogenous nutrient sources to egg formation. Following copulation at the colony, females then embarked on a pre-laying exodus lasting around 12-18 days, during which they completed the formation of their egg. While these long duration trips potentially allow females to range far from the colony, foraging destinations appeared to be flexible between years and within individuals. Although remotely sensed chlorophyll data provide only a (sometimes mismatched) proxy for prey distributions, the location in which females foraged appeared to be related to primary productivity close to the colony, in particular, the presence of dense patches of high productivity within the Celtic and Irish Seas. In years when local conditions are good, females may remain close to the colony, while in years with poorer conditions they range further, exploring the continental shelf slope. Even in years where females

appeared to work harder, foraging over larger areas, they were capable of forming an egg during trips of similar duration. This suggests that endogenous reserves occasionally may act to buffer egg formation at a cost to the female's body condition. However, in a long-lived species like the Manx shearwater, females would not be expected to severely compromise their own condition to produce an egg. Primary productivity close to the colony also appeared to influence the behaviour of males during the females' period of absence. In years when dense, patches of high productivity were present close to the colony, males were able to forage locally, increasing body condition whilst maintaining their presence at the colony. But in years with poorer conditions they foraged further afield, reducing their presence at the colony and potentially risking losing their burrow to other breeding pairs. This study provides the first high spatial precision data on the movements and at sea behaviour of the Manx shearwater (and perhaps any procellariiform) during the pre-laying exodus. Clearly, these data are of high value in conservation planning. Not only is the pre-laying period a critical stage of the breeding season, but also the distribution of birds – particularly pre-laying females – can be very different from that recorded during any other stage of the breeding season (Guilford *et al*. 2008; Dean *et al*. 2012; Chapter 3). The patterns described here are based only on three years of successful tracking of exodus behaviour: several more years of tracking in varying conditions would be desirable to confirm these. In addition, the patterns seen here may be strongly related to the location of Skomer Island in relation to the oceanographic features described. Further tracking of pre-laying movements from colonies across the species breeding range would likely yield further fascinating insights into this behaviour.

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Supplementary Material

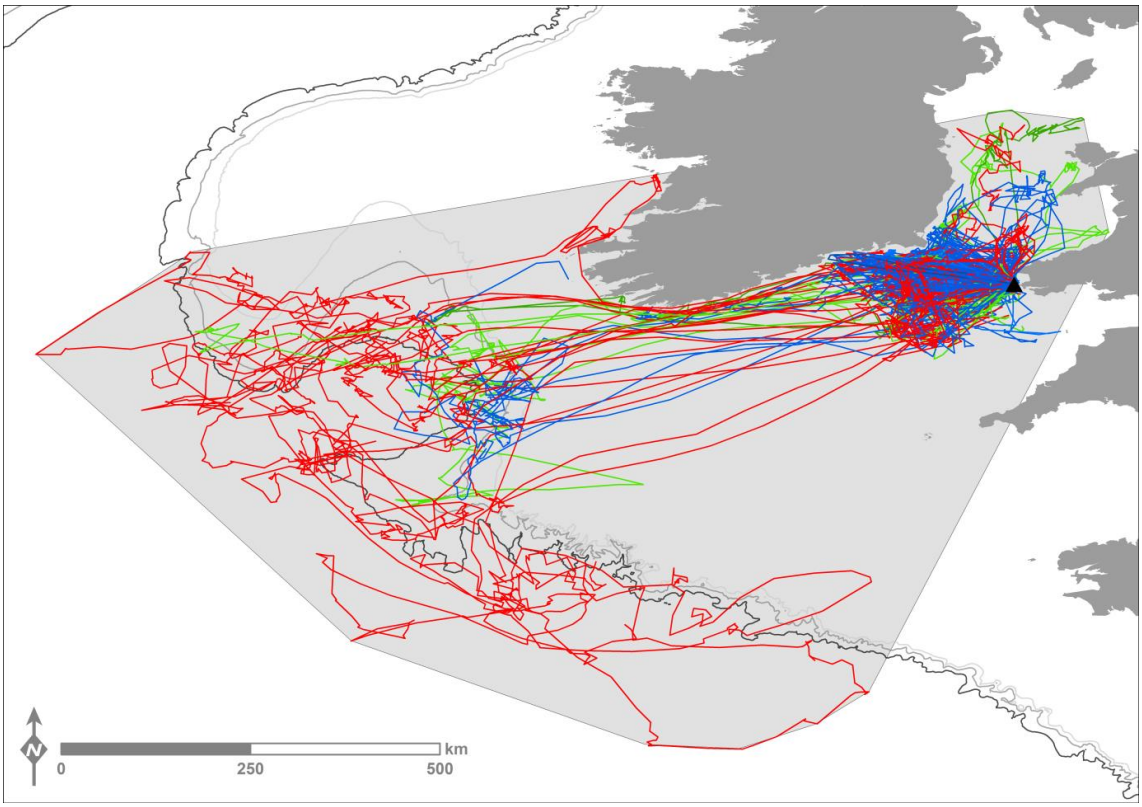

Figure S1. Extent of the 1 km grid of points from which null locations were randomly selected. All recorded tracks overlaid (males in blue, females in red, unsexed birds in green).

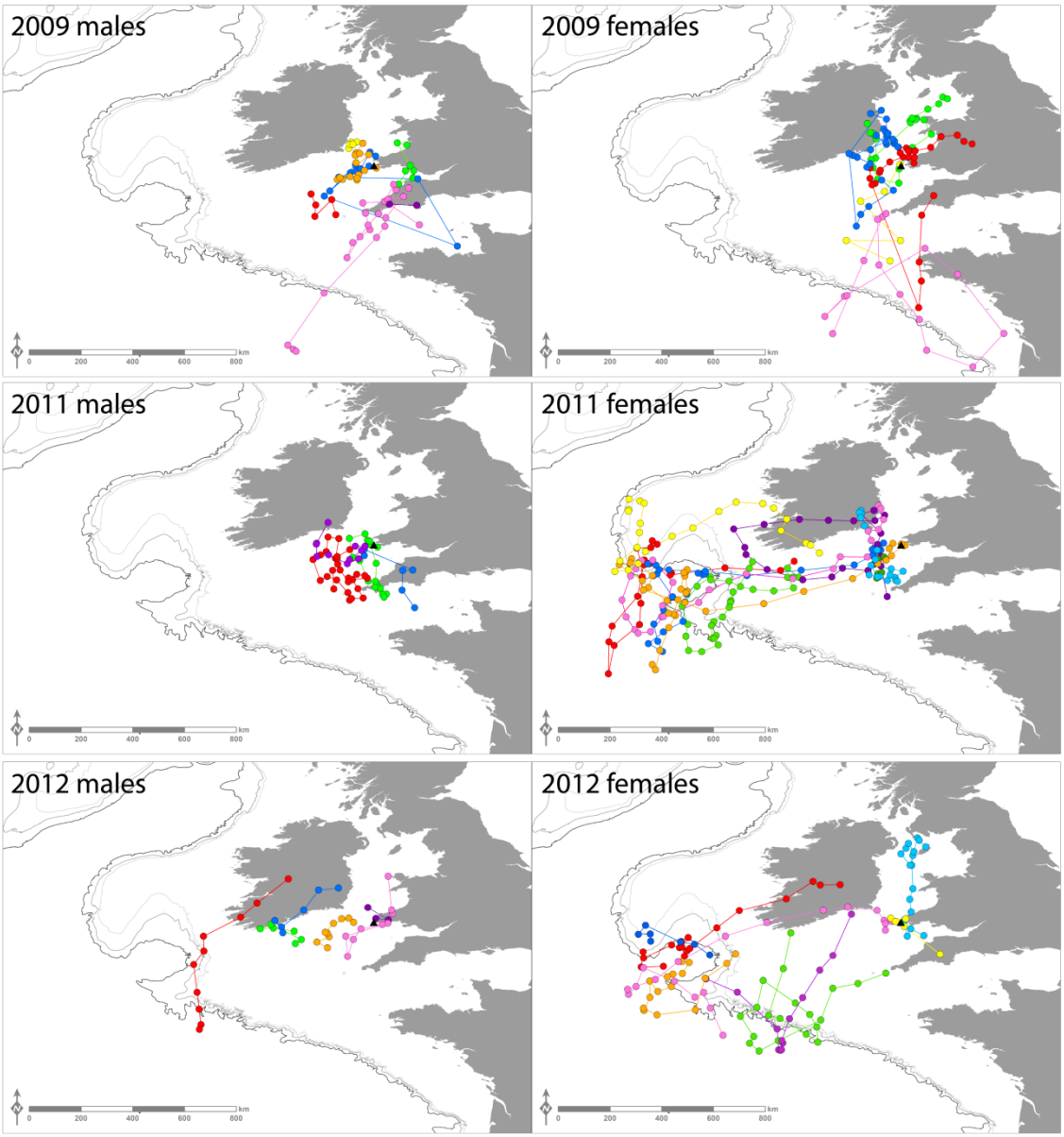

Figure S2. GLS location estimates (averaged over 3 days) from the geolocator-immersion loggers co-deployed in 2009, 2011 and 2012. These support the general patterns of distribution recorded by the GPS. Westward excursions, particularly by females, to the Porcupine Bight and continental shelf break were seen in 2011 and 2012, but not in 2009. GLS loggers lasted for the entire duration of deployments, although some daily locations were missing due to noisy light/dark transitions. GLS location estimates are much less precise than GPS: previous validation tests conducted on black-browed albatrosses *Thalassarche melanophrys* (Phillips *et al*. 2004) suggest a mean location error of 186 km. Some of the GLS locations for 2009 appear to show excursions south (male pink track, female pink, red and yellow track). However, the corresponding GPS locations indicate these birds were actually within the Celtic/Irish Sea during this time. Some locations were therefore up to 600 km out on the latitudinal axis, which appears

to have been far less accurate than the longitudinal accuracy. Light-level data were analysed in BasTrak software to provide approximate positions twice daily throughout the period (excluding days where noisy light/dark transitions prevented confident identification of the sunrise/sunset). Light/dark transitions were estimated using a standard light threshold of 10, linear interpolation, and filtering of apparent light or dark intervals <4 hours. Locations were calculated using a sun elevation angle of -3.5 which overall, gave the best correspondence between time-matched GLS and GPS locations (although see mismatches for some birds/loggers).

Table S1. Test statistics (Wilcoxon rank-sum) for environmental parameters for recorded bird locations and random null locations in figure 12. Table continued overleaf.

	Chlorophyll	**SST**	**Water Depth**
2009	Chl.: Random vs Males z(18) = 3.57, p < 0.001***	SST: Random vs Males z(18) = 3.57, p < 0.001***	Depth: Random vs Males z(18) = 3.57, p < 0.001***
	Chl.: Random vs Females rs(17) = 99, p < 0.001***	SST: Random vs Females rs(17) = 21, p < 0.001***	Depth: Random vs Females rs(17) = 99, p < 0.001***
	Chl.: Males vs Females rs(11) = 49, p = 0.366^{ns}	SST: Males vs Females rs(11) = 43, p = 0.945 ^{ns}	Depth: Males vs Females rs(11) = 35, p = 0.366 ^{ns}
2010	Chl.: Random vs Males rs(12) = 50, p = 0.002**	SST: Random vs Males rs(12) = 10, p = 0.002**	Depth: Random vs Males rs(12) = 50, p = 0.002**
	Chl.: Random vs Females rs(13) = 65, p < 0.001***	SST: Random vs Females rs(13) = 15, p < 0.001***	Depth: Random vs Females rs(13) = 59, p = 0.0193*
	Chl.: Males vs Females rs(7) = 25, p = 0.288^{ns}	SST: Males vs Females rs(7) = 19, p = 0.905^{ns}	Depth: Males vs Females rs(7) = 24, p = 0.413^{ns}
2011	Chl.: Random vs Males z(23) = 3.76, p < 0.001***	SST: Random vs Males z(23) = 3.9322, p < 0.001***	Depth: Random vs Males z(23) = 3.9322, p < 0.001***
	Chl.: Random vs Females z(24) = 0.43, p = 0.666^{ns}	SST: Random vs Males z(24) = -1.4013, p = 0.161^{ns}	Depth: Random vs Females z(24) = 0.3234, p = 0.746^{ns}
	Chl.: Males vs Females rs(15) = 100, p = 0.0055**	SST: Males vs Females rs(15) = 41, p = 0.0016**	Depth: Males vs Females rs(15) = 93, p = 0.0464*
2012	Chl.: Random vs Males z(25) = 1.6322, p = 0.102^{ns}	SST: Random vs Males z(25) = 3.8453, p < 0.001***	Depth: Random vs Males z(25) = 3.8453, p < 0.001***
	Chl.: Random vs Females z(26) = 2.0088, p = 0.0446*	SST: Random vs Females z(26) = 0.8900, p = 0.374^{ns}	Depth: Random vs Females z(26) = 0.9917, p = 0.321^{ns}
	Chl.: Males vs Females rs(13) = 76, p = 0.0205*	SST: Males vs Females rs(13) = 39, p = 0.0541^{ns}	Depth: Males vs Females rs(13) = 76, p = 0.0205*

Chapter 3

Simultaneous multi-colony tracking of the Manx shearwater reveals cross-colony utilization of a shared resource

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Abstract

Many studies of animal movements in the natural environment focus on relatively small datasets from a single population of animals. Here we present our analysis of a large, multi-year, multi-colony dataset simultaneously collected at four breeding colonies across the UK breeding range of the Manx shearwater. In total we recorded 529 foraging trips during 255 deployments on 169 individuals.

Analysis of the dataset indicated that the foraging areas of Manx shearwaters showed a relatively high degree of annual variation, but consistent patterns emerged. Birds from each colony consistently foraged within local waters, but birds from all four colonies also foraged within a single relatively restricted area of the Irish Sea, indicating co-foraging on a shared resource. The key area in which birds from all four colonies foraged was the vicinity of the Irish Sea Front and the stratified waters of the Western Irish Sea to the north and west. This area is likely to experience high productivity and the associated gyre currents may act as a retention mechanism for prey-fish.

During the early breeding season, this area may provide a predictable resource for off-duty incubating birds to recover body condition. During chick-rearing, longer duration trips to this area may be particularly important in regulating reproductive effort, allowing parents to recover body condition lost on shorter foraging trips close to the colony.

The frequency of recorded visits to this area declined with increasing distance of the colony, suggesting that the energetic net gain of foraging is significantly affected by the energetic costs of travelling to it. Nevertheless, this area is likely of key importance to birds breeding at colonies across the UK range.

Introduction

Seabirds are long-lived, widespread, upper-trophic marine organisms with high adult survival and slow population growth (Rickleffs 1990). As such they are vulnerable to a wide range of impacts at sea including pollution, incidental mortality in fisheries, incidental mortality and habitat loss associated with marine developments, and changes in prey resources as a result of changes in fishery management, oceanic conditions and climate change (González-Solís & Shaffer 2009). Seabirds therefore function as important indicators of ocean health (Einoder 2009; Lewison *et al*. 2012), particularly in light of global climate change (Grémillet & Boulinier 2009) and our increasing use of the seas at industrial scales (Halpern *et al*. 2008). However, a lack of detailed knowledge about at-sea movements and distributions of seabirds across species, colonies, sex, age classes and breeding status has presented a substantial challenge to seabird ecology (Lewison *et al*. 2012). The identification of important bird areas at sea, an understanding of their variability and an understanding of the environmental and ecological interactions that drive this variation are critical questions in marine conservation. Advances in miniature telemetry and data logging systems have revolutionized the remote observation of long-distance movements in seabirds and other elusive species (Burger & Shaffer 2008; Phillips *et al*. 2008; Rutz & Hays 2009; Bograd *et al*. 2010; Wilson & Vandenabeele 2012). This has enabled a vast number of tracking studies on a wide range of seabird species providing insights into many aspects of seabird behaviour and ecology (Phillips *et al*. 2008; Wilson & Vandenabeele 2012).

In particular, GPS and satellite tracking has provided a wealth of information about the foraging movements of individual birds at sea during the breeding season (e.g. Grémillet *et al*. 2004; Pinaud & Weimerskirch 2007; Weimerskirch *et al*. 2007; Guilford *et al*. 2008; Magalhães *et al*. 2008; Hamer *et al*. 2009; Pavia *et al*. 2010; Wakefield *et al*. 2011). However, there are several problems associated with the inference of colony or population level distributions from individual movement data (Holdo & Roach, 2012). Many studies necessarily follow only a small

number of individuals, either because of logistic or funding constraints, or out of a desire to minimise impacts on the population. Those individuals may be chosen for accessibility rather than representativeness. Of course the representativeness of individuals remains unknown without a comprehensive dataset for comparison, but generally the larger the sample the greater the confidence in recording a representative set of movements. Many studies follow individuals from only one, or a few, colonies that may not be representative of the range of the species. Some studies follow individuals only during one stage of the breeding season, or during only a single breeding season, yet distributions may change as a result of shifting resource distributions and oceanic features, or as a result of the different constraints of central place foraging at different stages of breeding. The extent to which snapshots of relatively small numbers of individuals are generalizable across time, colonies, or the population, is not clear.

Where birds are tracked from multiple colonies, tracking is often conducted at different sites asynchronously: either sequentially (e.g. Grémillet *et al*. 2004), or in different years (e.g. Hamer *et al*. 2001). As a result, the recorded foraging movements are likely to be sensitive to temporal variability in a range of factors, such as prey distributions (Fauchald 2009), weather (Finney *et al.* 1999; Garthe *et al*. 2009), oceanic features (Durazo *et al*. 1998; Garthe *et al*. 2009), moon phase (Riou & Hamer 2008; Yamamoto *et al*. 2008), or changing constraints of central place foraging at different stages of breeding. Potentially this may compromise comparisons of the foraging movements of birds from different colonies, particularly assessments of the extent to which birds from different colonies forage in the same areas. Yet, an understanding of the relative importance of different foraging areas to birds from different colonies is clearly crucial to assessing the conservation status of the species and of colonies, and indirectly the health of the marine resources on which they depend. Simultaneous tracking of birds from multiple colonies potentially would allow comparisons of foraging movements unaffected by temporal changes in environmental parameters that might be expected to influence those movements.

As animal tracking technologies have become increasingly inexpensive and reliable, tracking large numbers of birds simultaneously from multiple colonies has become a possibility. Here, we focus on the Manx shearwater (*Puffinus puffinus*), a small-medium (400 g) procellariiform seabird. The majority of the world population breeds in Britain and Ireland (Mitchell *et al*. 2004), predominantly in colonies at remote locations off the west coasts (figure 1). The breeding biology of the species therefore combines colonial breeding with central-place pelagic foraging involving long-distance movements over inshore waters and the open sea. Much of the breeding biology is known from studies of behaviour at colonies (e.g. Brooke 1990; Gray & Hamer 2001). In comparison, relatively little is known about the foraging movements of the species away from the colonies. Systematic ship-based surveys of seabird distributions in UK waters (Stone *et al*. 1994; Begg & Reid 1997) have provided valuable information on the distribution and abundance of foraging birds at sea, highlighting the locations of the main foraging concentrations. However, it is not possible to determine the provenance (colony of origin), or the breeding status of birds recorded in this way. More recent GPS tracking (Guilford *et al*. 2008) has provided finer-scale data on the routes and destinations of foraging trips, but only for a limited number of birds breeding on one colony. Little is known about the patterns of foraging at sea for large numbers of birds from different colonies.

The aim of this study was to assess the extent to which birds from different colonies foraged in the same locations at the same time and the consistency of those patterns across years. We used miniature GPS loggers deployed in combination with saltwater-immersion loggers to simultaneously record the foraging trips of a large number of Manx shearwaters from multiple colonies over three consecutive years. We tracked birds from two colonies (Copeland and Skomer) simultaneously during the incubation period and from up to four colonies (Rum, Copeland, Skomer and Lundy) simultaneously during the chick-rearing period. Using first-passage time analysis (Fauchald & Tveraa 2003) we identify the locations in which birds from each colony engaged in searching and foraging behaviour and validate these as a proxy for

foraging attempts (diving) using corresponding data from time-depth recorders co-deployed on a sub-sample of birds. We map the foraging distributions of birds tracked from each colony and visualise daily foraging distributions to reveal the extent of both spatial and temporal overlap in foraging activity. Additional data on chick meal sizes and adult mass changes for trips from one colony (Skomer) suggest that in the Manx shearwater, foraging trips to one region of the Irish Sea may be particularly important in regulating reproductive effort.

Materials and Methods

Data loggers

Logger deployments were made over three consecutive years on birds breeding at four separate colonies across the species' UK breeding range. During the incubation period (May-June 2009 - 2011), loggers were deployed on birds from Lighthouse Island in the Copelands group, Northern Ireland (Northern Irish Sea: 54°41'N, 5°31'W) and Skomer Island, Wales (Southern Irish Sea: 51°44'N, 5°17'W). During the chick-rearing period (July-August 2009 - 2011), loggers were deployed on birds from Copeland, Skomer and Lundy Island (Bristol Channel: 51°10'N, 4°40'W). During chick-rearing 2010 and 2011, loggers were also deployed on birds from Rum Island, Scotland (Inner Hebrides: 56°59'N, 6°17'W). As far as practicable, deployments were carried out over the same time period on different islands to allow us to examine the foraging distributions of birds from different colonies simultaneously (figure 1). However, due to the logistic constraints of the demanding tracking programme, deployments on Lundy were necessarily started 22 days earlier than the other colonies in 2010. Overall, a total of 264 deployments were made on 173 individuals (Table 1). Breeding adults were taken from their burrows by hand through a purpose-built inspection hatch, or using a purse net at the burrow entrance (Lundy only). Birds were weighed, devices deployed and birds returned to the burrow within 15 minutes. On return, birds were recaptured from the burrow, reweighed, devices removed and birds returned to the burrow within 10 minutes.

All birds were fitted with two devices: a global positioning system (GPS) logger (modified i-gotU GT-120: Mobile Action) and a British Antarctic Survey geolocator-immersion logger. GPS loggers were configured to record location once every 5 or 10 minutes. GPS were sealed in heat-shrink plastic and attached dorsally using thin strips of tesa marine cloth tape underlying a small number of contour feathers (Guilford *et al.* 2008). Geolocator-immersion loggers test for saltwater immersion every 3 seconds and record the number of samples immersed at the end of each 10-minute interval (Mk 13, 14, 15, 18L), or record each transition between the sea and air (Mk 19). Immersion loggers were attached by two lightweight cable ties to a leg ring so as to be immersed when the bird was sitting on the sea surface. Twenty five of the birds tracked from Skomer (Table 1) were additionally fitted with a CEFAS G5 time-depth recorder (TDR). TDRs were configured to record pressure every 1 second and were attached to the central four tail feathers using thin strips of tesa tape (similar to Wilson *et al.* 2009). GPS weighed 10.2 - 15g (depending on battery size, which was reduced for birds carrying TDRs). Geolocator-immersion loggers weighed 1.4g - 2.5g and TDRs 2.7g. The total mass of devices in each deployment was 18-19.5g. On return, parents were allowed to feed the chick before being recaptured from the burrow, reweighed, and devices inspected. If the devices had been deployed less than a week and were still well attached the bird was released, otherwise the devices were removed. Capture and deployment took <15 minutes, removal <10 minutes. The effects of tracking were tested on birds tracked from Skomer in 2009 and 2011 by comparison of hatching success, chick-growth and fledging success with a set of control nests where no tracking was carried out.

Monitoring mass changes

On Skomer, during the chick-rearing periods of 2010 and 2011, at each tracking nest, we carefully monitored the changes in mass of the chick and visiting adults throughout each night of deployment. This was done with the aim of calculating the change in adult mass and the amount of food delivered to the chick after each of the tracked foraging trips. Chicks were weighed at

the beginning of each night and the following day. During the night, small bamboo sticks were placed at the entrance of each burrow, which would be knocked down whenever an adult entered or left the nest. Regular inspection (every 20 minutes) allowed us to detect most visits. If an adult was present the entrance was temporarily blocked to allow the parent to feed the chick undisturbed without allowing it to escape. The adult was then removed, weighed and returned to the nest and the entrance was unblocked and the pegs reset. Once the adult had left the nest, the chick was reweighed. This protocol allowed us to attribute most feeds to individual parents. Where weighing the following day indicated that we had missed all or part of a feed (or feeds), we estimated the size of the missed feed(s) based on the rate of mass loss by ten chicks weighed every three hours between 22 and 24 July 2010 (mean 1.7 ± 0.6 g $hour^{-1}$). Where both parents were present at the nest simultaneously we assumed each parent delivered half of the total meal. Parents at nests on Skomer were sexed by cloacal inspection shortly after egg laying, when females' cloacae typically appear bruised and swollen.

Table 1. The number of birds tracked with GPS from each colony during each period of each year, with deployments for which we also recovered saltwater immersion data in round parentheses and those in which we co deployed a TDR in square parentheses. In italics below, the total number of foraging trips recorded. Approximate colony sizes (breeding pairs) are given.

		2009		2010		2011	
		Inc.	**Rear.**	**Inc.**	**Rear.**	**Inc.**	**Rear.**
Rum	**N birds**	-	-	-	9(9)	-	15(14)
(120k Pairs)	**N Trips**	-	-	-	*20(20)*	-	*58(52)*
Copeland	**N birds**	15(13)	20(13)	11(11)	20(18)	15(12)	22(21)
(4,633 Pairs)	**N Trips**	*16(13)*	*48(30)*	*11(11)*	*26(21)*	*19(12)*	*87(60)*
Skomer	**N birds**	9(9)	18[16](16)	8(8)	26[9](25)	13(11)	18(17)
(316k Pairs 365k Inc. adj. islands)	**N Trips**	*9(9)*	*24[20](20)*	*8(8)*	*69[14](63)*	*13(11)*	*47(43)*
Lundy	**N birds**	-	10(10)	-	11(11)	-	14(12)
(1,100 Pairs)	**N Trips**	-	*15(15)*	-	*29(28)*	-	*29(21)*

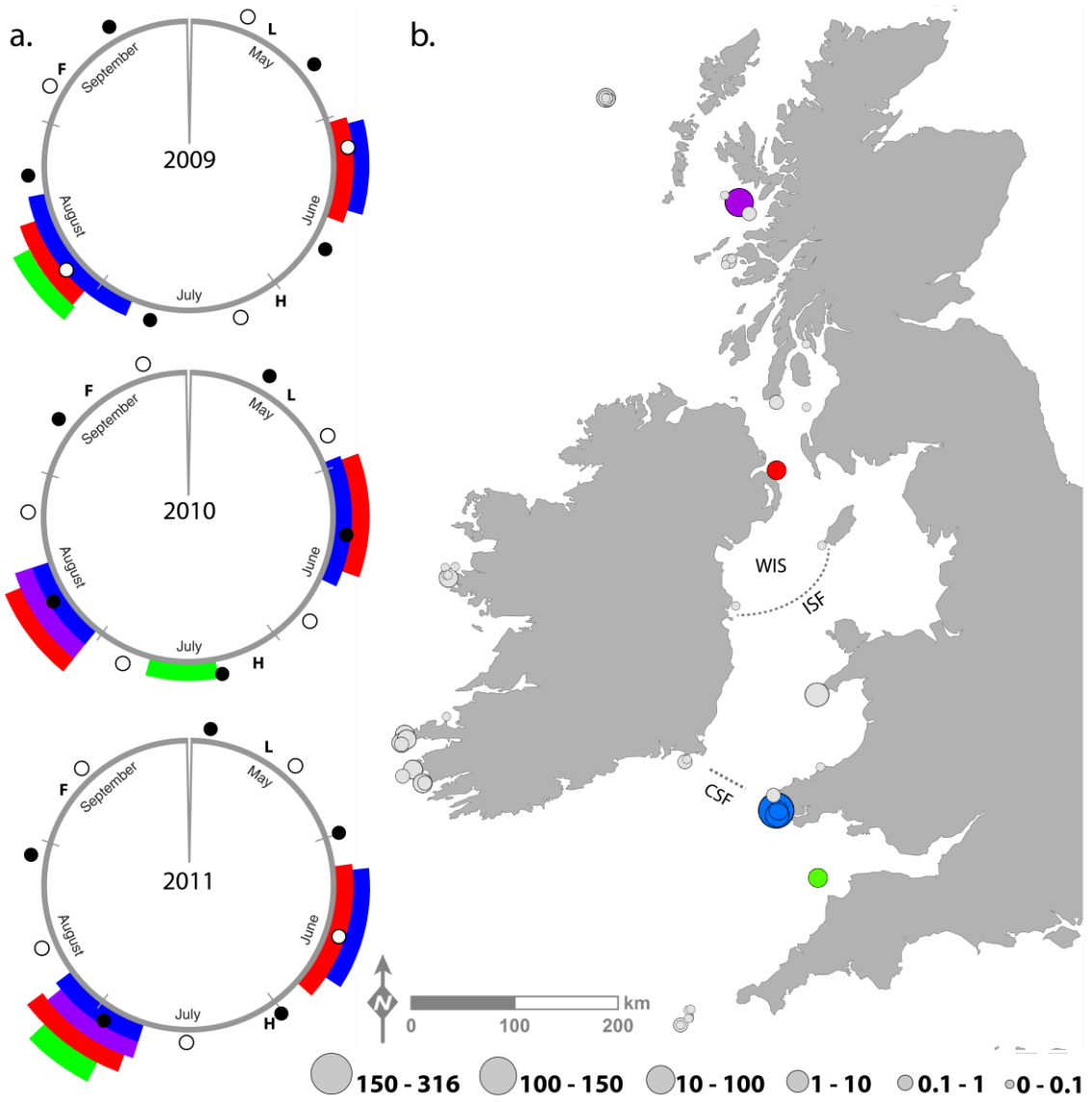

Figure 1. (a) Timing of deployments at each colony in each year with respect to the timing of breeding. Deployments are shown as coloured bands (from first to last recorded GPS fix): Rum (Purple), Copeland (Red), Skomer (Blue), Lundy (Green). The median lay (L), hatch (H) and fledge (F) dates are shown for nests monitored on Skomer. Moon phase is indicated as black circles (new moon) and white circles (full moon). (b) The locations of study colonies are shown, scaled by colony size (in thousands of pairs), and colour coded as in the deployment plots. The locations of all other significant colonies are also shown, scaled by colony size and coloured grey. Colony size data from Mitchell *et al.* (2004), Booker & Price (2010) and Perrins *et al*. (2012). The approximate positions of the Irish Sea Front (curved broken line) and Celtic Sea Front (broken straight line) are shown (Simpson & Hunter 1974).

Analysis of foraging movements

GPS tracks (which may contain multiple foraging trips) were segmented into individual trips based on the bird returning to within 1km of the colony between 20:00 and 03:00. Any trips that were incorrectly segmented using this method (usually where birds came close to the colony at night, but did not make landfall) were subsequently corrected manually. We used first-passage time analysis to identify those sections of the birds' tracks that were consistent with area-restricted search (ARS) and foraging behaviour. The first-passage time (FPT) is defined as the time required for an animal to cross a circular area with a given radius (Johnson *et al.* 1992; Fauchald & Tveraa 2003). Since slow, or tortuous movements will give greater FPTs than rapid direct movement, FPT has been used widely as a measure of ARS associated with foraging behaviour (Fauchald & Tveraa 2003; Pinaud & Weimerskirch 2005; Pinaud & Weimerskirch 2007; Weimerskirch *et al*. 2007; Bailleul *et al.* 2008; Pinaud 2008; Hamer *et al.* 2009; Pavia *et al.* 2010). We first determined the spatial scales over which Manx shearwaters engaged in ARS behaviour during foraging trips. Long periods of time spent sat on the water (e.g. roosting) are not strongly associated with foraging in the Manx shearwater (Dean *et al*. 2012) but typically result in very high peaks of FPT, increasing the variance in FPT and potentially masking patterns of ARS (Weimerskirch *et al.* 2007). We addressed this by removing bouts of sitting on the water (as in Pavia *et al*. 2010) - identified here using the co-deployed geolocator-immersion loggers - and interpolating the GPS tracks to give locations spaced 1km apart (as in Pinaud 2008; Pavia *et al*. 2010) using piecewise cubic hermite polynomials (as in Tremblay *et al*. 2006). To identify the spatial scale of ARS for each track we calculated FPT at each 1km location along the track using a series of radii (*r*) increasing in 1km steps from 1 to 250 km. We then identified the scale of ARS as the peak in the variance of log(FPT) plotted as a function of *r* as in (Fauchald & Tveraa 2003) (see figure 2 for example). To identify the most likely ARS and foraging locations along each track we then calculated FPT at each 1km location along the track using the colony mean scale

of ARS as the radius (*r*) (figure 3a). We then classified those GPS locations corresponding to the peaks in FPT as foraging locations (see figure 3 for example).

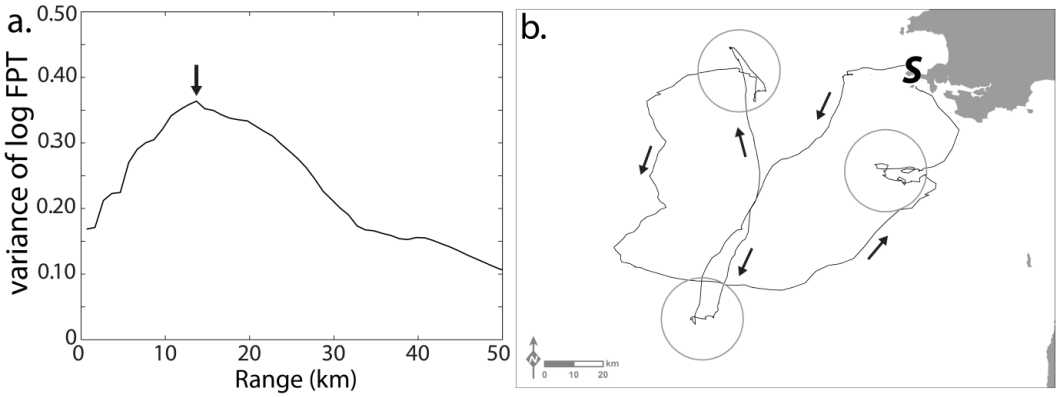

Figure 2. FPT analysis of a foraging trip for an example bird breeding on Skomer (***S***) (same bird as in figure 3): (a) variation in the log of FPT at increasing spatial scales reveals a peak at 14 km for this trip (arrow); (b) the GPS track with corresponding 14 km radius circles superimposed over the areas where FPT was highest (arrows indicate direction of travel).

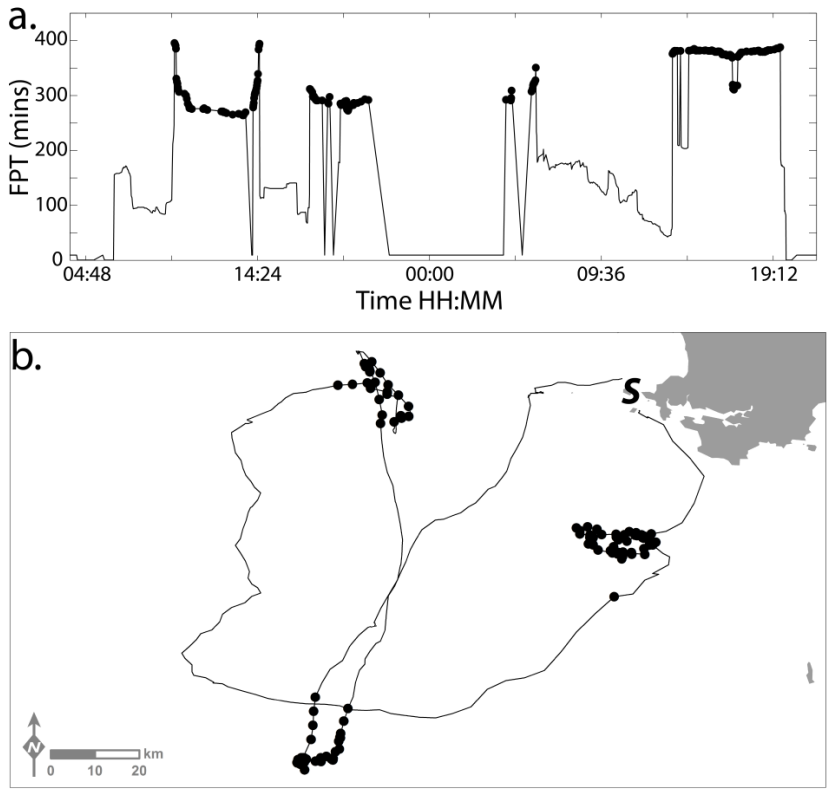

Figure 3. FPT analysis of a foraging trip for an example bird (same as in figure 2) breeding on Skomer (***S***): (a) FPT calculated at each 1km location as a function of time, using a radius of 19 km (the colony mean). Peaks in FPT corresponding with regions of ARS were classified as foraging and are highlighted by black points; (b) the GPS track with probable foraging locations (black points) identified by peaks in FPT.

Foraging distributions

Using the track locations classified as foraging from the FPT analysis (e.g. figure 3b) we calculated kernel density maps in ArcGIS over a grid of 1km^2 cells using a bandwidth (*h*) of 19km, chosen as the overall average scale of ARS. This bandwidth produced contiguous cores without over-smoothing (Supplementary Materials figure S1). Kernel density maps were calculated for all birds foraging from each colony during the incubation and chick-rearing periods of each year. Because overall density maps hide temporal patterns in foraging distributions, we also calculated kernel density maps for each day of tracking to visualise the spatial and temporal interactions of foraging birds from each of the colonies. Using the 95% kernel contours

calculated for each colony we also assessed the extent and distribution of overlap between the foraging ranges of birds from each colony. To validate our use of FPT to identify foraging locations, we compared the resulting foraging distributions with known diving locations. For each of the 25 birds from Skomer that carried TDRs, we calculated the proportion of all dives and the proportion of the total time spent submerged that fell within their own 95% kernel foraging contours.

Results

Impacts

The median duration of deployments was 8 days (interquartile range (IQR) 5-11) during incubation and 5 days (IQR 3-8) during chick rearing. Overall, incubation deployments recorded 1.1 foraging trips and chick rearing deployments recorded 2.4 trips. The departure masses of birds for each deployment were lighter during incubation than chick-rearing (405 ± 31 g and 424 ± 36 g respectively): two sample t-test t (260) = 3.88, $p < 0.001$. The masses of birds from different colonies in each period were not significantly different: Copeland incubation 407 ± 27 g, Skomer incubation 402 ± 37 g: two sample t-test t (69) = 0.67, p=0.505; Rum rearing 423 ± 47 g, Copeland rearing 428± 28 g, Skomer rearing 428 ± 38 g, Lundy rearing 412 ± 36 g: ANOVA $F(3,187) = 2.08$, $p = 0.104$. The combined device weight (18-19.5g) comprised approximately 4.5-5.2 % and 4.3-5.0 % of deployment body mass during incubation and chick-rearing respectively. For 51 nests from which adults were tracked on Skomer during incubation 2009 - 2011, hatching success was similar (70.6 %) to that of 120 nests where no incubation tracking had been carried out (74.2 %). For 39 nests from which adults were tracked on Skomer during chick-rearing 2009 - 2011, probable fledging success (actual fledging is difficult to assess) was similar (97.4 %) to that of 70 nests where no tracking had been carried out (98.6 %). During the tracking periods in 2009 and 2011, the mean growth rate of 24 chicks whose parents carried devices (6.9 ± 5.2 g day^{-1})

was slightly lower, but not significantly different to that of 23 chicks in control nests (7.5 ± 4.5 g day^{-1}): two sample t-test t (45) = 0.44, p = 0.66.

Foraging trips

We recorded 528 foraging trips during 259 deployments on 169 individuals (figure 4, table 1). Most tracks gave complete foraging trips: Copeland incubation 83%, Skomer incubation 77%, Rum chick-rearing 96%, Copeland rearing 97%, Skomer rearing 93% and Lundy rearing 100%. Incomplete tracks were excluded from calculations of trip duration. In only five trips did the GPS fail before the bird had reached its likely maximum range. These tracks were excluded from calculations of trip range. Plots of all foraging tracks recorded during incubation are given in figure 5 and during chick-rearing in figure 6. The average foraging trip metrics are given in Supplementary Materials (table S1) for each colony in each period of each year. Overlaying all 528 tracks (figure 4) shows that the foraging trips of Manx shearwaters from the four colonies studied here are largely restricted to the Irish and northern Celtic Seas, the Outer Bristol Channel, the North Channel and the inshore waters of the Outer Hebrides. The south-western extent in the Celtic sea is particularly striking. An additional 6 very long-range offshore trips into the Atlantic (Supplementary Materials figure S2) were excluded from the analysis as outliers because they (i) probably represent a different kind of rare foraging event, and (ii) for practical reasons they would distort the analyses herein.

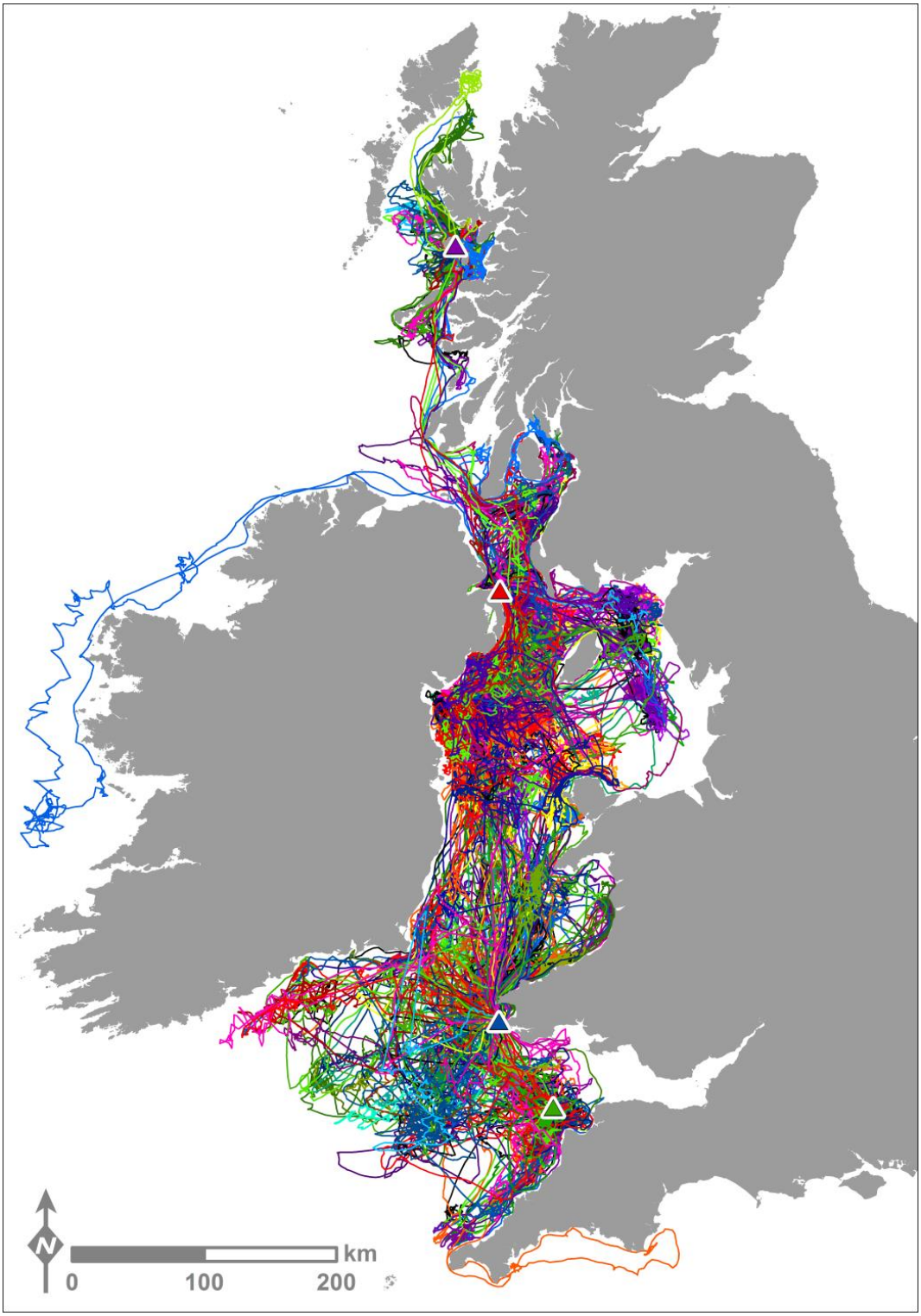

Figure 4. All 528 foraging trips recorded during incubation and chick-rearing from the four colonies: Rum (purple triangle), Copeland (red triangle), Skomer (blue triangle) and Lundy (green triangle). Tracks are coloured by individual (some colours re-used).

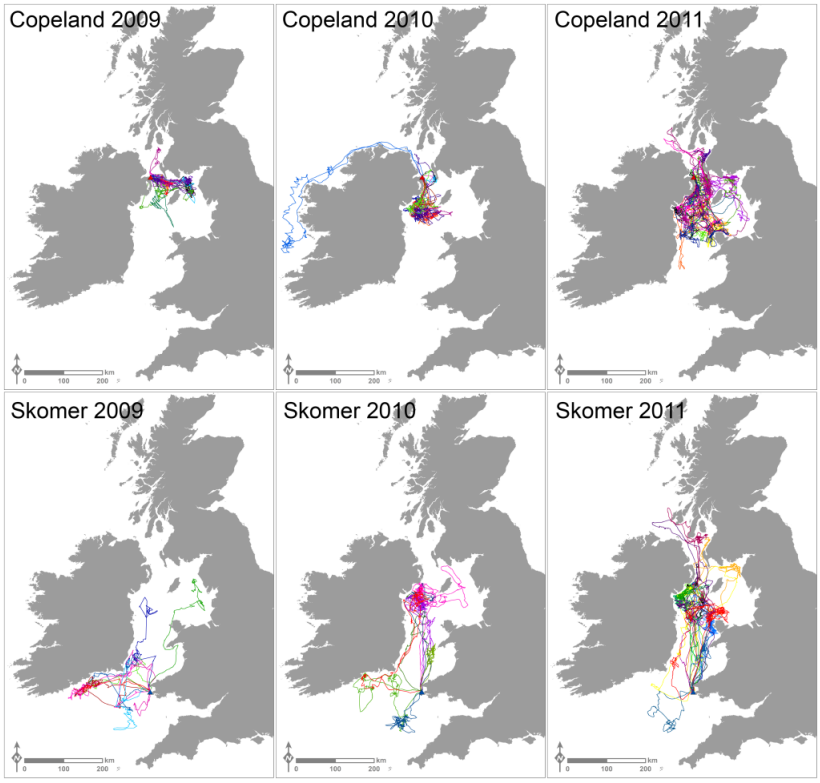

Figure 5. Foraging trips recorded during incubation from each of the two colonies in each year: Copeland (red triangle), Skomer (blue triangle). Trips coloured by individual (some colours re-used).

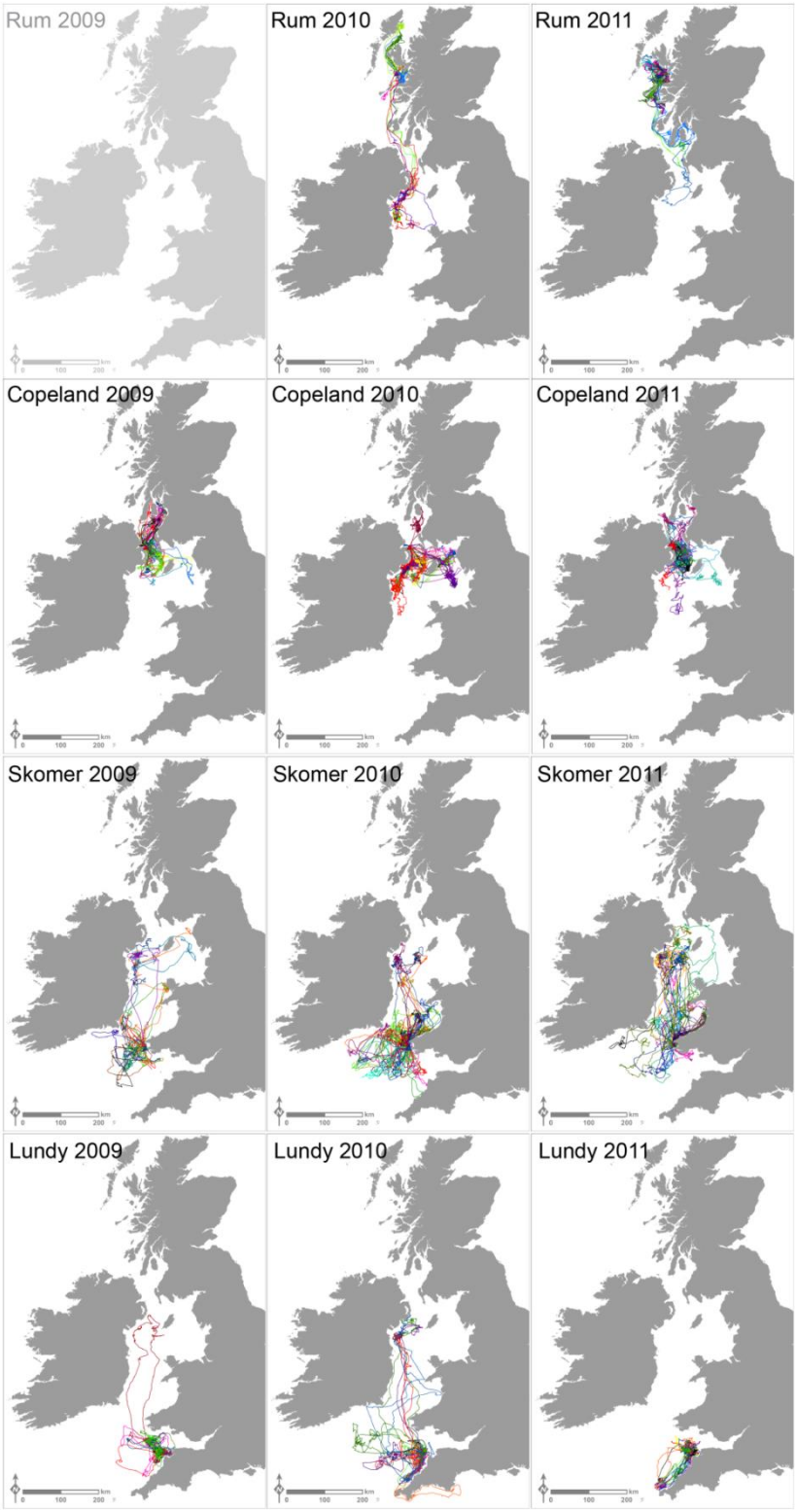

Figure 6. Foraging trips recorded during chick-rearing from each of the four colonies in each year: Rum (purple triangle), Copeland (red triangle), Skomer (blue triangle) and Lundy (green triangle). Trips coloured by individual (some colours re-used).

Foraging distributions

Because we used the co-deployed saltwater-immersion loggers to remove long periods spent on the water prior to FPT analysis, we only included the 437 foraging trips for which we had corresponding saltwater-immersion data in the density mapping. Most (67%) Manx shearwater foraging trips showed a peak in variance of log(FPT) indicating that ARS typically occurred at scales between 10 and 40 km; the overall mean was 19.2 ± 8.4 km. Some trips, particularly very short looping trips, did not show a clear peak in variance of log(FPT) indicating that those birds did not concentrate search effort at any particular spatial scale (Fauchald & Tveraa 2003). The mean scale of ARS for each colony in each period of each year is shown in the Supplementary Materials (table S1). Most trips (87%) showed peaks in FPT as a function of time, indicating periods of slower, more tortuous movement consistent with searching and foraging. In the remainder (13%) of tracks birds did not appear to concentrate search effort in a particular area and so we classified the whole track (excluding periods on the water) as foraging. Kernel density maps of foraging locations (figure 7) from simultaneous tracking (figure 1) show the contemporary foraging distributions of birds from two colonies during incubation and three-four colonies during chick-rearing. Ninety-five per cent kernel contours for individual birds equipped with TDRs contained 78.5 ± 16 % of all dives accounting for 79.8 ± 17 % of total time submerged (Supplementary Materials figure S3, table S2). Some diving occurred in areas where no ARS or peaks in FPT were identified, particularly *en route* between the colony and the main foraging areas, but in general the kernel density maps represent the majority of foraging activity.

During the incubation and chick-rearing periods there was substantial inter-annual variability in the foraging distributions of birds from all colonies. However, some consistent patterns emerged. During incubation, birds from Copeland foraged much closer to their colony than did birds from Skomer. Birds from Skomer frequently travelled north to forage in areas of the Irish Sea that were also used by birds from Copeland, particularly in 2010 and 2011, leading to a high

degree of overlap (8-62 % of Copeland's distribution and 4-65 % of Skomer's distribution) between the two foraging distributions in the vicinity of the Western Irish Sea Front (ISF) and Western Irish Sea (WIS) (Simpson & Hunter 1974) (figure 8, Supplementary Materials table S2). During chick rearing, birds from all four colonies engaged in foraging close to their respective colonies (figure 7). The only local foraging distributions that overlapped were those of Skomer and Lundy (75 km apart), where there was an area of overlap approximately equidistant from both colonies that varied in extent between years (2-20 % of Skomer's distribution and 8-45 % of Lundy's distribution [figure 8, Supplementary Materials table S4]). However, the foraging distributions of birds from all four colonies overlapped in one important area, the ISF and WIS (figures 7 and 8). We visualised the spatio-temporal interactions of foraging by birds tracked from each of the colonies during the simultaneous tracking periods (Supplementary Materials visualisations V1-V6). These reveal that not only do the overall foraging distributions overlap, but that on many occasions in different years and periods of the breeding season, birds tracked from different colonies foraged in the same areas at the same time. Indeed, in some instances, birds from different colonies appear to track the same resources over consecutive days, particularly within the ISF/WIS area.

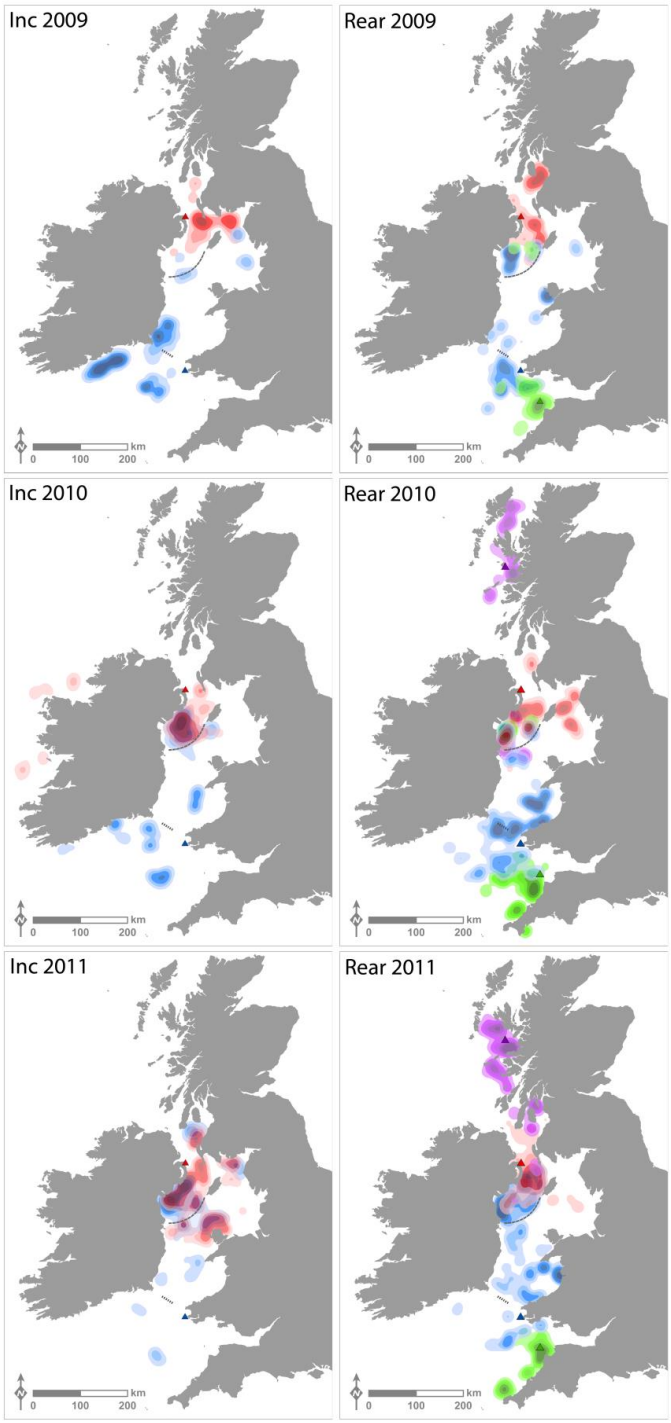

Figure 7. Foraging density maps calculated for incubation and chick-rearing in each year. Kernel densities were calculated using those locations classified as foraging using FPT. Distributions for each colony: Rum (purple), Copeland (red), Skomer (blue) and Lundy (green) are shaded from lightest (95% occupancy contour) to darkest (20% occupancy contour) and are translucent to show overlap between colonies. The approximate positions of the Irish Sea Front (curved broken line) and Celtic Sea Front (broken straight line) are shown.

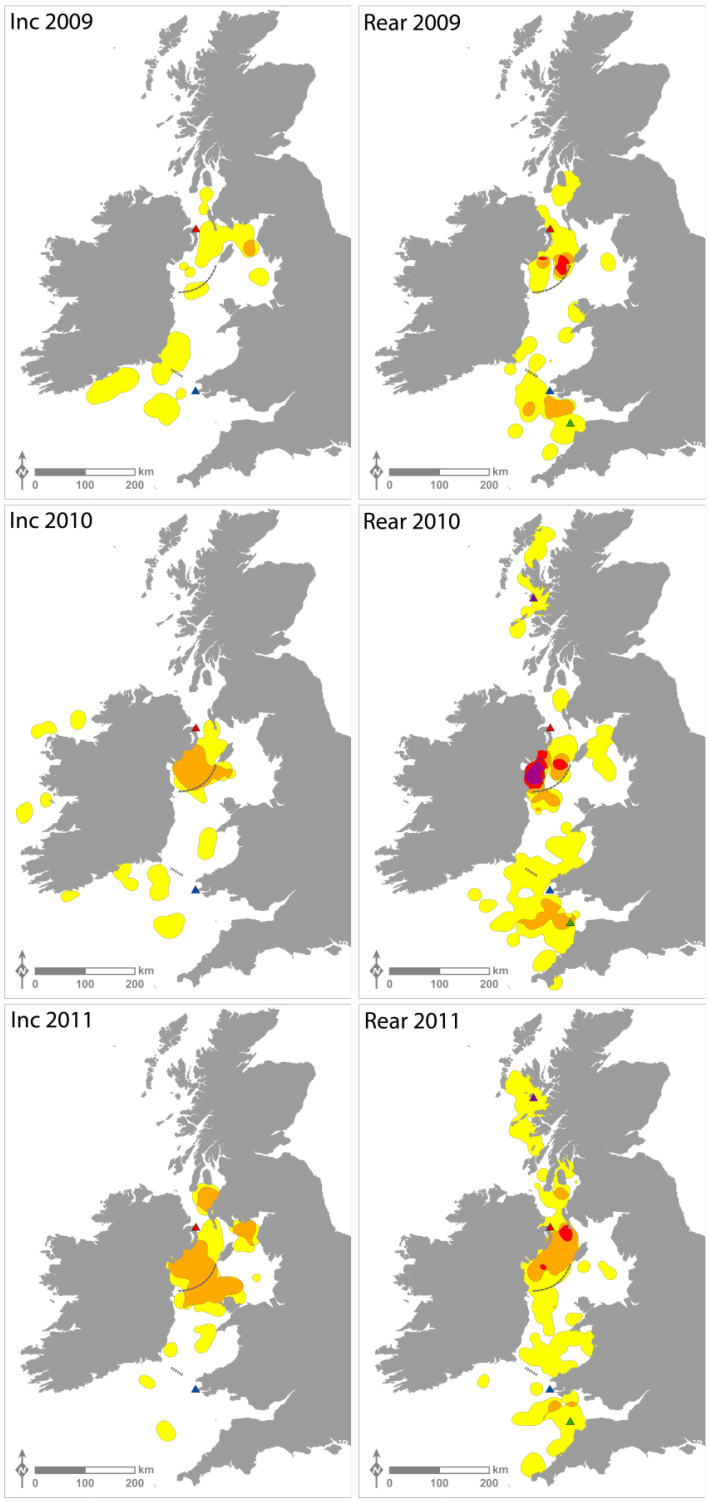

Figure 8. Size and extent of overlap between foraging ranges (95% kernel contours) for each colony during incubation and chick-rearing in each year. Yellow areas represent foraging by birds from one colony, orange two colonies, red three, and purple four. The approximate positions of the Irish Sea Front (curved broken line) and Celtic Sea Front (broken straight line) are shown.

Trip range and duration in relation to the ISF

During incubation and chick-rearing, trip duration was correlated with trip range and (except for incubation trips from Skomer) trip range was correlated with distance travelled per day (figures 9 and 10). During incubation, most trips from Copeland were of less than 200km range. Sixty three per cent of these visited the ISF/WIS (figure 9). Most incubation trips from Skomer were between 100 and 300 km range and 50% of these visited the ISF/WIS. The majority of birds travelling over 200km from Skomer visited the ISF/WIS (figure 9). During chick-rearing, the majority of trips from all four colonies were relatively local (within 200 km of the colony), but birds from Rum, Skomer and Lundy also made less frequent long-range trips. All long-range trips from Skomer and most long-range trips from Rum and Lundy visited the ISF/WIS area (figures 10 and 11). The percentage of trips visiting the ISF/WIS decreased monotonically with distance of the colony from the approximate position of the ISF: 5% from Rum (~375km from ISF), 7% from Lundy (~280km from ISF), 15% from Skomer (~215km from ISF) and 44% from Copeland (~120km from ISF) (Supplementary Materials figure S4). For birds of known sex (Skomer only) there were no significant differences in median trip duration or range for males and females during incubation and chick-rearing: Incubation duration (F=10.5 days, M=8 days), range (F=290 km, M=244 km): Wilcoxon Rank-sum (10) = 31, p = 0.23; (15) = 89, p = 0.11. Chick-rearing duration (F=2 days, M=2 days), range (F=108 km, M=96 km): Wilcoxon Rank-sum *z* (40) = 0.31, p = 0.76; *z* (41) = 0.33, p = 0.74. The probability of us recording a trip to the ISF/WIS area was not significantly higher for males (incubation = 0.55, rearing = 0.14) than for females (incubation = 0.37, rearing = 0.07) Fisher exact tests: incubation p = 0.25, rearing p = 0.08.

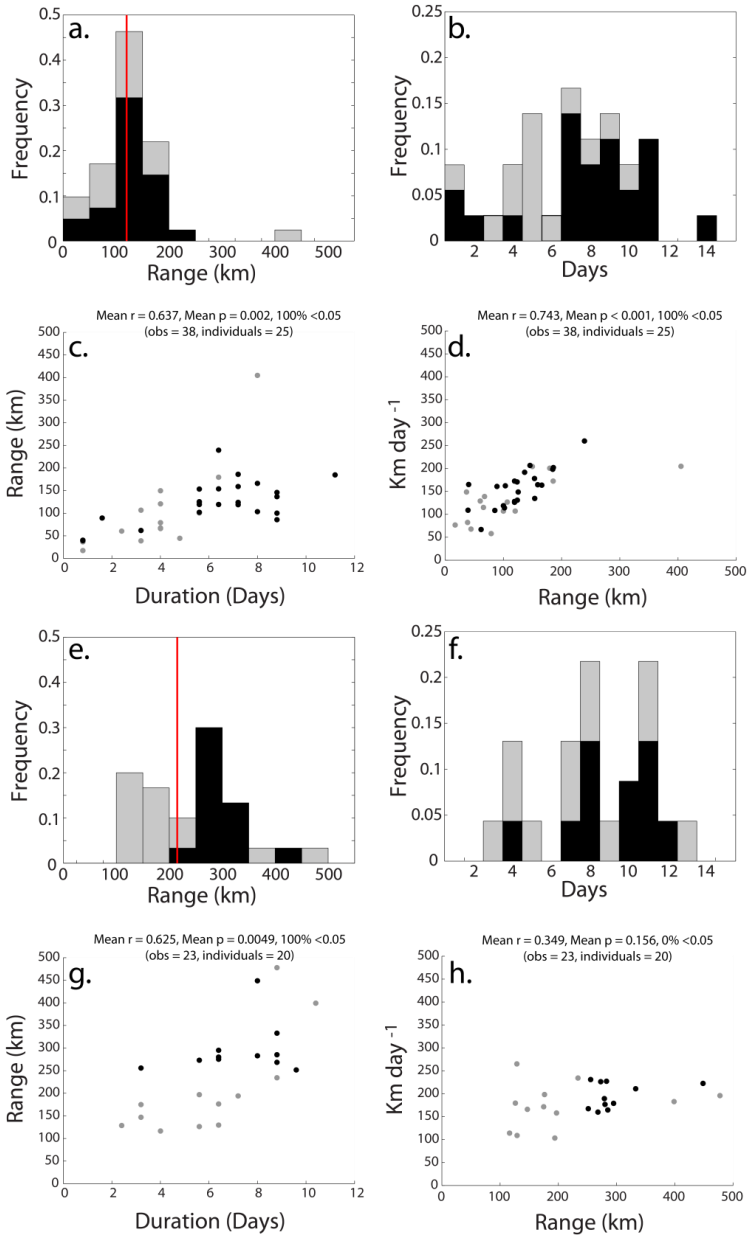

Figure 9. Frequency distributions of foraging trip range (maximum straight-line distance from colony) and duration for incubation trips from Copeland (a, b) and Skomer (e, f). Black bars represent trips made to the ISF/WIS, grey bars trips to other areas, red lines show the straight-line distance from the colony to the middle of the ISF. Scatter plots show the relationship (Spearman's rank correlation) between duration and range and range and distance travelled per day for Copeland (c, d) and Skomer (g, h). Black points represent trips made to the ISF/WIS, grey points trips to other areas. Because we had multiple trips for some individuals we randomly selected one trip per individual and tested the Spearman's rank correlation, repeated 100 times and took the mean r and p values as well as the percentage of iterations in which $p<0.05$.

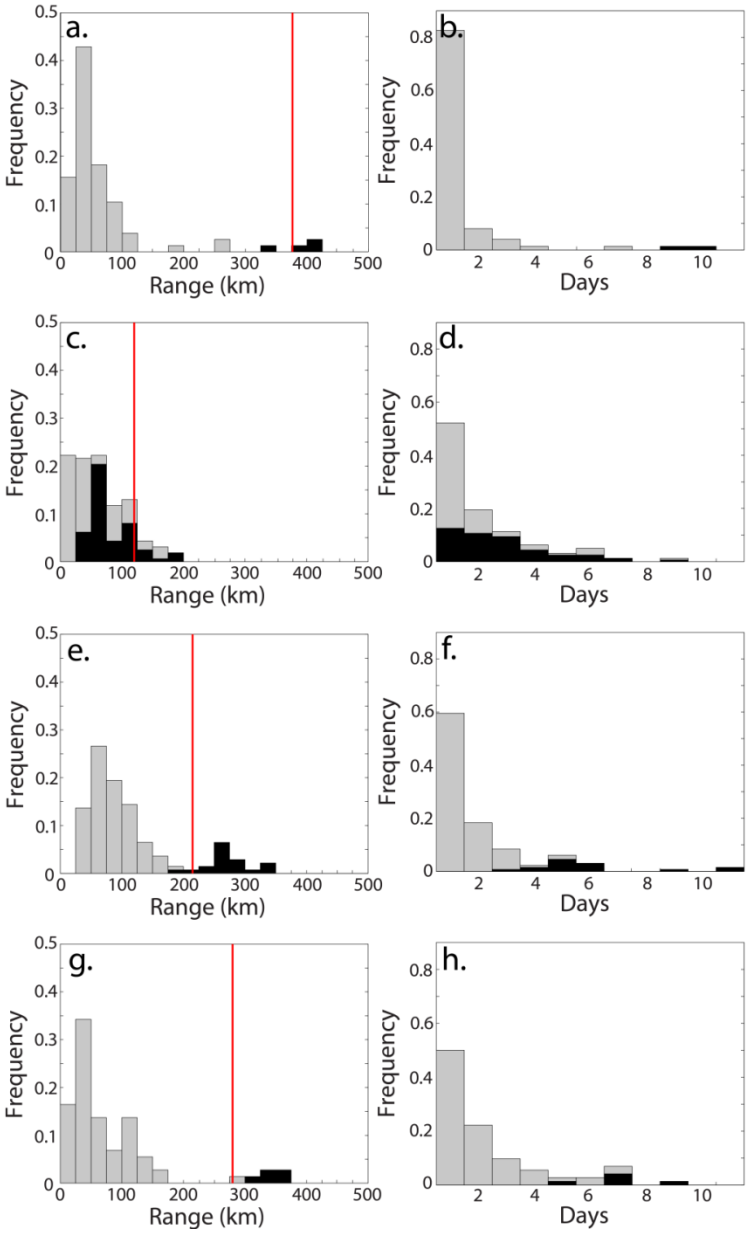

Figure 10. Frequency distributions of foraging trip range (maximum straight-line distance from colony) and duration for chick-rearing trips from Rum (a, b), Copeland (c, d), Skomer (e, f), Lundy (g, h). Black bars represent trips made to the ISF/WIS, grey bars trips to other areas, red lines show the straight-line distance from the colony to the middle of the ISF.

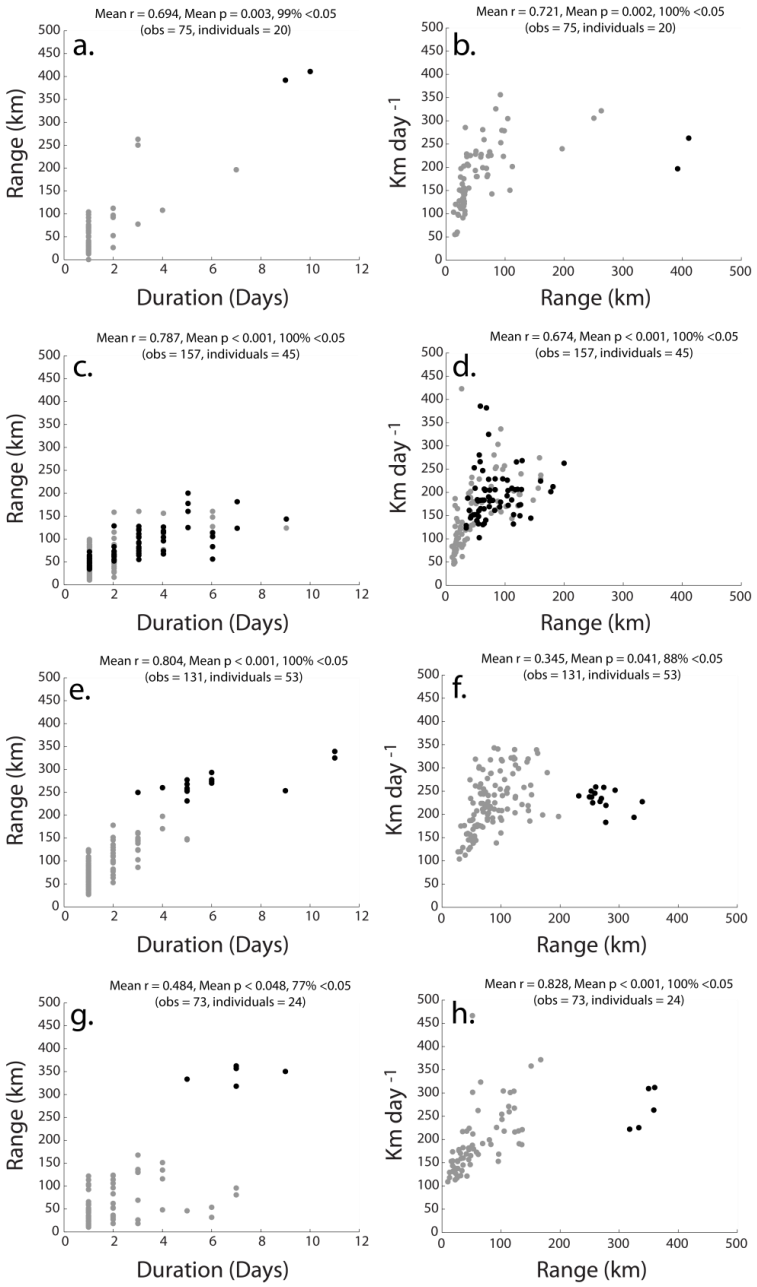

Figure 11. Scatter plots show the relationship (Spearman's rank correlation) between duration and range and range and distance travelled per day for chick-rearing trips from Rum (a, b), Copeland (c, d), Skomer (e, f), Lundy (g, h). Black points represent trips made to the ISF/WIS, grey points trips to other areas. Because we had multiple trips for some individuals we randomly selected one trip per individual and tested the Spearman's rank correlation, repeated 100 times and took the mean r and p values as well as the percentage of iterations in which $p<0.05$.

Mass changes during foraging trips

Using linear mixed effect models of mass changes on trip duration, with individual as a random effect, we found no significant relationship between foraging trip duration (days) and an adults net mass change (g), or mass change per day (g day^{-1}) during incubation foraging trips from Copeland or Skomer (figure 12). During chick-rearing, the total mass change by the parent over a foraging trip can be split into the mass of the meal fed to the chick and the net mass change by the parent (after feeding the chick). Using linear mixed-effect models of mass changes on trip duration, with individual as a random effect we found that the total mass change (g) by the parent increased slightly with trip duration (days), but that the daily total mass change (g day^{-1}) decreased with the log of trip duration (figure 13). Similarly the mass of the meal fed to the chick (g) increased slightly (but not significantly) with trip duration, but the daily rate of food delivery (g day^{-1}) decreased with the log of trip duration. The net change in parent's mass (g) tended to be negative for short trips and increased slightly with trip duration (but not significantly), as did the daily net mass change (g day^{-1}).

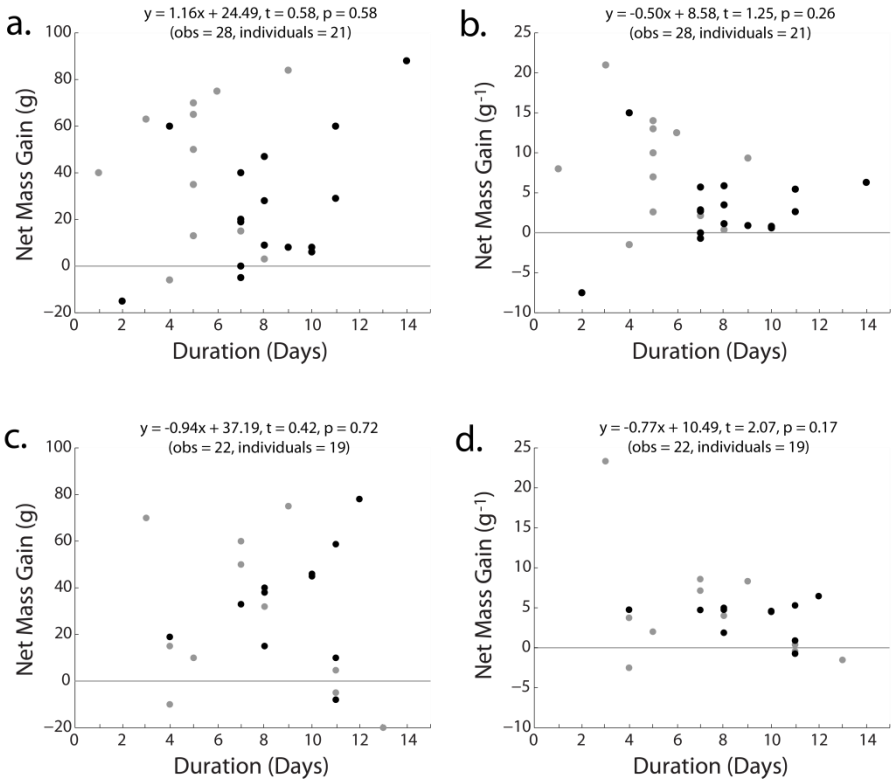

Figure 12. Net mass changes in g (a, c) and g day^{-1} (b, c) for adults on foraging trips from Copeland (a, b) and Skomer (c, d). Black points represent trips made to the ISF/WIS, grey points trips to other areas. Using linear mixed effect models with individual as a random effect there were no significant relationships between Net mass change and trip duration.

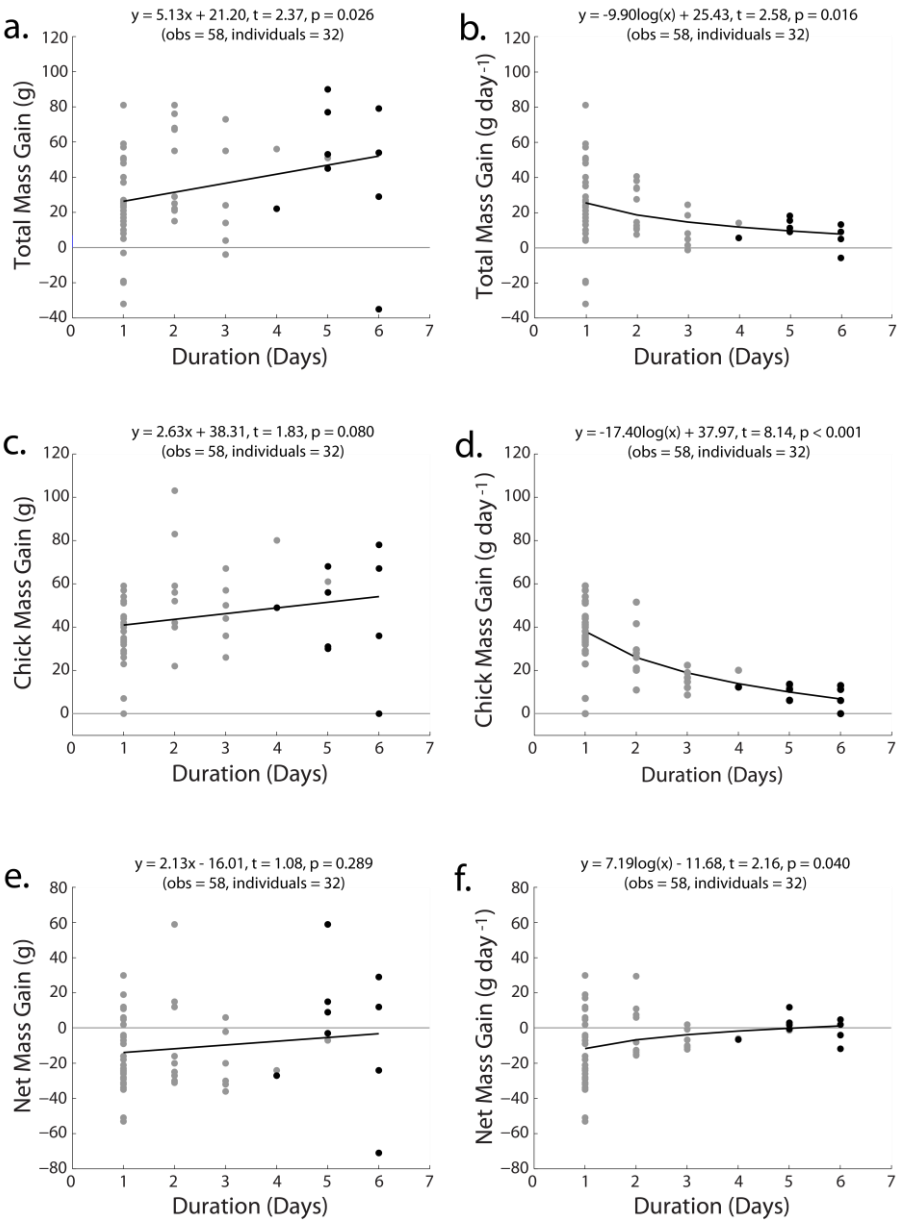

Figure 13. Linear mixed effect models with individual as a random effect showing the relationship between: foraging trip duration and total mass changes (parental net gain + meal fed to chick) in (a) g and (b) g day^{-1} for chick-rearing parents from Skomer; the relationship between foraging trip duration and the mass of meals subsequently fed to chicks in (c) g and (d) g day^{-1}; and the relationship between foraging trip duration and net mass change (parental net gain after feeding the chick) in (e) g and (f) g day^{-1}. Black points represent trips made to the ISF/WIS, grey points trips to other areas.

Discussion

Impacts and success of tracking

We recorded a large number of foraging trips (528) made by a large number of individual Manx shearwaters (169) from four colonies across the UK range, during the two main stages of the breeding season, over three consecutive years (figure 1, 5 and 6). We found considerable variability between years in foraging distributions (figure 7). Some of this variability may have been due to tracking different individuals in each year. This highlights the importance of continuing tracking studies over several (preferably consecutive) years in order to capture as much of the natural inter-annual variation as possible. We tracked birds from two colonies simultaneously during the incubation period and up to four colonies simultaneously during the chick-rearing period. Unfortunately, considerable logistic challenges forced us to undertake tracking earlier on Lundy in 2010. These data have an advantage over tracking data collected from single colonies, or from different colonies asynchronously because they allow us to compare the foraging movements of birds from different colonies unaffected by temporal changes in environmental parameters that might be expected to influence those movements. Even so, it should be noted that differences in the timing of breeding between the colonies made it impossible to track birds from different colonies simultaneously *and* during identical stages of the breeding season. Previous work suggests that there is a tendency for shearwaters breeding at higher latitudes to lay later in the season and in any year, the median laying date on Rum could be 1-2 weeks later than on Skomer (Brooke 1990).

The combined mass of devices in these deployments comprised approximately 4.3-5.2 % of the body mass of the birds tracked in this study. Previous studies of procellariiforms (Sæther *et al*. 1993; Phillips *et al*. 2003) have demonstrated negative impacts including nest desertion, increased trip duration and reduced meal sizes on a range of species carrying loads comprising 0.6–6.0% of body weight, although many of those deployments were of longer duration than

here. In addition, it is likely that birds experience increased diving and flight costs and stress (Burger & Shaffer 2008), which probably are passed on to the offspring in the form of reduced incubation effort, provisioning rate and meal sizes (Sæther *et al*. 1993; Mauck & Grubb 1995). Our control tests suggest that our devices did not have detectable medium-term (breeding season) effects on reproductive success. There were small effects on provisioning by parents, but these differences were not significant. It is also possible that the devices had some small effects on the at-sea behaviour and recorded trip duration. However, the mass of devices as a percentage of body mass was similar between colonies, so comparison of foraging trips between colonies should not be biased by differential device mass effects. Nevertheless, the data on the at-sea movements of Manx shearwaters presented here must therefore be interpreted with the caveat that these birds are carrying devices that may have affected their behaviour.

Foraging distributions

Our results indicate that our use of FPT to identify foraging locations and the subsequent use of kernel density mapping to represent the spatial distribution of foraging behaviour identified the majority of locations in which diving occurred (Supplementary Materials figure S3, table S2). These results are broadly in agreement with Hamer *et al*. (2009), but contrary to Robinson *et al*. (2007). Even so, not all dives corresponded with peaks in FPT: these were typically short lived bouts of diving during commuting flights between the colony and foraging areas. These may be opportunistic foraging events, where prey or other foraging birds were encountered during commuting flight; prey may be ingested even during rapid and directed flight (Catry *et al*. 2004) and such encounters may not always trigger ARS behaviour (Weimerskirch *et al*. 2007).

During incubation, trip duration (median 7-8 days) is likely to be controlled by a complex trade-off between the ability of the incoming partner to fast during the following incubation stint and the time needed for the outgoing partner to recover body condition lost during the previous incubation stint. Our data show that birds from Copeland made relatively local trips (less than

200 km range), the majority of which were to the ISF/WIS (figure 9). Birds from Skomer also made relatively local trips, but most trips were longer range (greater than 200 km) and the majority of those were to the ISF/WIS. In this area in 2010 and 2011, there was a high degree of temporal and spatial overlap in the foraging areas of birds from both colonies (figure 8). In general, most longer duration (>6 days) and (from Skomer) longer range (>200 km) trips visited the ISF/WIS. Birds from Copeland travelled more kilometres per day on these longer trips than on shorter trips. We found no effect of trip duration on net mass gain during incubation and so these longer trips primarily to the ISF/WIS did not result in greater mass gains for foraging birds (figure 12). During the early breeding season, reliable aggregations of prey may be limited and this area may provide a predictable, but not necessarily highly profitable resource for off-duty incubating birds to recover body condition. Given the distribution of colonies (figure 1) and the duration of incubation stints (7-8 days), it seems likely that birds from other colonies also foraged there with some regularity.

During chick-rearing, birds from all four colonies foraged in relatively local areas (within 200 km) as expected for a central place forager constrained to return frequently (median 1-2 days) to provision it's chick. The only local foraging distributions that overlapped were those of Skomer and Lundy, which are only 75 km apart. In addition to frequent short duration, short-range trips, birds from Rum, Skomer and Lundy also made less frequent long-range (>200 km) and long-duration (>4 days) foraging trips (figure 10). All long-range trips from Skomer and most from Rum and Lundy visited the ISF/WIS. Copeland birds also made frequent local foraging trips to this area. As a result, there was spatial and temporal overlap of foraging birds from up to four colonies within this relatively restricted area of the Irish Sea, indicating co-foraging on a shared resource (figure 8). For birds from Skomer, these longer-duration, longer range trips tended to result in slightly larger meals fed to the chick, but at a lower rate of provisioning (g day^{-1}) than for shorter trips (figure 13). The energy density of these meals may have been greater, since they may have contained a higher proportion of partially digested stomach oils (Chaurand &

Weimerskirch 1994), but in Manx shearwaters, chicks are typically fed relatively undigested Clupeid fish (Brooke 1990) and so it seems likely that the rate of energy delivery to chicks over these longer-range trips to the ISF/WIS area was lower than for shorter duration local trips. Importantly, birds tended to lose net mass (in g and g day^{-1}) on for short trips, but tended to lose less mass over longer trips, most of which visited the ISF/WIS. Whether this was simply the result of foraging, digesting and accumulating integrated body condition for longer, or was in some way facilitated by the quality of the foraging location is unknown. These results suggest that in common with many procellariiforms (Chaurand & Weimerskirch 1994; Weimerskirch *et al*. 1994; Weimerskirch *et al*. 1997; Weimerskirch 1998; Gray & Hamer 2001; Magalhães *et al*. 2008), but not all (Phillips *et al*. 2009), the foraging and provisioning strategy of Manx shearwaters may allow parents to regulate reproductive effort by combining short trips to local areas (which maximise food delivery rate to the chick at a net energetic cost to parents) with less frequent, longer trips to more distant productive areas (which result in a lower rate of food delivery, but which allow parents to recover body condition lost on short trips). In Manx shearwaters (at least those breeding on Skomer) it may be the specific foraging location of the ISF/WIS that is important in this role.

Given the relative sparsity of our sampling (a relatively small proportion of each population tracked), these data suggests potentially high levels of interaction between birds from different colonies, particularly in this area. In some cases birds from different colonies appeared to track the same mobile prey resources within the WIS (Supplementary Materials visualisations V1-V6). Again, it seems likely that birds from other untracked colonies also foraged there with some regularity, but since the frequency of recorded visits to this area declined with increasing distance of the colony, the net energetic gain of foraging there is probably significantly affected by the energetic costs of travelling to it. Perhaps at some range greater than 375km (the distance between Rum and the ISF/WIS) the costs of travel may outweigh the benefits of foraging there. The movements of birds from colonies such as St Kilda (≈500km northwest of ISF)

and the Scilly Isles (≈450km south of ISF), may reveal this. The notion that birds may prefer to forage there but for their central place foraging constraint is supported by the distribution of Manx shearwaters during September and October, when the chicks have fledged and the parents are no longer constrained to visit the colonies, which shows a marked concentration in this area (Stone *et al*. 1994).

Previous surveys (Stone *et al*. 1994) have shown that this area supports high densities of Manx shearwaters during the breeding season, although the provenance (colony of origin) and breeding status of these birds was previously unknown. The ISF is a seasonal tidal mixing front that extends in an arc from the southern tip of the Isle of Man to Dublin Bay (Simpson & Hunter 1974) (figure 1). The dynamics of most of the Irish Sea are dominated by strong tidal currents, which keep the water column vertically mixed. In the WIS, tidal currents are weak, which permits the development of a thermocline from early April–May until the end of October (Simpson and Hunter 1974; Hill *et al.* 1994). To the west of the ISF, currents flow as a cyclonic gyre around the centre of the WIS (Hill *et al.* 1994). The aggregation of seabirds at frontal systems is well documented (Stone *et al.* 1994; Schneider 1990; Begg & Reid 1997; Durazo *et al.*. 1998; Vliestra *et al.* 2005; Le Fèvre 1986) and the ISF area is likely to provide profitable feeding opportunities. Increased primary production associated with fronts (Savidge 1976; Beardall *et al.* 1982; Le Fèvre 1986; Yoder *et al.* 1994) and aggregation (Scrope-Howe & Jones 1985), or physical retention by currents of zooplankton and nektonic organisms (Herman *et al.* 1981; Yoder *et al.* 1994) are likely to attract high densities of pelagic fish (Laurs *et al.* 1977; Alemany *et al.* 2009). In addition, the currents of the cyclonic gyre are likely to function as physical retention mechanism, allowing fish larvae spawned in coastal regions (Dickey-Collas *et al.* 2001) to circulate within the WIS, but ensuring that they return and recruit into the adult population (Hill *et al.* 1994; Dickey-Collas *et al.* 1997). This seasonal stability in recruitment may provide a reliable prey resource for higher trophic levels including seabirds (Durazo *et al.* 1998). That birds breeding at colonies across the UK range use this area to varying extents, throughout the

breeding season highlights its importance. In addition to breeding birds, the area is likely to be of importance to non-breeders. In any year, possibly as much as half of the population may not breed; mainly immature birds, not yet of breeding age (up to 7 years; Brooke 1990), but also divorced or widowed birds searching for a new mate. While each of these potential future breeders will be associated with a particular colony, they may not return there with the regularity of breeders. Hence their foraging patterns at sea are likely to be less constrained than those of breeding birds.

Intraspecific competition at foraging grounds is likely to increase as a function of conspecific density and may be significant enough to cause prey depletion, limit colony size and foraging ranges, and to select for differential foraging strategies between sexes (Ashmole 1963; Furness & Birkhead 1984; Birt *et al*. 1987; Cairns 1989; Lewis *et al*. 2001; Grémillet *et al*. 2004; Wakefield *et al*. 2011). Why then should breeding birds pay the travel costs of commuting several hundred kilometres to forage within an area of extremely high conspecific density? Several mutually inclusive (and not exhaustive) possibilities may account for this. First, the energetic costs of travelling these distances may be low for Manx shearwaters, which like other procellariiform seabirds are able to use shear, or dynamic soaring techniques to exploit wind energy close to the sea surface (Wilson 1975; Pennycuik 2002; Sachs 2005). Second, the availability of prey within the ISF/WIS area may be high enough that intense intraspecific competition does not limit foraging efficiency. Finally, Manx shearwaters may not experience high levels of intraspecific competition, even at the high densities found in the ISF/WIS area. This could arise if the benefits of social foraging at these densities outweigh the costs of competition. The formation of large, high density flocks may actually increase the foraging success of individual members (Götmark *et al*. 1986), aggregating prey into more vulnerable, easily captured groups.

Conclusions

We analysed a large seabird tracking dataset in which deployments were made simultaneously at up to four colonies, during incubation and chick-rearing stages of three consecutive breeding seasons. This gives us a high level of confidence in the robustness of inferring colony and population foraging distributions. The data indicate that the foraging areas of Manx shearwaters were variable between stages of the breeding season and between years. Nevertheless, consistent patterns emerged.

Birds from each colony consistently foraged within relatively local areas, but birds from all colonies also foraged within a single relatively restricted area of the Irish Sea, the ISF and WIS, indicating co-foraging on a shared resource. Visualisations of foraging movements also suggest that within this area birds from different colonies may follow mobile resources together. This key area in which birds from all four colonies foraged may provide a predictable resource during the early breeding season, while later in the season high densities of prey may make the area particularly important in regulating reproductive effort, allowing parents to recover body condition lost on shorter foraging trips close to the colony. Given the distribution of other colonies, it is likely that this area is of importance to birds breeding at colonies across the Irish and Celtic Seas and the west coast of Scotland. Coupled with previous surveys of Manx shearwaters in UK waters, these data highlight both the importance of local foraging areas and the importance of this shared resource.

In addition to allowing robust inferences to be made about large scale colony and population distributions, these data present an opportunity to investigate the mechanisms that drive the large scale annual variation seen in these distributions. The combined GPS and saltwater-immersion data from a large number of individuals also present opportunities to examine the fine scale behaviour of foraging birds from different colonies at different stages of the breeding

season, with a view to understanding details of search and foraging behaviour as well as the mechanisms that drive individual variation in foraging locations.

Acknowledgements

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Supplementary Material

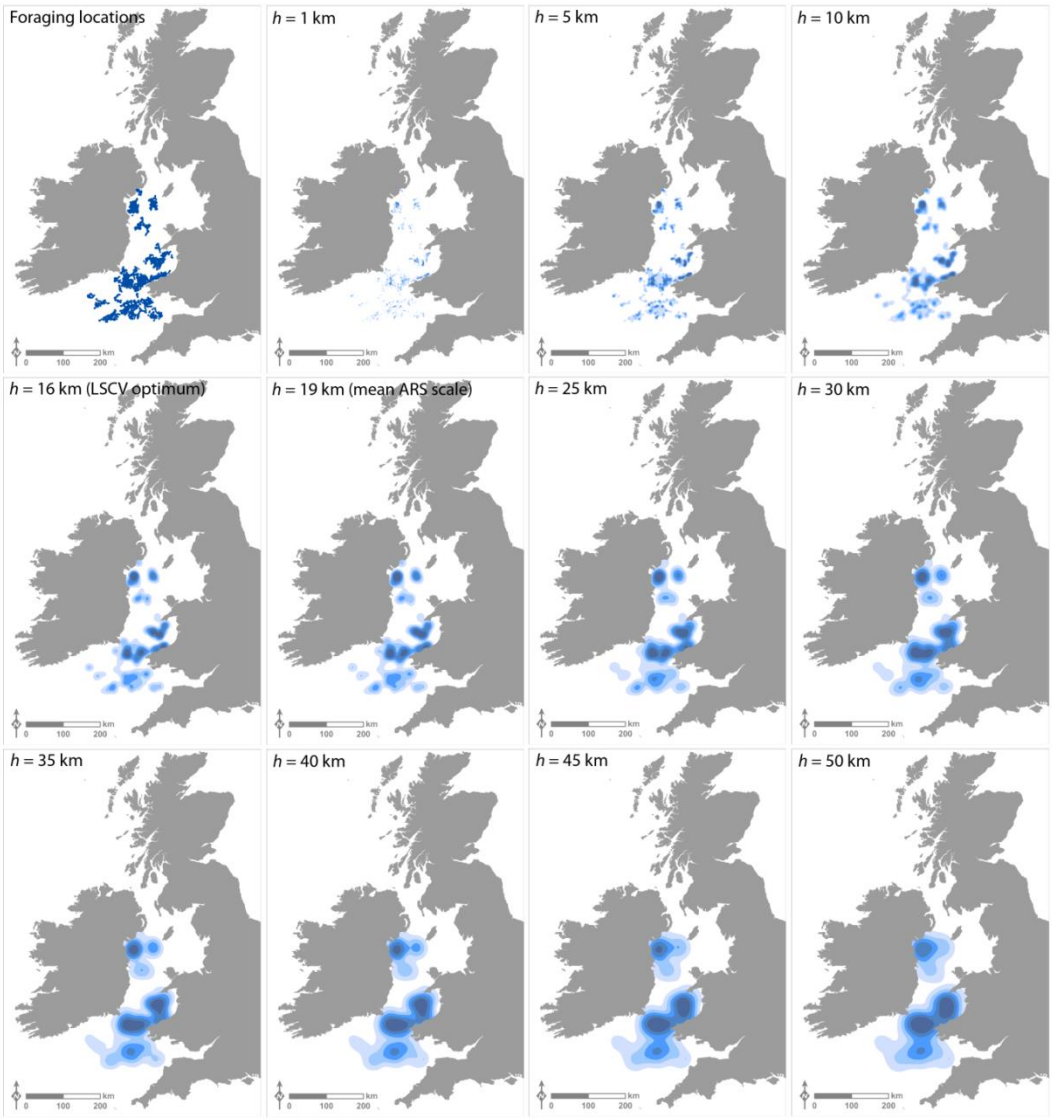

Figure S1. Validation of bandwidth (*h*) choice. Example original foraging (classified using FPT) locations from Skomer during chick-rearing 2010 (top left panel) and kernel density estimates made using a range of bandwidth (*h*) parameters from 1-50km. Kernel occupancy contours (95%, 80%, 60%, 40%, 20%) are coloured from light-dark blue. The mean scale of ARS 19km was used in this study, which produced contiguous core without over-smoothing the data. For comparison, least-squares cross-validation (which can produce under-smoothed surfaces) selected an optimum value of 16km, which did not produce a markedly different kernel estimate from 19km.

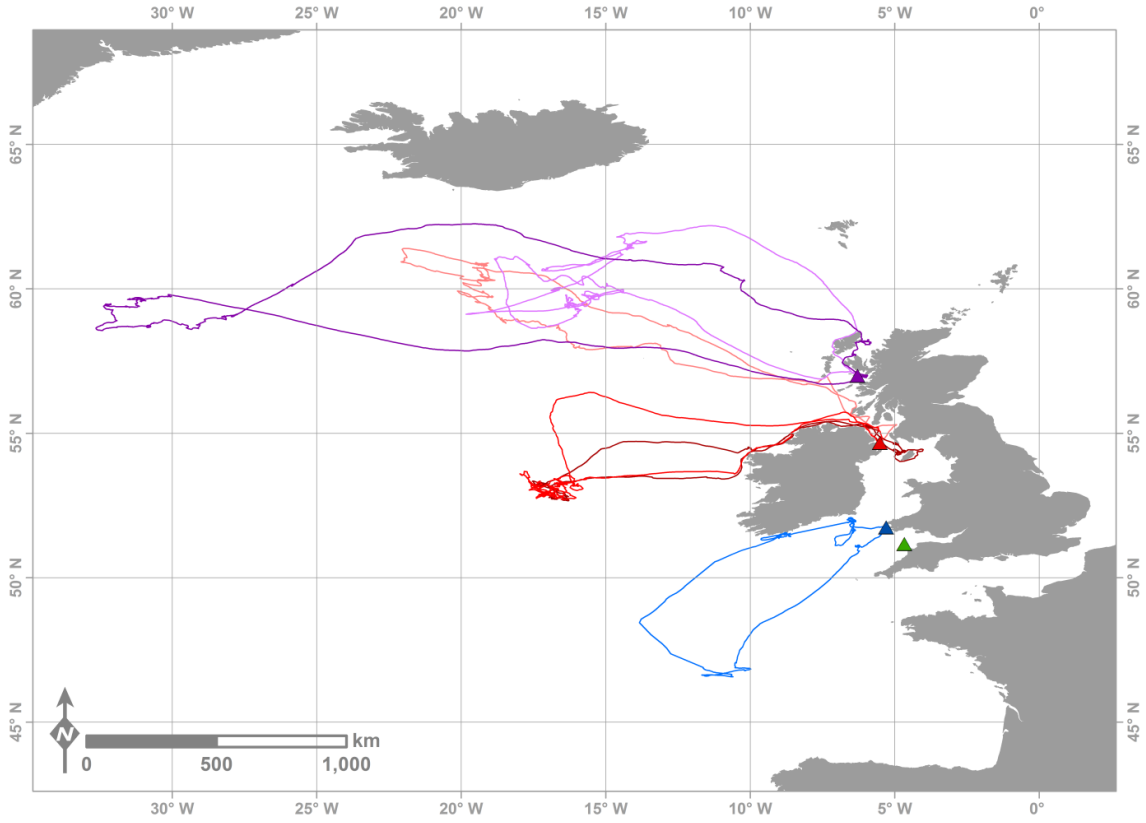

Figure S2. Six very long-range offshore trips into the Atlantic, two from Rum, three from Copeland and one from Skomer. These were excluded from the analysis as outliers because they (i) probably represent a different kind of rare foraging event, and (ii) for practical reasons they would distort the analyses.

Table S1. Average trip metrics for foraging trips recorded from each colony in each period of each year: Median (IQR) track length, maximum range from colony, duration and distance covered per day; and mean (± SD) scale of ARS.

		2009		2010		2011		Overall	
		Inc.	Rear.	Inc.	Rear.	Inc.	Rear.	Inc.	Rear.
Rum 120,000 pairs	track (km)	-	-	-	**2789** (152-421)	-	**177** (120-228)	-	**184** (128-274)
	range (km)	-	-	-	**64** (30-108)	-	**32** (26-63)	-	**35** (29-72)
	dur (d)	-	-	-	**1** (1-2)	-	**1** (1-1)	-	**1** (1-1)
	Km day^{-1}	-	-	-	**202** (145-275)	-	**160** (120-225)	-	**179** (128-226)
	scale ARS (km)	-	-	-	**18.3** ± 9.8	-	**14.5** ± 5.7	-	**15.8** ± 7.5
Copeland 4,633 pairs	track (km)	**536** (329-737)	**257** (128-465)	**978** (329-1307)	**836** (608-1240)	**1604** (1281-2014)	**179** (92-335)	**1058** (522-1558)	**255** (129-548)
	range (km)	**93** (66-120)	**73** (34-94)	**118** (92-124)	**124** (95-140)	**156** (141-182)	**42** (25-61)	**120** (88-154)	**56** (27-93)
	dur (d)	**5** (4-7)	**1** (1-2)	**7** (4-9)	**4** (3-6)	**9** (8-10)	**1** (1-2)	**7** (5-9)	**1** (1-3)
	Km day^{-1}	**108** (78-128)	**174** (146-258)	**131** (116-158)	**206** (183-228)	**178** (165-202)	**145** (87-187)	**139** (114-171)	**169** (120-206)
	scale ARS (km)	**17.6** ± 7.1	**15.4** ± 5.5	**22.4** ± 10.8	**19.8** ± 7.5	**25.2** ± 7.5	**17.7** ± 7.6	**21.6** ± 8.9	**17.7** ± 7.2
Skomer 316,000 pairs	track (km)	**808** (628-1018)	**320** (263-563)	**1412** (1006-1713)	**263** (187-516)	**1983** (1475-2295)	**307** (209-821)	**1517** (925-2117)	**297** (203-581)
	range (km)	**194** (165-219)	**83** (57-141)	**254** (153-274)	**79** (63-105)	**285** (263-350)	**110** (64-205)	**254** (176-295)	**86** (61-134)
	dur (d)	**6** (4.5-8)	**1** (1-2)	**8** (7-10)	**1** (1-2)	**10** (7.5-11)	**1** (1-4)	**8** (7-11)	**1** (1-2)
	Km day^{-1}	**136** (109-165)	**262** (208-290)	**177** (162-194)	**218** (177-254)	**203** (181-227)	**224** (186-255)	**180** (165-219)	**223** (186-259)
	scale ARS (km)	**20.6** ± 11.7	**17.0** ± 5.1	**27.1** ± 11.3	**18.0** ± 8.0	**28.5** ± 12.1	**20.7** ± 8.6	**26.0** ± 11.8	**18.6** ± 7.8
Lundy 1,100 pairs	track (km)	-	**726** (379-1174)	-	**263** (180-456)	-	**272** (133-425)	-	**305** (169-592)
	range (km)	-	**48** (33-111)	-	**65** (46-113)	-	**28** (22-72)	-	**49** (29-107)
	dur (d)	-	**4** (2-6)	-	**1** (1-2)	-	**2** (1-2)	-	**2** (1-3)
	Km day^{-1}	-	**179** (144-247)	-	**223** (171-279)	-	**153** (131-190)	-	**181** (152-225)
	scale ARS (km)	-	**20.7** ± 8.9	-	**17.9** ± 5.4	-	**19.2** ± 3.9	-	**19.3** ± 6.2

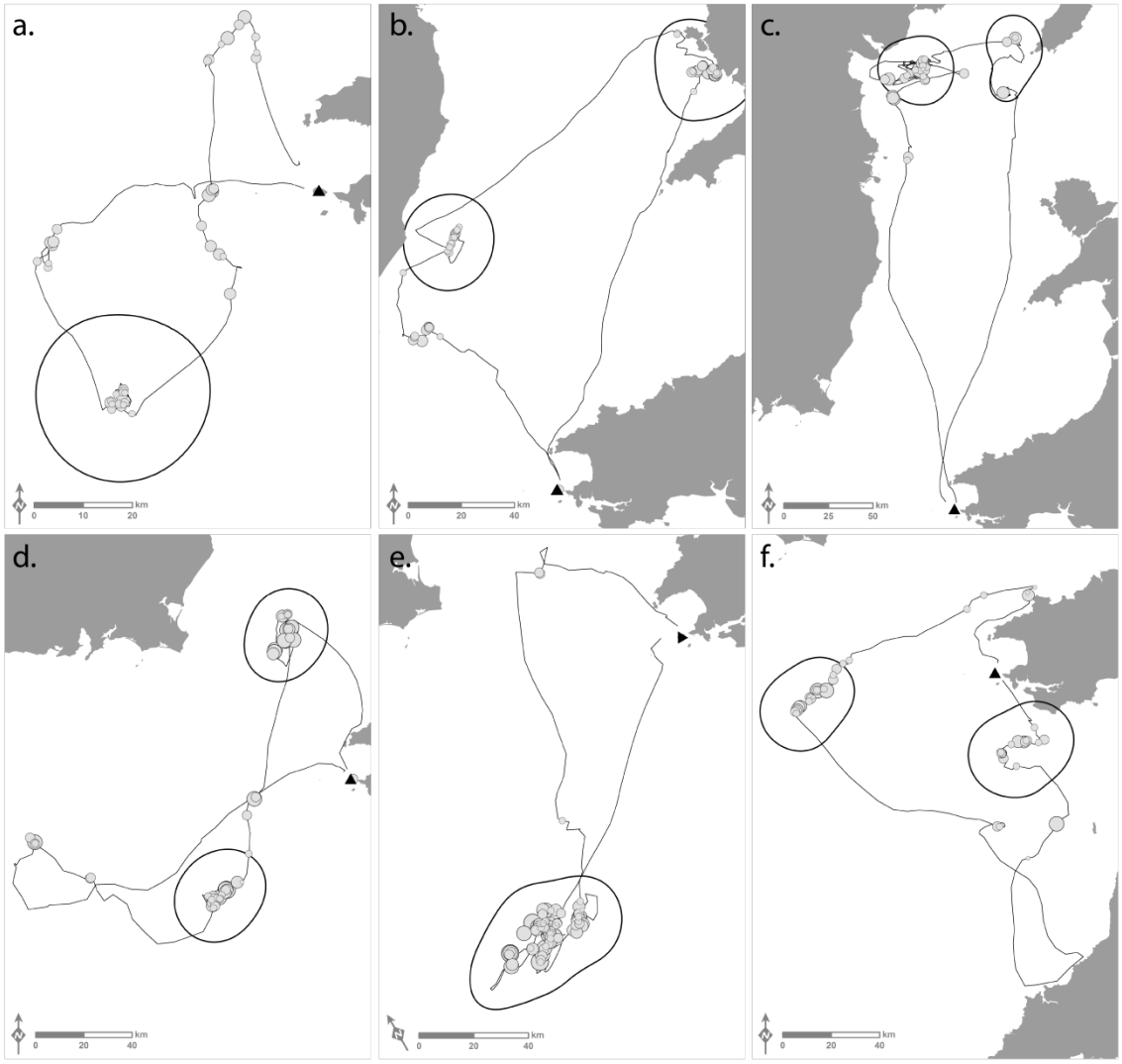

Figure S3. Validation of the FPT kernel density mapping as representation of actual foraging attempts (dives). Example comparisons of 95% kernel density contours (calculated using locations identified as ARS based on FPT) and the locations of diving activity for 4 of the 25 birds simultaneously carrying GPS, geolocator-immersion loggers and TDRs.

Table S2. Validation of kernel density mapping as representation of actual foraging attempts (dives). For each bird carrying a TDR, the percentage of dives and time submerged falling within the 95% contour. Superscripts reference examples birds in figure S3.

Bird	Time submerged (s)	N. dives	FPT T sub (s)	FPT N. dives	% time submerged	% N. dives
1	2267	178	1535	128	67.7	71.9
2	1231	109	1231	109	100.0	100.0
3	1349	119	891	80	66.0	67.2
4	3910	311	3778	303	96.6	97.4
5	1419	147	907	93	63.9	63.3
6 [a]	**1934**	**121**	**379**	**33**	**19.6**	**27.3**
7	2517	204	2128	161	84.5	78.9
8	491	52	342	30	69.7	57.7
9	3062	331	2658	277	86.8	83.7
10	2742	229	2076	172	75.7	75.1
11 [b]	**1402**	**132**	**1068**	**98**	**76.2**	**74.2**
12	966	54	677	42	70.1	77.8
13	1438	123	1383	116	96.2	94.3
14 [c]	**699**	**61**	**495**	**50**	**70.8**	**82.0**
15	2087	144	1733	117	83.0	81.3
16	1147	115	1097	109	95.6	94.8
17 [d]	**2093**	**218**	**1745**	**177**	**83.4**	**81.2**
18	2503	179	2191	129	87.5	72.1
19	2777	221	1741	140	62.7	63.3
20	2278	217	2108	197	92.5	90.8
21	3529	172	2679	121	75.9	70.3
22 [e]	**3620**	**211**	**3569**	**204**	**98.6**	**96.7**
23	1973	118	1962	112	99.4	94.9
24	1787	201	1637	182	91.6	90.5
25 [f]	**1055**	**112**	**852**	**86**	**80.8**	**76.8**
Mean					**79.8**	**78.5**
±SD					**±17.4**	**±15.9**

Table S3. Spatial overlap of the foraging range of each colony with the other colonies tracked during the incubation periods. Percentage overlap shows the overlap of the colony in the row header with the colony in the column header, as a percentage of the total range of the colony in the row header.

		range km^2	% overlap w Skomer
2009	**Copeland**	8103	7.78
		range km^2	**% overlap w Copeland**
	Skomer	17112	3.69
		range km^2	**% overlap w Skomer**
2010	**Copeland**	13140	44.79
		range km^2	**% overlap w Copeland**
	Skomer	16843	34.94
		range km^2	**% overlap w Skomer**
2011	**Copeland**	20664	62.18
		range km^2	**% overlap w Copeland**
	Skomer	19844	64.75

Table S4. Spatial overlap of the foraging range of each colony with the other colonies tracked during the chick-rearing periods. Percentage overlap shows the overlap of the colony in the row header with the colony in the column header, as a percentage of the total range of the colony in the row header.

2009		**range km^2**	**% overlap w Skomer**	**% overlap w Lundy**	
	Copeland	9121	14.58	10.88	
		range km^2	**% overlap w Copeland**	**% overlap w Lundy**	
	Skomer	17984	7.39	20.38	
		range km^2	**% overlap w Copeland**	**% overlap w Skomer**	
	Lundy	8101	12.25	45.24	
2010		**range km^2**	**% overlap w Copeland**	**% overlap w Skomer**	**% overlap w Lundy**
	Rum	12723	23.04	28.70	13.08
		range km^2	**% overlap w Rum**	**% overlap w Skomer**	**% overlap w Lundy**
	Copeland	13034	22.49	27.15	18.50
		range km^2	**% overlap w Rum**	**% overlap w Copeland**	**% overlap w Lundy**
	Skomer	27856	13.11	12.70	18.93
		range km^2	**% overlap w Rum**	**% overlap w Copeland**	**% overlap w Skomer**
	Lundy	13169	12.63	18.31	40.05
2011		**range km^2**	**% overlap w Copeland**	**% overlap w Skomer**	**% overlap w Lundy**
	Rum	13115	10.93	5.99	0.00
		range km^2	**% overlap w Rum**	**% overlap w Skomer**	**% overlap w Lundy**
	Copeland	12050	11.89	54.20	0.00
		range km^2	**% overlap w Rum**	**% overlap w Copeland**	**% overlap w Lundy**
	Skomer	28195	2.79	23.16	2.16
		range km^2	**% overlap w Rum**	**% overlap w Copeland**	**% overlap w Skomer**
	Lundy	7790	0.00	0.00	7.80

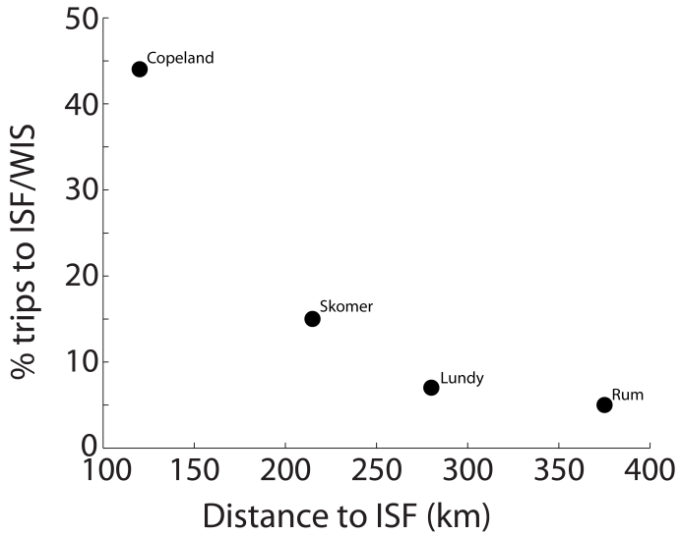

Figure S4. The percentage of foraging trips visiting the ISF/WIS area decreased monotonically with distance of the colony from the approximate position of the ISF.

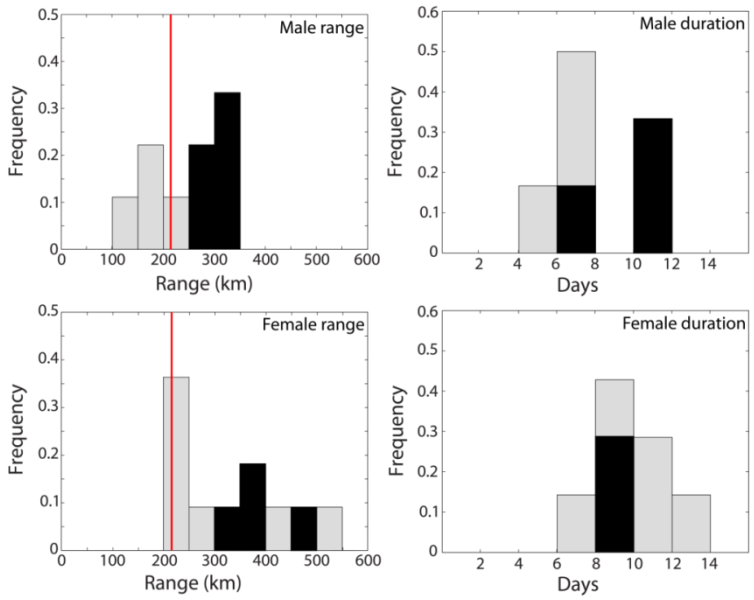

Figure S5. Frequency distributions of foraging trip range and duration for male and female birds from Skomer during the incubation period. Black bars represent trips made to the ISF/WIS, grey bars trips to other areas.

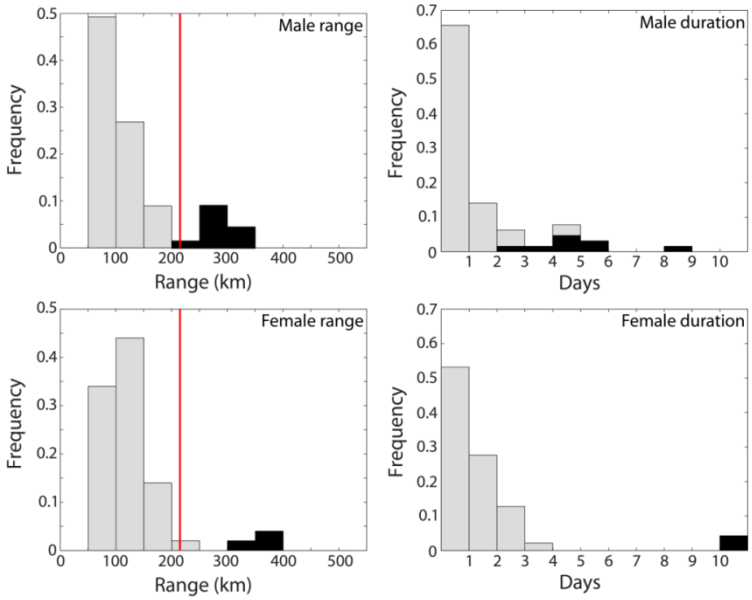

Figure S6. Frequency distributions of foraging trip range and duration for male and female birds from Skomer during the chick-rearing period. Black bars represent trips made to the ISF/WIS, grey bars trips to other areas.

Table S5. Median (and interquartile range) of trip range, duration and kilometres travelled per day for individual male and female birds from Skomer during incubation and chick-rearing.

	Male Incubation	**Female Incubation**	**Male Rearing**	**Female Rearing**
Range (km)	**243.7** (133 – 281)[1]	**289.7** (223 – 390)[1]	**108.3** (69 – 136)[4]	**96.1** (79 – 125)[4]
Duration (d)	**8** (7 – 11)[2]	**10.5** (10 – 11)[2]	**2** (1 – 3)[5]	**2** (1 – 2)[5]
Km day^{-1}	**157.9** (113 – 171)[3]	**182.4** (151 – 224)[3]	**208.8** (193 – 251)[6]	**233.1** (209 – 261)[6]

Wilcoxon rank-sums: [1](15) = 89, p = 0.11; [2](10) = 31, p = 0.23; [3](15) = 90, p = 0.093; [4]z(41) = 0.33, p = 0.74; [5]z(40) = 0.31, p = 0.76, [6]z(41) = 1.01, p = 0.31.

Visualisations (V1-V6) of daily foraging patterns (V1 incubation 2009; V2 incubation 2010; V3 incubation 2011; V4 chick-rearing 2009; V5 chick-rearing 2010; V6 chick-rearing 2011) can be found as mp4 format movies on the accompanying disk. Individual frames (days) from each visualisation are also provided as images on the accompanying disk.

Chapter 4

The diving behaviour of the Manx shearwater

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Abstract

Although shearwaters of the genus *Puffinus* morphologically are well adapted for swimming under water and while species in this group have long been known to engage in pursuit plunging and pursuit diving, little detailed information exists on the typical dive performance of these species. We successfully co-deployed miniature, high-sampling-rate TDRs alongside miniature Global Positioning System (GPS) loggers on a large sample of birds (32 individuals) during the chick-rearing period of three consecutive breeding seasons (2009-2011). These data provide the first insights into the diving behaviour of the Manx shearwater and the first large dataset providing detailed information on the diving behaviour of a *Puffinus* shearwater.

Diving was highly constrained to daylight and crepuscular hours, during which birds made 4.1 ±SD 1.6 dives per hour, most of which were in bouts of repeated diving activity. The mean of median depths reached for each bird was 5.7 ±SD 1.5 m and the mean median duration 12.9 ±SD 2.7 s. Shearwaters also made some much deeper dives. The mean maximum depth reached was 32.7 ±SD 8.2 m and the overall maximum depth reached by any bird was 55.5 m. Like other Puffinus shearwaters, the maximum diving depth was close to the allometric relationship between body mass and maximum diving depths previously calculated for penguins and alcids. However, few dives exceed 40-60 s duration, which may represent their aerobic dive limit. The diving performance of males and females was similar.

By linking diving information with the co-deployed GPS loggers, we demonstrate the fine-scale spatial distribution of diving for example birds. Most dives occurred in bouts of activity separated by periods of rest, aerial searching, or commuting to different foraging areas. Diving activity continued through the day, but peaked during the evening, possibly reflecting a foraging strategy that minimises the cost of carrying large payloads of food. Diving activity was widespread throughout the Irish and North Eastern Celtic Sea and the recorded distribution was

variable between years. Nevertheless, several areas of consistent high density diving activity were apparent and are likely to be of high conservation importance for Manx shearwaters.

Introduction

Many procellariiform seabirds perform foraging dives beneath the ocean to capture prey. The diving performance of different species varies greatly across the order. At one end, the albatrosses with long wings and light bodies are not structurally adapted for diving and typically perform shallow (<5m) dives (Prince, Huin & Weimerskirch 1994; Hedd *et al*. 1997). At the other extreme are the diving petrels (*Pelecanoides*), which are highly adapted for underwater pursuit of food by wing propulsion, reaching mean maximum depths of 25-39 m (Chastel 1994; Prince & Jones 1992; Zavalaga & Jahncke 1997; Bocher *et al.* 2000). Shearwaters of the genus *Puffinus* also possess several anatomical adaptations for swimming under water using their wings and feet for propulsion, including a robust sternum and pelvis, laterally compressed tarsi, flattened humeri and relatively short wings with high wing-loading (Wahram 1977; Brown, Bourne & Wahl 1978). From observations of foraging birds at sea, species in this group have long been known to engage in pursuit plunging and pursuit diving (King 1974; Jones 1975; Brown, Bourne & Wahl 1978; Brooke 1990). Studies using maximum depth gauges (Burger & Wilson 1988) or low-sampling rate archival pressure loggers have revealed a wide range of mean maximum diving depths for six different species of *Puffinus* shearwaters (5-58 m) (Weimerskirch & Sagar 1996; Weimerskirch & Cherel 1998; Keit *et al.* 2000; Burger 2001; Peck & Congdon 2006; Shaffer *et al.* 2009; Rayner *et al.* 2011). These maximum diving depths are typically allometrically scaled and clustered close to the allometric regression of maximum depths for penguins and alcids (Burger 1991; Burger 2001).

While studies using maximum depth gauges have provided a wealth of information on the maximum diving capabilities of many species of diving animal, they cannot provide detailed

information on the typical depths, durations, or profiles of dives. Neither can they provide information on dive frequency and temporal patterns of diving. The increasing miniaturisation of time-depth recorders (TDRs), which record time-series pressure (depth) data at high sampling frequencies, has made the collection of detailed data on diving behaviour possible for *Puffinus* shearwaters, which range in size from the little shearwater (*Puffinus assimilis* c. 240 g) to the great shearwater (*Puffinus gravis* c. 850 g). Yet, to date only two studies have made use of these devices to study the diving behaviour of the genus. Aguilar *et al*. (2003) presented preliminary data on the diving behaviour of a single Balearic shearwater (*Puffinus mauretanicus*), recorded at 4-s resolution, and Ronconi *et al.* (2010) presented detailed data on the diving behaviour of two female great shearwaters, recorded at 2-s resolution.

We report the first deployments of TDRs on the Manx shearwater *Puffinus puffinus*, a small-medium sized Puffinus shearwater (c. 400g) that breeds predominantly in colonies at remote locations off the west coasts of Britain and Ireland. During the chick-rearing period, parents make foraging trips to sea lasting from one to several days (Brooke 1990, Guilford *et al.* 2008; Gray & Hamer 2001), returning at night to provision their chick. While at sea, foraging birds make long distance movements (Guilford *et al.* 2008; Chapter 3), engaging in area-restricted search (Chapter 3) and frequent transitions between the air and the sea, including plunge and pursuit diving (King 1974; Jones 1975; Dean *et al.* 2012), using their wings and feet for propulsion (King 1974; Jones 1975; Brown *et al.* 1978). Much of their foraging behaviour occurs in large dense flocks (King 1974; Jones 1975; Stone *et al.* 1994). The primary type of prey recorded from regurgitates, crop and gizzard contents are Clupeid fish, but also some squid (Brooke 1990). However, no information exists on the typical depths to which foraging Manx shearwaters routinely dive, the maximum depths they are capable of reaching, the frequency with which they dive and how diving effort translates into foraging success. Yet, information on diving behaviour is critically important in understanding the foraging behaviour and movements of shearwaters at sea. In this study we co-deployed miniature, high-sampling-rate TDRs

alongside miniature Global Positioning System (GPS) loggers and geolocator-immersion loggers to provide detailed data on the diving behaviour of Manx shearwaters during the chick-rearing period of three consecutive breeding seasons.

Materials and Methods

Data loggers

Time-depth recorders were deployed on birds breeding on Skomer Island, Wales (Southern Irish Sea: 51°44'N, 5°17'W). Deployments were made on chick-rearing parents during July and August in three consecutive years: 2009, 2010 and 2011. All birds were simultaneously fitted with a CEFAS G5 time-depth recorder (TDR) and a global positioning system (GPS) logger (modified i-gotU GT-120: Mobile Action). Most birds also carried a British Antarctic Survey geolocator-immersion logger (data not used here). TDRs were configured to record pressure every 1-second, with a resolution of <0.1 m, for a maximum of seven days. TDRs were attached to the central four tail feathers using thin strips of tesa tape (as in Dean *et al.* 2012). GPS loggers were refitted with smaller batteries, configured to record locations every 5-20 minutes, sealed in heat-shrink plastic and attached dorsally using thin strips of tesa marine cloth tape underlying a small number of contour feathers (Guilford *et al.* 2008; Dean *et al*. 2012). Geolocator-immersion loggers were attached by two lightweight cable ties to a leg ring so as to be immersed when the bird was sitting on the sea surface. GPS weighed 10.2 -11.3 g. Geolocator-immersion loggers weighed 1.4g - 2.5 g and TDRs 2.7 g. The total mass of devices in each deployment was approximately 17.5-19 g. Breeding adults were taken from their burrows by hand through a purpose built inspection hatch. Birds were then weighed, devices deployed and birds returned to the burrow within 15 minutes. On return, birds were recaptured from the burrow, reweighed, and devices inspected. If the attachment had deteriorated such that it was likely to fail, or if the dive logger had stopped recording, the devices were removed and birds returned to the burrow

within 10 minutes. Tracked birds were sexed where possible by cloacal inspection shortly after egg laying, when females' cloacae typically appear bruised and swollen.

Analysis of dive logs

Data were downloaded from retrieved loggers using the supplied software and exported as time-series data (time-stamped pressure measurements at a 1-second recording interval). Recorded pressure values were converted to depth using the recommended conversion (10 Bar = 101971.621 millimetres of water at 4˚C) (CEFAS G5 Manual). The modal depth (representing the surface) was calculated and a zero offset value calculated as the difference between the modal depth and zero. Corrected depth values were then obtained by adding the zero offset to the measured depth values (figure 1a). By plotting depth as a function of time, dives could be seen as negative departures from zero. However, the depth logs also contained some noise, which may be recording error, or actuations of the pressure sensor by wave action or preening (figure 1b). Individual dive events were identified as deviations from zero greater than a threshold value of 1.5 m and lasting longer than 3 seconds (figure 1c). These thresholds were the minimum required to exclude erroneous identification of recorder noise as dives. For each dive we calculated the maximum depth reached, dive duration, descent and ascent rates, and the dive depth:duration ratio. Lower ratio values indicate more U-shaped dive profiles, with more time spent at depth, or more depth fluctuations. Higher ratio values indicate more V-shaped dives with little or no time spent at depth. We also calculated the post dive interval (PDI) as the number of seconds between the end of each dive and the beginning of the next. PDI was used to estimate the behavioural aerobic dive limit (bADL) as in Tremblay *et al.* (2005). Descent and ascent rates were calculated as the maximum depth divided by the time from the surface to maximum depth and from maximum depth to the surface respectively. They do not therefore represent actual swimming velocities.

Mapping of diving activity

We interpolated GPS tracks to 10-minute resolution using piecewise cubic hermite polynomials as in (Tremblay *et al*. 2006). For each interpolated track location we then summed the number of dives starting within each 10-minute interval centred on the GPS location. We then calculated the total number of bird hours recorded, the total number of dives recorded, and finally the number of dives per bird-hour, over a grid of 5 km^2 cells.

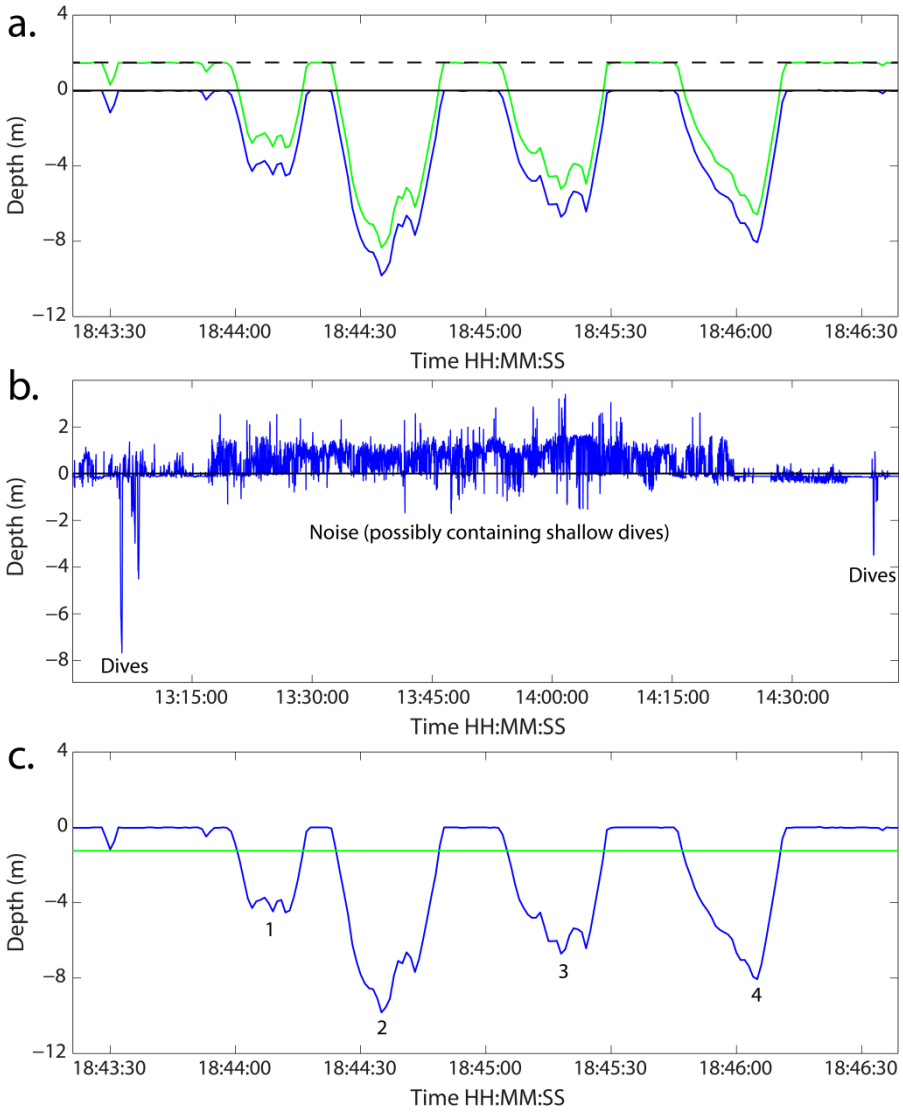

Figure 1. (a) Recorded depth values (corrected using the CEFAS correction factor) plotted as a function of time (shown in green) and the modal depth value (shown as a broken black line). The difference between the modal value (broken line) and the water surface (0 m shown as an unbroken black line) is the zero offset value. The corrected depth, shown in blue, is the sum of the recorded depth and the zero offset. (b) Example of noise in the dive log. (c) The corrected depth (shown in blue) and the dive ID threshold (1.5 m shown in green). Deviations from zero greater than the threshold and lasting longer than three seconds were identified as individual dives (e.g. numbered 1-4).

Results

We successfully deployed combined loggers on 18 birds in 2009 (5 males, 11 females, 2 unknown), nine in 2010 (4 males, 4 females, 1 unknown) and ten in 2011 (8 males and 2 females), The GPS was not recovered from one bird in 2009 (sex unknown). Deployments of loggers were short (median 3 days, interquartile range (IQR) 2-10 days), recording a median of 3 days (IQR 2-7) of diving activity over a median of 1 trip per deployment (IQR 1-2 trips). The mean departure mass was 420.6 ± 37 g and the combined device mass (17.5-19 g) comprised approximately 4.0-4.8% of body mass. The median recorded foraging trip was 1 day (interquartile range 1-3, range 1-8) after which tracked parents fed chicks a mean mass of 48.1 ± 20.7 g and during which parents net mass changed by -12.8 ± 15.5 g. Corrupted data from four TDRs (1 male in 2009, 2 males and 1 female in 2011) were discarded.

Diving behaviour

In total we recorded 7,417 dives during 122 bird days from 33 deployments: 3,004 dives in 53 days from 17 birds in 2009, 1,969 dives in 28 days from nine birds in 2010; and 2,444 dives in 41 days from seven birds in 2011 (Table 2). One female was tracked twice (once in 2009 and once in 2010) and the second deployment was excluded from statistical analyses. Plotting corrected depth as a function of time for individual birds shows the pattern and timing of diving (figure 2). In particular, diving was highly constrained to daylight hours. On inspection the rare dives made at night appeared to be mechanical actuations of the pressure sensor while the bird was on the colony, particularly during handling. Figure 3a & b shows detail from a bout of diving shown in figure 2b. Figure 3c shows detailed dives from figure 2c. For each dive in figure 3b and c we give the maximum depth, dive duration, descent rate, ascent rate and depth/duration in table 1.

Median dive depth and duration, mean descent rate, ascent rate and depth/duration, as well as maximum recorded dive depth and dive rate (dives daylight hour^{-1}) are given for each bird tracked in Table 2. Most dives made were towards the shallow end of each birds recorded depth

range: frequency distributions of dive depths were skewed towards shorter shallower dives, with longer deeper dives being made less frequently (figure 4a-c, table 3). Scatter plots of dive depth versus duration (figure 4) suggest a physical upper limit overall to the maximum depth that Manx shearwaters can reach per unit time: approximately 0.77 m per s total dive time. Mean descent rates (0.959 ± 0.064 m s^{-1}) were significantly slower than ascent rates (0.993 ± 0.066 m s^{-1}): Wilcoxon rank-sum z (62) = 2.15, p = 0.031. Dive duration increased linearly with dive depth, although the variation between individuals increased with depth (figure 5a). Descent rate increased with dive depth from 1-30 m, after which it plateaued (figure 5b). Ascent rate increased with dive depth from 1-20 m, after which it plateaued, then appeared to decrease with increasing dive depth beyond 30 m (figure 5c). Depth:duration ratio was lowest (indicating more U-shaped dives with time spent at depth) for shallow dives, and increased (progressively more V-shaped dives) with depth. Dives deeper than 30 m had similarly high ratios indicating that most dives deeper than 30 m were typically V-shaped (figure 5d). Behavioural ADL was estimated (as in Tremblay *et al.* 2005) as the dive duration at which the minimum PDI increases, indicated by the line joining the lower values in figure 6. Overall, this appeared to occur at approximately 40-60 s duration (figure 6a), but the relationship for individuals varied between approximately 20 and 60 s (figure 6b) with no clear differences between males and females. The maximum diving depth recorded (55.5 m) was similar (when scaled for body mass) to those recorded for several other Puffinus shearwaters and similar to the allometric relationship calculated by Burger (1991) for penguins and alcids (figure 7).

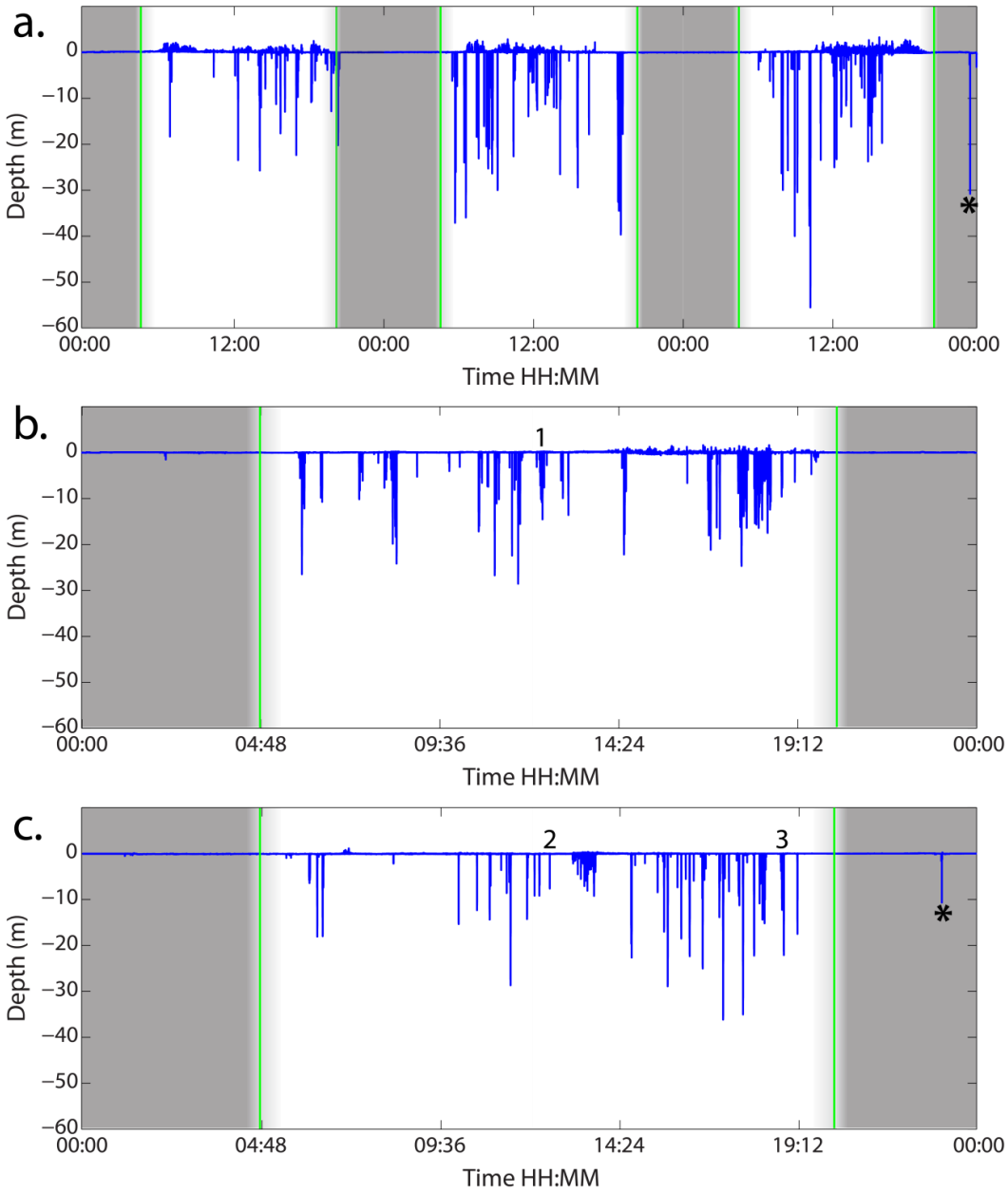

Figure 2. Example time-depth plots for three different birds. (a) shows diving behaviour during a three-day foraging trip. Time is given in GMT. (b & c) Show the diving behaviour of a paired male (b) and female (c) bird on one-day foraging trips made two days apart. The nocturnal 'dives' at the end of deployments (a) and (c) (marked *) were recorded during removal of the device. Vertical green lines show the timing of sunrise and sunset in the centre of the Irish Sea during the logging period. Number 1 in figure b indicates the bout of diving that can be seen in more detail in figure 3 b and c. Numbers 2 and 3 in c indicate the V and U-shaped dives shown in figure 3 c.

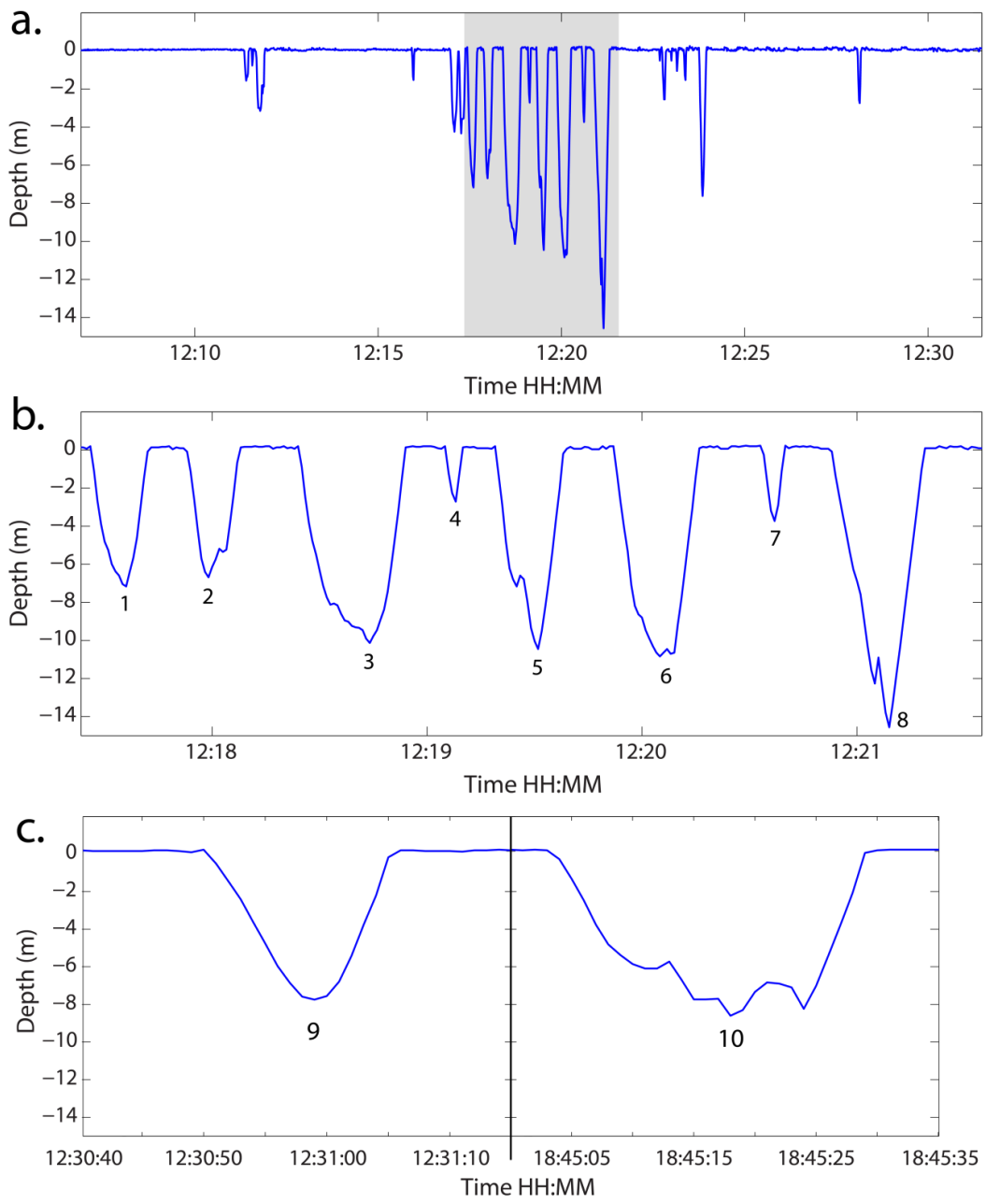

Figure 3. (a) Shows in greater detail a four-minute bout of dives (1 in figure 2 b) made by the male of the pair. The highlighted section is shown in greater detail in (b): a series of eight dives occurring during the bout. (c) shows two dives of similar depth, but different profile shapes (V versus U) made by the female of the pair (2 and 3 in figure 2 c). For the dives numbered 1-10 in (b) and (c) we give the depth, duration, descent and ascent rates and depth/duration in table 1. Time is given in GMT.

Table 1. Depth, duration, descent and ascent rates and depth/duration are given for each dive in figure 3. The descent and ascent rates for each dive are based on the duration of the entire descent to (or ascent from) maximum depth and therefore do not represent true swimming velocities.

Dive	Max. depth (m)	Duration (s)	Desc. Rate (m s^{-1})	Asc. Rate (m s^{-1})	Depth/dur (m s^{-1}).
1	7.2	16	0.72	1.19	0.450
2	6.7	15	1.11	0.74	0.467
3	10.1	30	0.51	1.01	0.337
4	2.7	5	0.90	1.36	0.540
5	10.5	20	0.87	1.31	0.525
6	10.8	24	0.83	0.99	0.450
7	3.7	7	0.93	1.24	0.529
8	14.6	26	0.91	1.46	0.562
9	7.65	16	0.85	1.09	0.478
10	8.38	26	0.59	0.69	0.322

Table 2. Number of days recorded for each bird tracked, the sex of each bird (M=male, F=female, U=unknown), and the average (mean ±SD or median and interquartile range) dive metrics recorded. One female (F*) was tracked twice – once in 2009 and once in 2010. Table continued overleaf.

Year	Sex	Days Rec.	N. Dives Rec.	Dives Daylight hr^{-1}	Median Depth (m)	Depth IQR	Median Duration (s)	Dur. IQR	Mean Desc. Rate ($m\ s^{-1}$)	Des. Rate SD	Mean Asc. Rate ($m\ s^{-1}$)	Asc. Rate SD	Mean Depth:Dur. ($m\ s^{-1}$)	Depth: Dur. SD	Max. Depth (m)
2009	**F**	2	126	3.7	3.5	2.5-6.8	11.0	6-17	0.87	0.33	0.94	0.30	0.4344	0.14	24.35
	F	1	119	7.0	7.4	3.9-11.8	16.0	9-25	0.96	0.29	1.02	0.29	0.4779	0.12	29.84
	F	7	149	1.3	4.4	2.3-8.1	11.0	6-20	0.95	0.34	0.91	0.31	0.4450	0.15	39.63
	F	1	106	6.2	5.7	2.2-10	12.0	6-21	0.95	0.27	0.99	0.25	0.4729	0.12	35.02
	F	1	89	5.2	4.7	3.3-6.7	10.0	7-15	0.95	0.26	1.04	0.31	0.4786	0.11	16.92
	F	2	121	3.6	5.4	3.0-9.7	11.0	7-19	1.00	0.30	1.04	0.30	0.4916	0.13	25.90
	F	2	221	6.5	5.2	3.0-8.8	12.0	7-20	0.95	0.28	0.92	0.27	0.4516	0.11	39.25
	F	7	180	1.5	4.7	2.4-9.0	10.0	6-18	1.00	0.32	1.02	0.27	0.4904	0.13	36.00
	F	2	110	3.2	6.9	3.8-11.4	14.0	9-23	1.08	0.31	1.03	0.32	0.5131	0.14	25.28
	F*	2	109	3.2	6.2	3.1-10.0	14.0	7-19	0.97	0.30	1.14	0.32	0.5060	0.13	25.58
	F	3	190	3.7	5.7	3.4-9.0	14.0	8-22	0.89	0.32	0.98	0.34	0.4436	0.14	39.54
	M	2	172	5.1	6.2	3.0-10.0	13.0	7-23	1.00	0.28	1.00	0.26	0.4832	0.12	24.47
	M	1	135	7.9	7.4	3.6-11.9	15.0	8-26	0.95	0.27	1.01	0.26	0.4766	0.11	26.74
	M	1	88	5.2	6.0	3.4-9.9	16.0	8-23	0.98	0.34	1.02	0.31	0.4812	0.15	34.93
	M	5	299	3.5	5.8	3.3-9.5	14.0	8-21	0.94	0.32	1.01	0.31	0.4689	0.13	28.27
	U	7	412	3.5	4.0	2.4-7.0	9.0	6-16	0.95	0.31	0.92	0.26	0.4475	0.12	25.36
	U	7	378	3.2	5.7	3.1-9.8	12.0	7-19	0.99	0.33	1.08	0.30	0.5019	0.14	32.54

Table 2. Continued.

Year	Sex	Days Rec.	N. Dives Rec.	Dives Daylight hr^{-1}	Median Depth (m)	Depth IQR	Median Duration (s)	Dur. IQR	Mean Desc. Rate ($m\ s^{-1}$)	Des. Rate SD	Mean Asc. Rate ($m\ s^{-1}$)	Asc. Rate SD	Mean Depth:Dur. ($m\ s^{-1}$)	Depth: Dur. SD	Max. Depth (m)
2010	**F**	3	216	4.2	4.3	2.7-6.8	10.0	7-16	0.91	0.30	0.97	0.28	0.4526	0.12	28.68
	F	1	114	6.7	9.5	6.0-14.5	18.0	14-25	1.01	0.28	1.07	0.22	0.5093	0.11	28.55
	F*	3	182	3.6	4.5	2.7-7.1	10.0	6-16	0.91	0.29	1.05	0.32	0.4685	0.13	26.48
	F	2	115	3.4	4.9	2.7-9.1	10.0	6-18	1.06	0.32	1.08	0.28	0.5252	0.13	30.50
	M	7	584	4.9	4.3	2.4-7.9	9.0	5-17	0.99	0.29	1.04	0.27	0.4957	0.12	42.38
	M	3	208	4.1	6.8	3.7-14.0	14.5	8-27	1.03	0.29	1.02	0.26	0.4994	0.12	55.51
	M	3	183	3.6	9.6	4.6-16.5	19.0	10-31	1.07	0.31	1.04	0.23	0.5140	0.11	41.80
	M	3	210	4.1	5.7	3.7-9.3	16.0	9-21	0.89	0.30	0.96	0.32	0.4420	0.13	31.36
	U	3	157	3.1	6.7	3.2-15	14.5	7-27	1.09	0.32	1.08	0.25	0.5295	0.13	39.58
2011	**F**	7	731	6.1	4.6	2.1-10.5	11.0	5-23	0.93	0.26	0.96	0.23	0.4607	0.10	44.29
	M	4	301	4.4	7.6	4.1-12.3	17.0	10-26	0.95	0.28	0.98	0.29	0.4640	0.12	36.83
	M	2	119	3.5	3.3	2.2-8.2	10.0	5-16	0.91	0.29	0.97	0.32	0.4507	0.14	18.80
	M	7	231	1.9	5.3	2.6-8.4	12.0	7-20	0.86	0.27	0.91	0.26	0.4245	0.11	32.75
	M	7	376	3.2	4.7	2.7-9.2	13.0	7-23	0.86	0.32	0.89	0.28	0.4197	0.13	33.84
	M	7	316	2.7	5.2	2.7-9.8	15.0	8-24	0.85	0.30	0.86	0.28	0.4085	0.13	44.94
	M	7	370	3.1	4.2	2.4-7.8	11.0	6-18	0.91	0.29	0.89	0.27	0.4309	0.12	29.26
Mean (±SD)		**3.7 ±2.4**	**226.1 ±148.0**	**4.1 ±1.6**	**5.7 ±1.5**	-	**12.9 ±2.7**	-	**0.96 ±0.06**	-	**0.99 ±0.07**	-	**0.47 ±0.03**	-	**32.8 ±8.2 Max. 55.5**

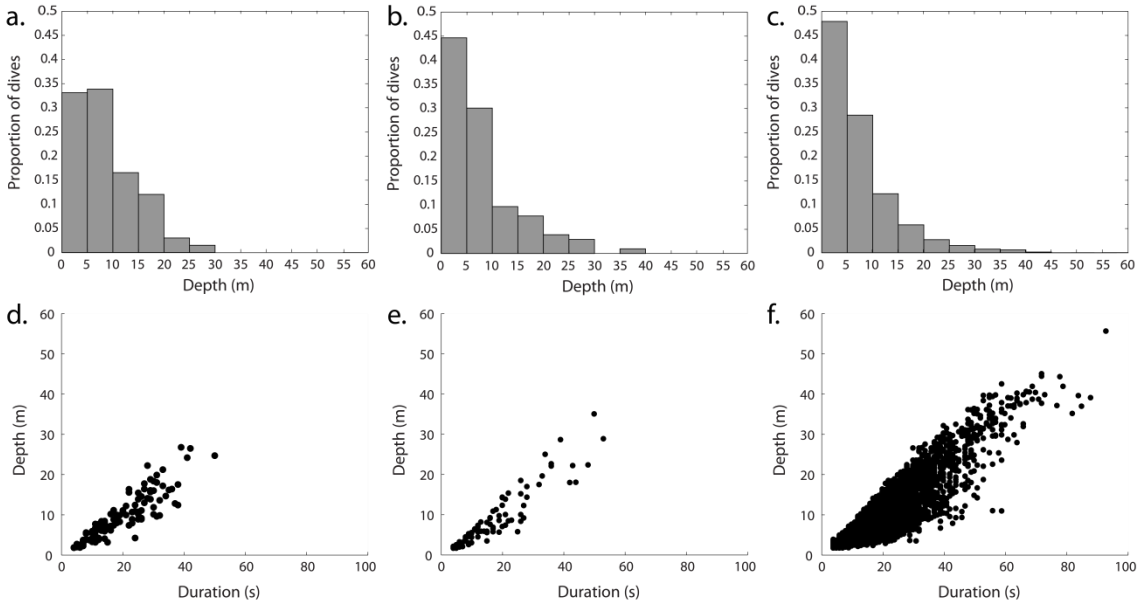

Figure 4. Frequency distributions (a-c) of dive depth and scatter plots of dive depth versus duration (d-f) for (a & d) the male bird featured in figure 2 b, (b & e) the female bird featured in figure 2 c, and (c & f) all recorded dives in this study. The upper edge to the point cloud in scatter plot (f) suggests a physical upper limit overall to the maximum depth that can be reached per unit time (approximately 0.77 m per s total dive time) with most dives falling well below this.

Table 3. Percentiles of all recorded dive depths and durations.

Percentile	**10**	**20**	**30**	**40**	**50**	**60**	**70**	**80**	**90**	**100**
Depth (m)	≤1.9	≤2.4	≤3.2	≤4.1	≤5.3	≤6.6	≤8.5	≤11.1	≤16.0	≤55.5
Duration (s)	4	≤6	≤8	≤10	≤12	≤15	≤19	≤23	≤31	≤93

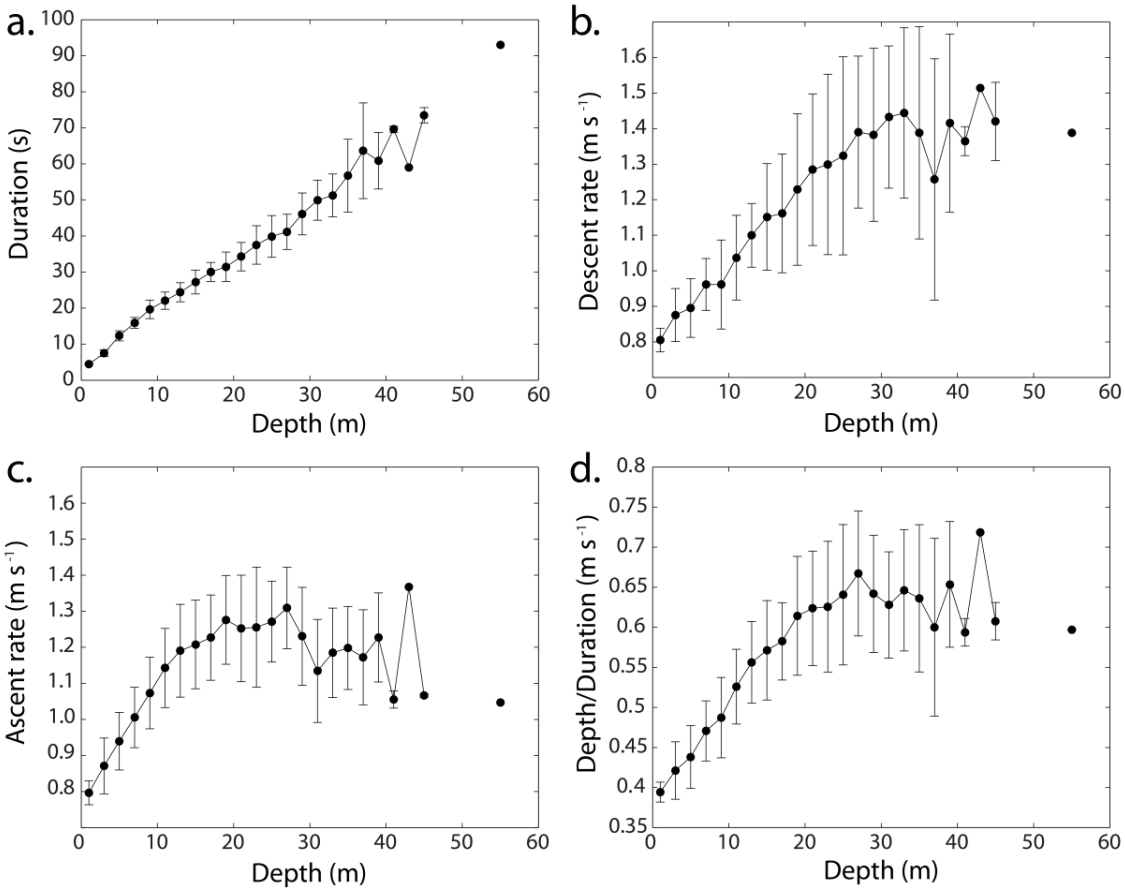

Figure 5. Changes in dive duration (a) descent (b) and ascent (c) rates, and depth:duration ratio (d) with dive depth (2 m bins). Points represent the mean ±SD (bars) of individual bird means in each 2 m bin. Dive duration increased linearly with dive depth, while descent and ascent rates and depth:duration ratios increased with depth until around 30 m, after which they plateaued or decreased (ascent rate).

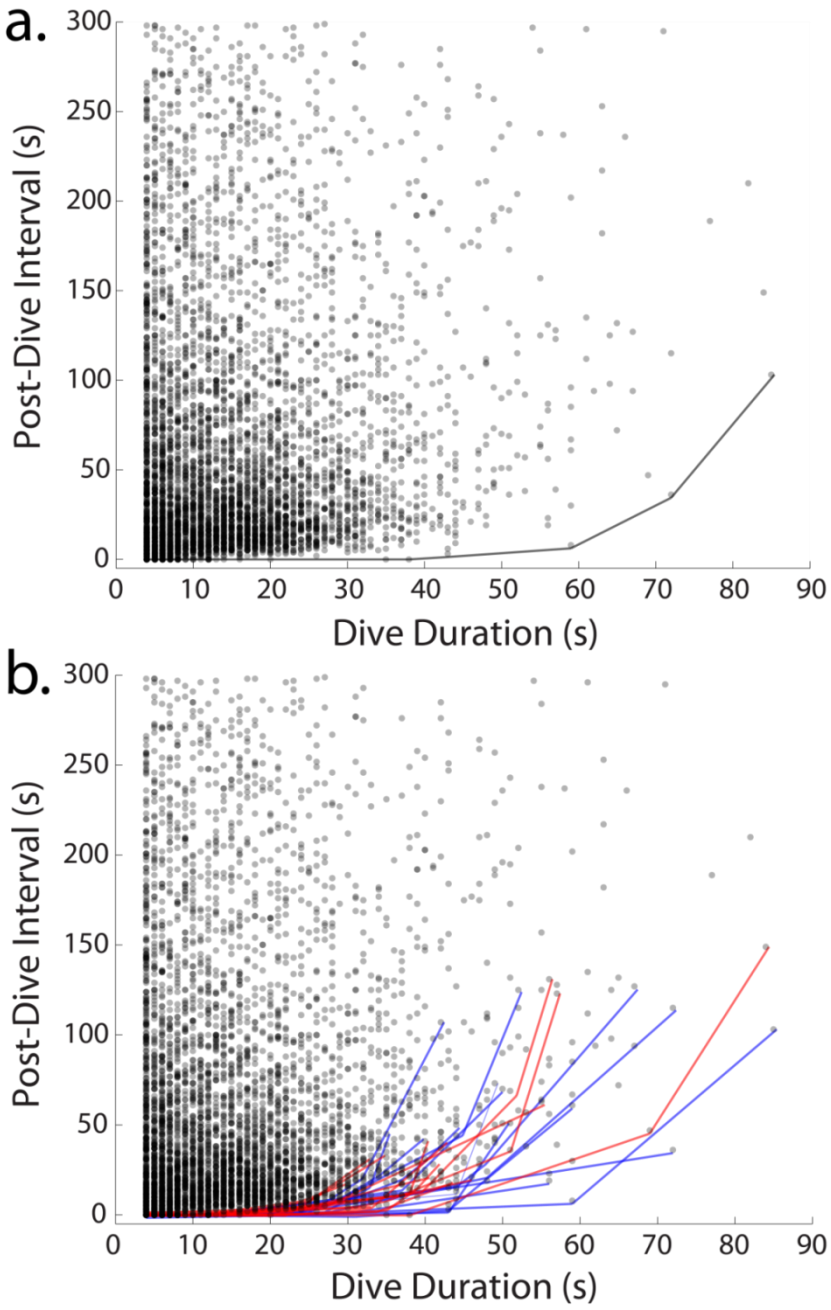

Figure 6. The relationship between dive duration and post-dive interval (PDI) for all dives recorded in this study. PDI is truncated here at 300s. The slope change in the line joining the lowest values of PDI theoretically defines the behavioural aerobic dive limit (bADL). Overall this was estimated to be approximately 40-60 s (a), but the relationship for individuals varied between 20-60s (b) with no clear differences between males (blue) and females (red). Dives lasting less than the bADL should be entirely aerobic, dives lasting beyond the bADL should be increasingly anaerobic.

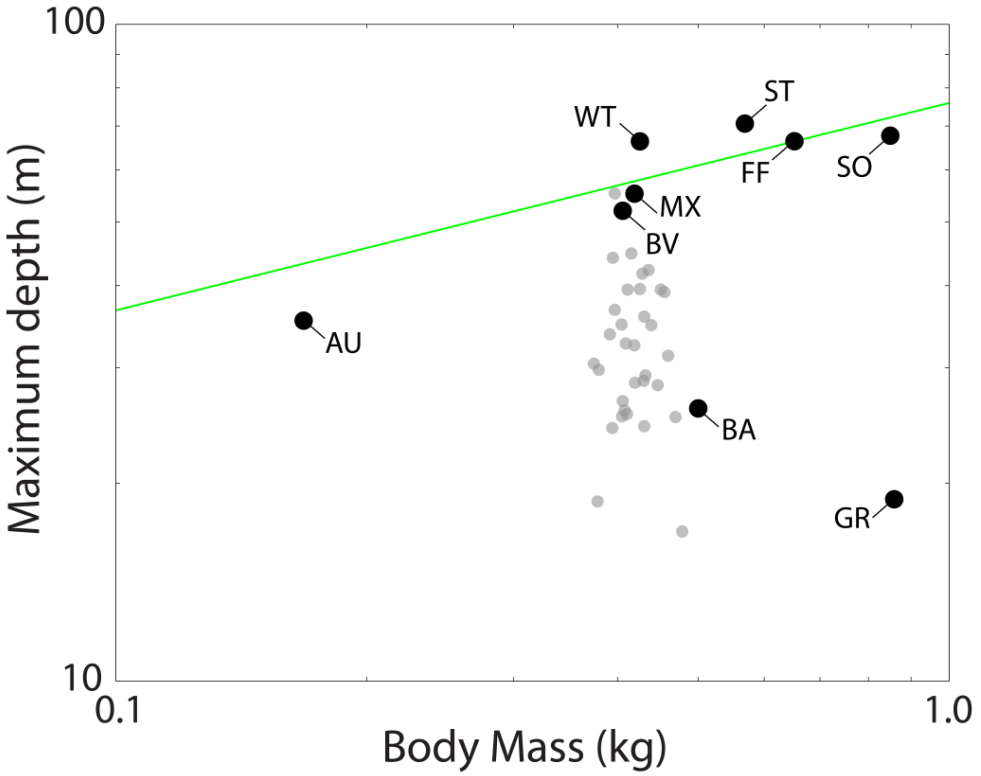

Figure 7. Log-log plot of maximum recorded diving depths against body mass reconstructed from the data in Burger (2001) comparing five species of *Puffinus* shearwaters from studies using maximum depth gauges: Wedge-tailed *Puffinus pacificus* (WT) and Audobon's *Puffinus lherminieri* (AU) shearwaters (Burger 2001); Black-vented *Puffinus opisthomels* (BV) (Keitt *et al*. 2000); Sooty *Puffinus griseus* (SO) (Weimerskirch & Sagar 1996; Shaffer *et al.* 2009); Short-tailed *Puffinus paciftenuirostris* (ST) (Weimerskirch & Cherel 1998). Added to the plot are data from a study of three Flesh-footed shearwaters *Puffinus carneipes* (FF) using low sampling rate pressure loggers (Rayner *et al*. 2011) and from two studies using higher sampling rate TDRs on a single Balearic shearwater (BA) (Aguilar *et al*. 2003) and on two female Great shearwaters (GR) (Ronconi *et al*. 2010). Our data for Manx shearwaters (MX) are also shown (Maximum recorded depth and average body mass). Grey points indicate the maximum depth-body mass relationships for each of the individual birds tracked in this study. The green line represents the allometric equation derived by Burger (1991) from maximum diving depths of penguins and alcids: $mD = 75.905*M^{0.316}$ where mD is maximum depth (m) and M is mass (kg).

The mean mass of males tracked in this study (419.3 ± 23.5 g) was not significantly different to the mass of females (419.3 ± 31.8 g) two sample t test t (27) = 0.001, p = 0.999. Diving frequency (dives daylight hour^{-1}) was not significantly different between males (4.08 ± 1.4

dives hr^{-1}) and females (4.38 ± 1.8 dives hr^{-1}): Wilcoxon rank-sum *z* (27) = 0.59, p = 0.56. The median and maximum dive depths were similar for males (5.87 ± 1.6 m and 34.4 ± 9.4 m) and females (5.54 ± 1.5 and 31.29 ± 7.44): Wilcoxon rank-sum *z* (27) = 0.74 and 0.85, p = 0.46 and 0.39. The median duration of dives was similar for males (13.9 ± 2.8 s) and females (12.3 ± 2.4 s): Wilcoxon rank-sum *z* (27) = 1.67, p = 0.095. Mean descent and ascent rates of males (0.942 ± 0.066 m s^{-1} and 0.970 ± 0.062 m s^{-1}) and females (0.966 ± 0.06 m s^{-1} and 1.006 ± 0.064 m s^{-1}) were also similar: Wilcoxon rank-sum *z* (27) = 1.07 and 1.33, p = 0.28 and 0.18. The ratio of dive depth and duration: was also similar for males (0.461 ± 0.033) and females (0.477 ± 0.029): Wilcoxon rank-sum *z* (27) = 1.20, p = 0.23.

Regressions of mean body mass on each of the calculated dive metrics indicated that diving performance was not significantly related to body mass. We found that body mass explained only small percentages of variation in dive performance metrics and none of the relationships was significant (figure 8). For the small number (n = 7) of individual foraging trips where we were able to calculate the total mass gain (total fed to chick plus the adult's net gain), total mass gain (g day^{-1}) roughly increased with each of the dive metrics, although only the relationship with ascent rate was significant, explaining approximately 85% of variation in total mass gain, P = 0.033.

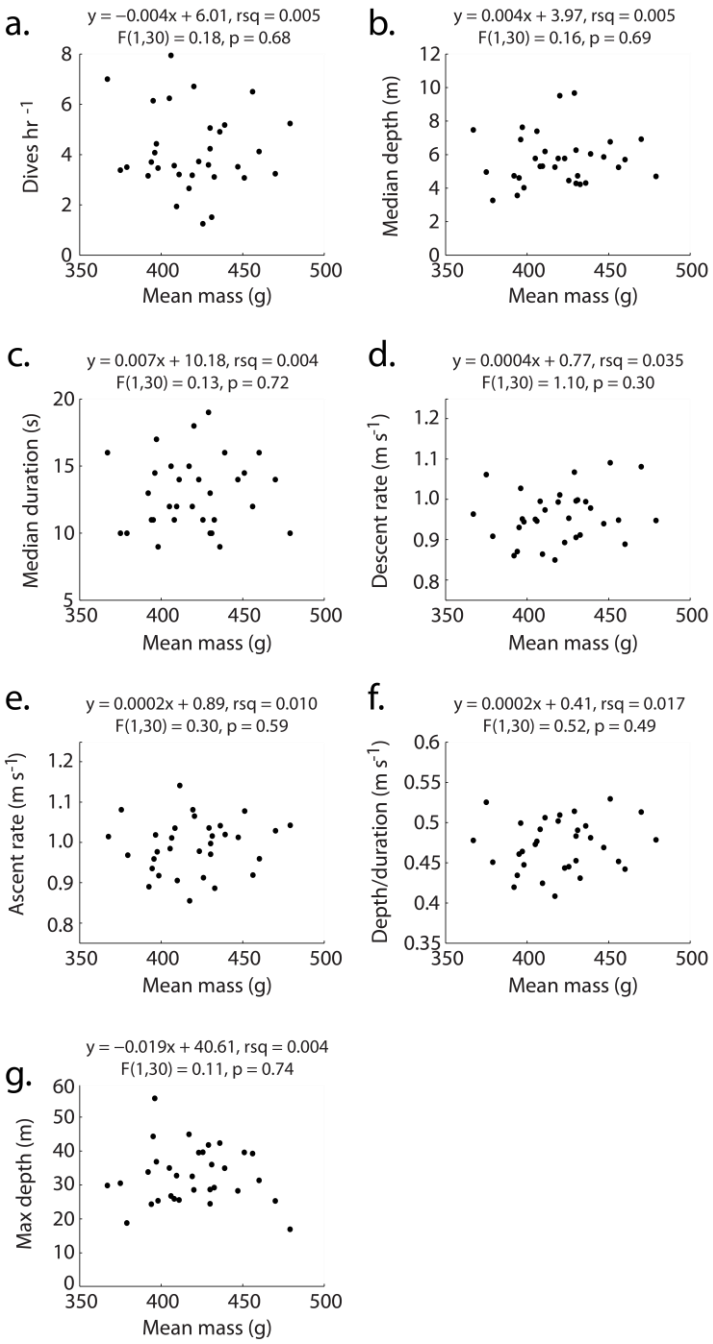

Figure 8. The relationship between birds' mean body mass and several measures of dive performance: (a) Dive rate (dives hr^{-1}), (b) Median dive depth, (c) Maximum dive depth, (d) Median dive duration, (e) Mean descent rate, (f) Mean ascent rate, (g) Mean depth/duration. The linear regression line, equation, r^2, F and p values are given. Body mass explained only small percentages of variation in dive performance metrics and none of the relationships was significant.

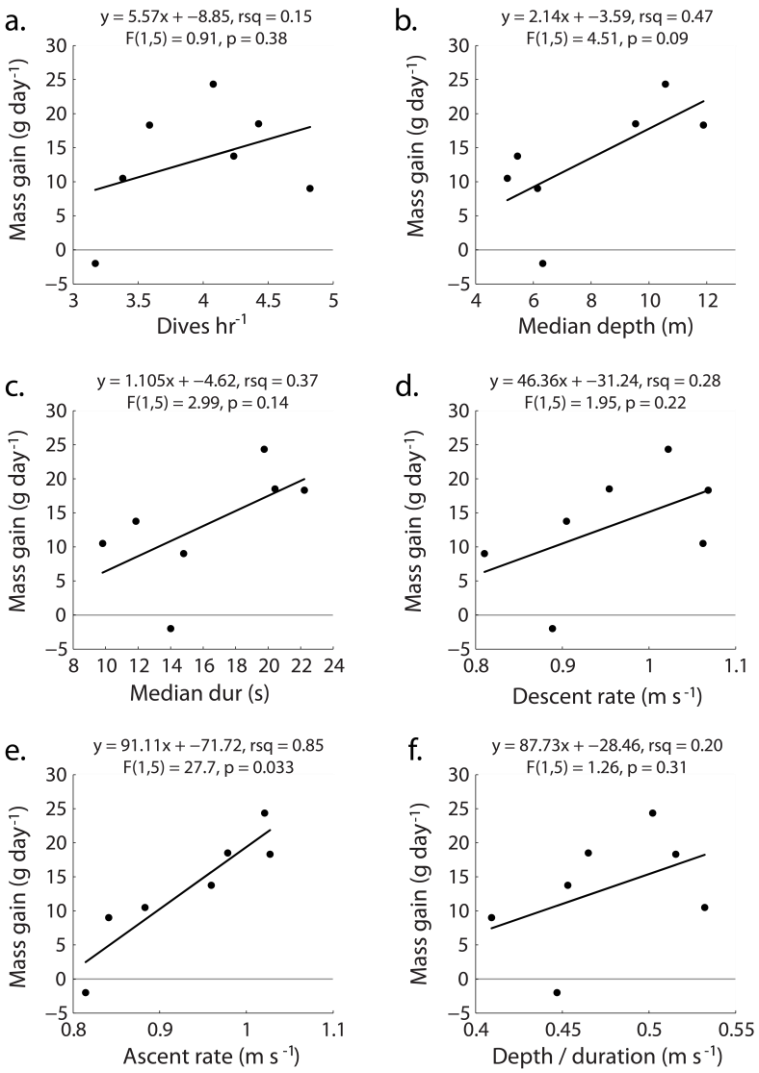

Figure 9. The relationship between total mass gain (g day^{-1}) and several measures of dive performance: (a) Dive rate (dives hr^{-1}), (b) Median dive depth, (c) Median dive duration, (d) Mean descent rate, (e) Mean ascent rate, (f) Mean depth/duration. The linear regression line, equation, r^2, F and p values are given. Total mass gain (g day^{-1}) roughly increased with each of the parameters, although only ascent rate was significant, explaining approximately 85% of variation in total mass gain, P=0.033.

Temporal pattern of diving behaviour

To look at the average temporal distribution of diving behaviour, we calculated the median (±IQR) (across individuals) proportion of all dives, median dive depth, maximum dive depth, median duration, descent and ascent rates and depth:duration ratios that occurred in each

hour of the day (figure 10). These results confirm that on average, diving activity commenced and increased rapidly at first light (figure 10a). Diving activity continued throughout the day, reaching a peak at around 17:00 - 18:00 GMT, before rapidly decreasing at sunset. Median dive depth, duration, descent and ascent rate and depth:duration ratio were relatively stable throughout the daylight hours. Maximum dive depth increased through the morning, was deepest in the afternoon and decreased rapidly prior to sunset.

Spatial distribution of diving behaviour

Diving typically occurred in bouts of high-intensity activity lasting 5-20 minutes and separated by periods of no, or infrequent dives (figures 2 and 3). Spatially, this typically could be seen as periods of high-intensity diving activity within spatially restricted areas (figure 11), separated by periods that are likely to be commuting flight between foraging locations, or rest. However, some brief periods of diving occurred along relatively linear sections of the birds tracks (figure 11). Grid maps of diving intensity (number of dives recorded per hour of bird activity figure 12) show that diving behaviour was widespread within the Irish and Celtic Seas and variable between years (or perhaps between birds tracked in each year). Several areas of high diving activity could be seen in each year, with some areas showing consistently high diving activity between years: in particular, the western Irish Sea and the location of the Western Irish Sea Front, coastal areas of St Cardigan Bay, the southwest coast of Anglesey, southwest of the LLyn Peninsular and the waters within 100 km of Skomer. The intermediate maps used to calculate dives bird-hr^{-1} (number of recorded bird hours and number of recorded dives) are shown in the Supplementary Material (figures S1 and S2).

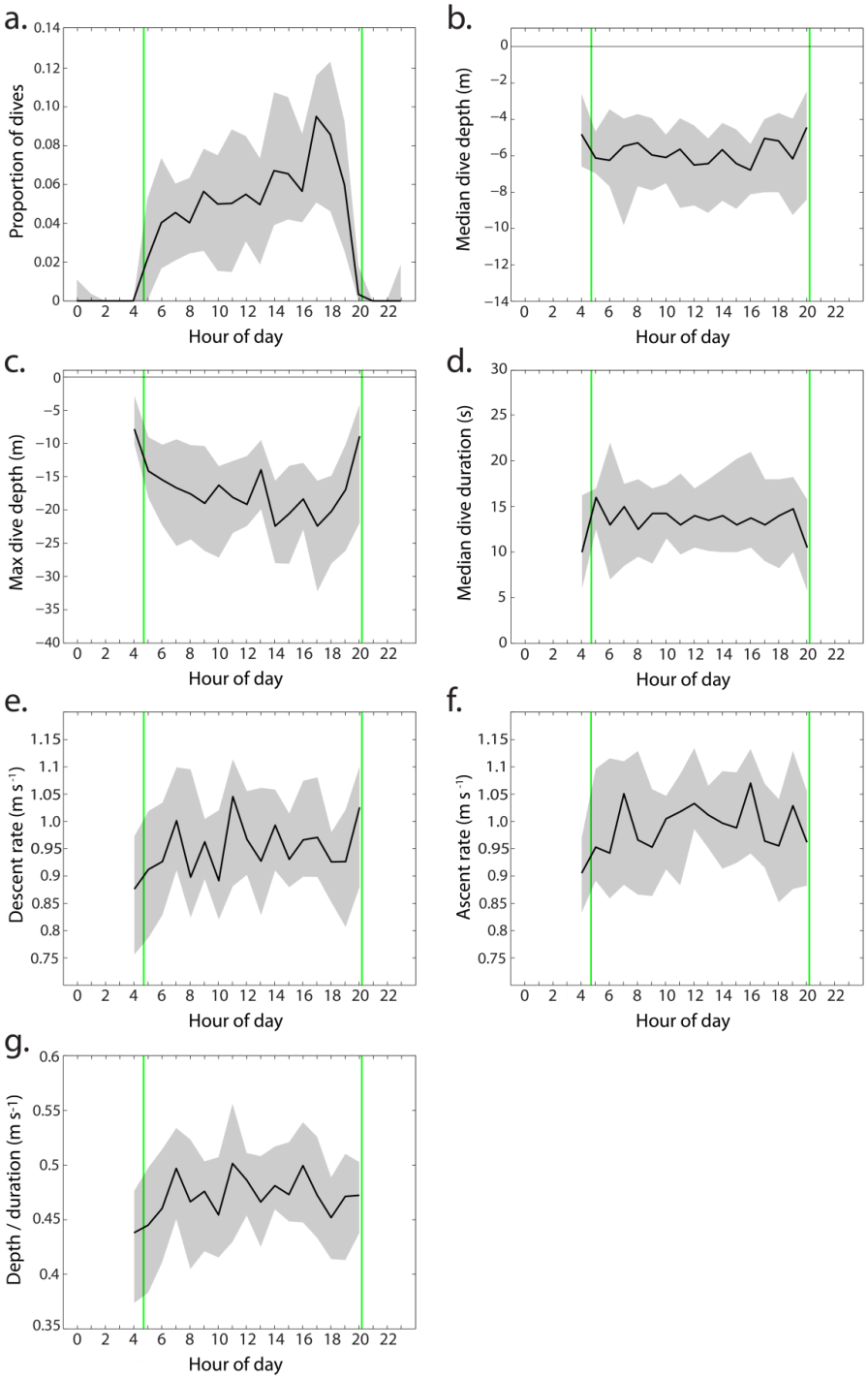

Figure 10. The average (median ± interquartile range) timing (GMT) of diving behaviour for all birds: (a) proportion of all dives that occurred in each hour of the day, (b) median dive depth, (c) maximum dive depth, (d) median dive duration, (e) descent rate, (f) ascent rate, (g) depth/duration. Vertical green lines show the timing of sunrise and sunset in the centre of the Irish Sea during the logging period.

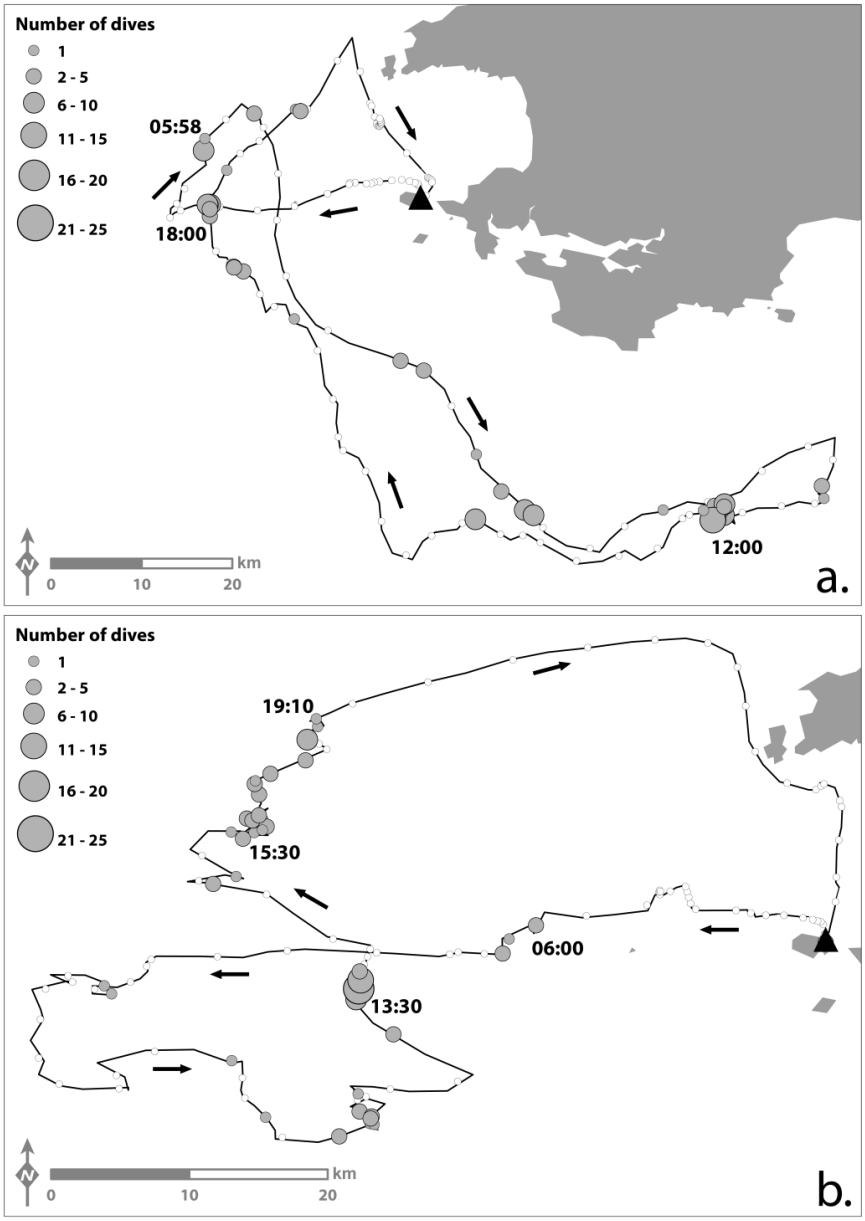

Figure 11. Number of dives within 10-minute segments of GPS tracks for the two birds featured in figure 3b and c. Figure 7a corresponds to the dive profile for the male bird in figure 3b (and detailed in figure 4). Figure 7b corresponds to the dive profile for the female bird in figure 3c. GPS locations where dives occurred are coloured grey, scaled according to the total number of dives made. Locations where no dives occurred are indicated by small open circles. Arrows indicate the direction of travel and time labels indicate the timing (GMT) of some diving bouts for comparison with figure 3b and c. The location of the colony on Skomer Island is indicated by a black triangle.

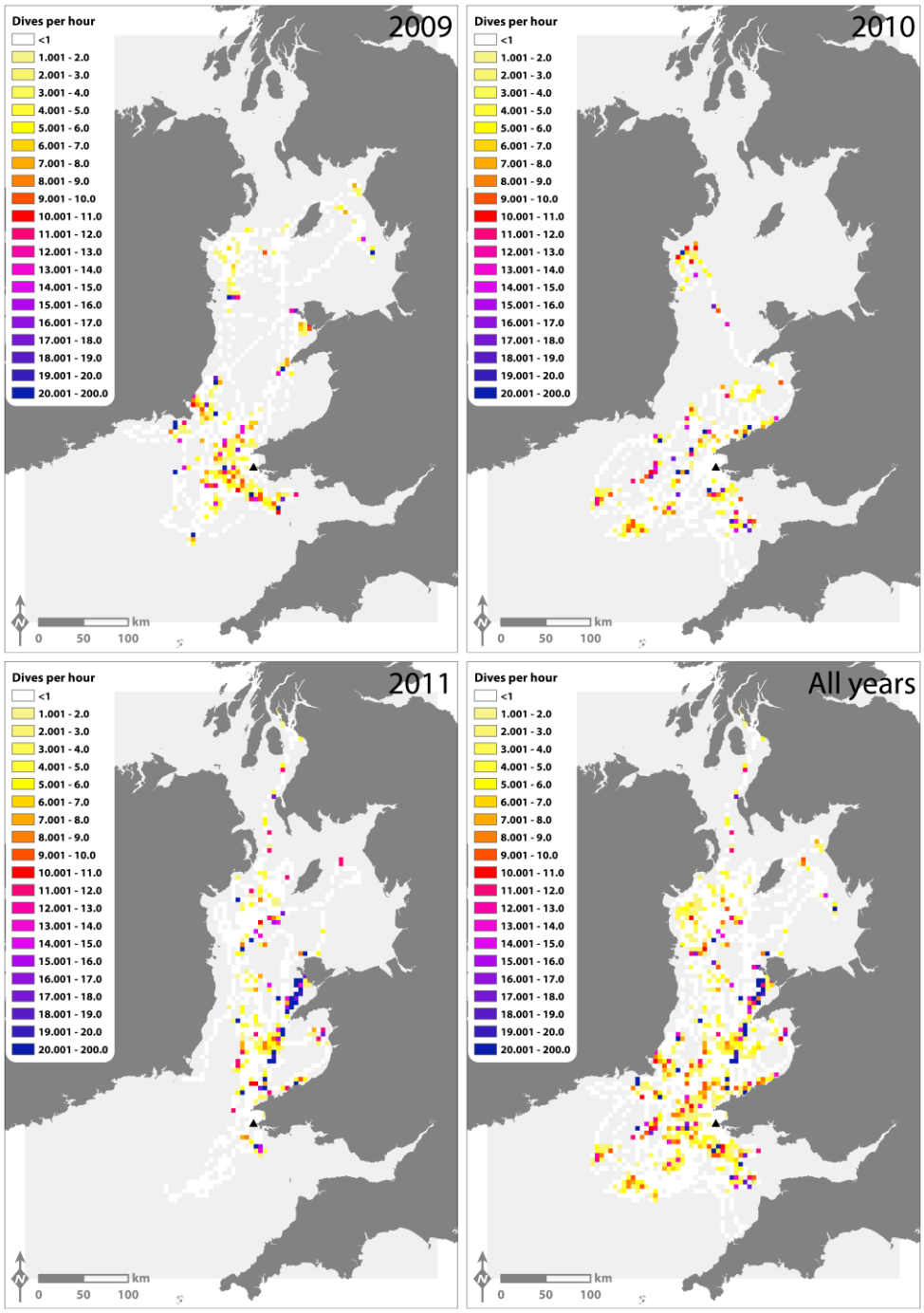

Figure 12. The intensity of diving activity (dives hr^{-1}) in the Irish and Celtic Seas in 2009, 2010, 2011 and overall. 5 km^2 grid cells are coloured from yellow (low) to blue (high). The location of the colony on Skomer is indicated by a black triangle. The total hours of bird presence and the total number of recorded dives used to calculate these grids are shown in the Supplementary Material (figures S1 and S2).

Discussion

Impacts and success of dive logging

We co-deployed miniature, high-sampling-rate TDRs alongside miniature Global Positioning System (GPS) loggers on a large sample of birds (32 individuals) during the chick-rearing period of three consecutive breeding seasons (2009-2011). These data provide the first insights into the diving behaviour of the Manx shearwater and the first large dataset providing detailed information on the diving behaviour of a *Puffinus* shearwater. The use of high-sampling-rate dive loggers (1 Hz in this study) is critical for capturing fine-scale diving behaviour and accurately calculating dive parameters. Reduction of the sampling rate changes the apparent shape of dive profiles, masking fluctuations in depth during the descent, bottom, and ascent phases of dives, increasing the apparent incidence of V shaped dives. Lower sampling rates also lead to under estimation of the number of dives performed, overestimation of dive duration and potentially underestimation of dive depth (Wilson and Pütz 1995). It is recommended (Wilson and Pütz 1995) that in order to calculate dive parameters reasonably accurately, researchers should use recording intervals of 10%, or less of the dive duration. Our sampling rate of 1 Hz was 8.5 % of the median dive duration. Our use of a 1.5 m/3 s threshold for identifying diving events was necessary to exclude uncertain dive events during periods of noise in the recordings. As a result, we may have excluded some genuine short, shallow dives from the analysis.

The combined mass of devices in these deployments comprised approximately 4.0-4.8% of body mass. Previous studies of procellariiforms (Sæther *et al.* 1993; Phillips *et al.* 2003) have demonstrated negative impacts including nest desertion, increased trip duration and reduced meal sizes on a range of species carrying loads comprising 0.6–6.0% of body weight, although many of those deployments were of longer duration than here. In addition, it is likely that birds experience increased diving and flight costs and stress (Burger & Scaffer

2008), which probably are passed on to the offspring in the form of reduced incubation effort, provisioning rate and meal sizes (Sæther *et al.* 1993; Mauck & Grubb 1995). The median recorded foraging trip was 1 day (interquartile range 1-3, range 1-8) after which tracked parents fed chicks a mean mass of 48 g, compared to 49 g for untagged parents (Hamer & Hill 1997) and 56 g for parents carrying devices <1% body mass (Gray & Hamer 2001) in different years with potentially different food availability. During foraging trips parents' net mass changed by a mean of -12.8 g, although net mass loss may be typical on short duration trips (Weimerskirch *et al.* 1997). A previous comparison of untracked birds and birds tracked with similar device loads (Chapter 3) suggests that any impacts on provisioning and breeding success over these short deployments were likely to be minimal. However, the data on the diving behaviour of Manx shearwaters presented here must be interpreted with the caveat that these birds are carrying devices that may have affected their behaviour.

Diving behaviour

Approximately 50% of all dives were less than 6 m deep, but all birds routinely dived deeper, with all but one bird recorded diving to over 20 m. The mean maximum depth for all birds was 33 m and the deepest dive recorded was 55.5 m. This was highly similar (when scaled for body mass) to maximum depths recorded (using maximum depth gauges or low sampling rate pressure loggers) for several other Puffinus shearwaters: Sooty shearwaters during chick-rearing (Weimerskirch & Sagar 1996; Shaffer *et al.* 2009); Short-tailed shearwaters during chick-rearing (Weimerskirch & Cherel 1998); Black-vented shearwaters during both incubation and chick-rearing (Keitt *et al*. 2000); pre-breeding Wedge-tailed shearwaters (Burger 2001); non-breeding Flesh-footed shearwaters (Rayner *et al*. 2011); and Audubon's shearwaters (breeding status unknown) (Burger 2001). Like other Puffinus shearwaters, the maximum dive depth for Manx shearwaters was similar to the allometric

relationship between body mass and maximum dive depth calculated by Burger (1991) for penguins and alcids.

Two previous studies of the diving behaviour of Puffinus shearwaters using high sampling rate TDRs - a single Balearic shearwater logged at 4-s resolution during chick-rearing (Aguilar *et al*. 2003) and two female Great shearwaters logged at 2-s resolution incubation (Ronconi *et al*. 2010) – recorded maximum depths that were substantially lower (scaled for body mass) than maximum depths recorded for other Puffinus shearwaters using TDRs and maximum depth gauges. In the case of the Balearic shearwater, which is behaviourally and structurally highly similar to the Manx shearwater, the large difference in recorded maximum diving depth is unlikely to result from physiological, or structural differences. The average (typical) diving depths of Manx and Balearic shearwaters were similar (approximately 5 m). The depths of recorded dives are likely to reflect the depths to which birds need to dive in order to reach the prey available in a particular location at a particular time. Since these depths rarely may be close to the maximum depth set by the physiological limits of the individual or species, the probability of recording depths close to an individual's maximum depth will increase with the length of logger deployment and the probability of recording depths close to a species' maximum depth will increase with the number of birds tracked. Hence the lower than expected maximum dive depths recorded for Balearic shearwaters (and probably Great shearwaters) are most likely the result of the low sample sizes in those studies. Plotting the distribution of individual birds in this study on figure 7 indicates the wide variation in diving performance recorded for Manx shearwaters. Despite there being an allometric relationship between body mass and maximum diving depth across several species of Puffinus shearwaters (Burger 2001) as well as penguins and alcids (Burger 1991), we found no relationships between diving performance and body mass within the birds in this study (figure 8). Body mass within a species is a confusing indication of body size, since a large bird in poor condition, a small bird in excellent condition, or a

small bird that has recently ingested a large amount of prey, may have similar masses. Large stores of lipids may affect a bird's diving performance by increasing buoyancy, while larger muscle mass may enhance a bird's propulsive swimming abilities.

The rates of energy expenditure and oxygen consumption during propulsive swimming increases rapidly with speed (Hind & Gurney 1997). Breath-holding diving species therefore are assumed to descend and ascend at speeds that minimize energy expenditure per unit distance travelled and maximize the potential duration of foraging at depth (Thompson *et al.* 2003). The descent and ascent rates in this study are based on the duration of the entire descent to (or ascent from) maximum depth and therefore represent average velocities over the whole descent/ascent, which may not be linear, especially where time is spent at depth. They are therefore probably slightly slower than actual descent and ascent swimming velocities. Nevertheless, the mean descent and ascent rates (0.959 m s^{-1} and 0.993 m s^{-1}) were similar to those reported for one Balearic shearwater (approximately 1 m s^{-1}) (Aguilar *et al.* 2003) and for Brünnich's guillemots (*Uria lomvia*) (0.94 and 0.86 m s^{-1}) (Croll *et al.* 1992), but slower than those reported for Great shearwaters (1.14 and 1.35 m s^{-1}) (Ronconi *et al.* 2010). Descent rates might be expected to be slower than ascent rates, since a diving shearwater must overcome its own buoyancy to descend through the water column, but can use its buoyancy to assist the ascent (or make slower passive ascents without swimming).

In conjunction with increasing descent and ascent rates, the mean depth:duration ratio increased with depth to around 30 m (figure 5), indicating that deeper dives were increasingly V-shaped, with increasingly direct descents and ascents and relatively little time spent at depth. Beyond 30 m the depth:duration ratio reached a plateau presumably indicating the point at which deeper dives cannot become more V-shaped due to constraints

on the maximum attainable descent and ascent rates at those depths. Two factors - aerobic capacity and buoyancy - are likely to influence this relationship.

When seabirds undertake dives below the surface they have only the oxygen they take with them, stored in the respiratory and circulatory systems and muscles. The availability of those stores and the rate at which they are utilized in overcoming buoyancy and drag and in thermoregulation will determine the duration for which the bird can remain submerged and metabolize aerobically (Butler 2001). Dives made beyond this duration (the aerobic dive limit, ADL) should result in increased blood lactate concentration, which subsequently must be metabolised during extended recovery periods on the surface. Hence deeper dives may become increasingly V shaped to avoid diving beyond the bird's ADL. Anaerobic dive limits have been calculated (cADL) for several species of diving seabird: 48 s for Brünnich's guillemot (Croll *et al.* 1992), 78-120 s for Gentoo penguins *Pygoscelis papua* and 126 s for King Penguins *Aptenodytes patagonicus* (Butler 2001) and estimated behaviourally (bADL) as 27-29 s for Imperial shags *Phalacrocorax atriceps* (Quillfeldt *et al.* 2011) and 240 s for Crozet and Kerguelen shags *Phalacrocorax melanogenis* and *Phalacrocorax verrucosus* (Tremblay *et al.* 2005; Cook *et al.* 2008). Our overall estimate (bADL) of 40-60 s and between 20-60 s for individual Manx shearwaters falls within this range (figure 6). Less than 4% of dives exceeded 40 s duration, suggesting that shearwaters rarely dive beyond their aerobic limit. However, anaerobic dives occasionally may be profitable when they permit long duration dives to fully exploit dense, but mobile and hard-to-find concentrations of prey before they escape or become depleted (Ydenberg & Clark 1989).

The effects of buoyancy also change with depth and are greatest during shallow dives, since increasing compression of air spaces (in plumage, bones, and respiratory system comprised of air sacs) by increasing hydrostatic pressure reduces buoyancy with increasing depth. Work on Brünnich's guillemots (Lovvorn et al. 1999) and Kergulen shags *Phalocrocorax*

verrucosus (Cook *et al*. 2010) shows that buoyancy decreases rapidly during the top 20 m and that at greater depths diving birds may attain neutral, or even negative buoyancy. The depth at which neutral buoyancy is reached (ca. 62 m for Brünnich's guillemots and 40-70 m for Kergulen shags) appears to vary due to species body composition (Lovvorn *et al*. 1999), individual body condition and the loading of respiratory air prior to the dive, which some species may control to optimize the costs and benefits of buoyancy at their expected depth (Sato *et al*. 2002; Cook *et al*. 2010). In Manx shearwaters, increasing descent rate with depth is likely to be facilitated by a rapid reduction in buoyancy with depth. However, decreased buoyancy also affects ascent rates since birds at or beyond their neutrally buoyant depth must actively swim to ascend. Mean Ascent rate appears to plateau at around 20 m and decrease beyond 30 m (figure 5) suggesting that Manx shearwaters may reach neutral buoyancy at a depth of approximately 30 m. Less than 2% of dives exceeded 30 m duration, suggesting that shearwaters rarely dive beyond their neutrally buoyant limit.

During pursuit dives, it is likely that shearwaters need to put on bursts of additional speed in order to capture prey. During shallow dives where buoyancy is high, horizontal velocities are expected to be greater than vertical descent velocities, even though wingbeat frequency may be reduced (Lovvorn *et al*. 1999). Croll *et al.* (1992) recorded descent and (presumably passive) ascent velocities of 0.94 and 0.86 m s^{-1} for Brünnich's guillemots, much slower than the horizontal underwater swimming velocity (2.18 m s^{-1} at 1 m deep) recorded for Common guillemots *Uria aalge* in pursuit of Clupeid fish *Sprattus sprattus* (Swennen & Duiven 1991). Buoyant ascent at shallower depths may also provide a mechanism for increasing pursuit velocity. By approaching prey from below and making small ascents (e.g. figure 3c dive 10), a diving shearwater potentially could take advantage of buoyancy to rapidly increase its attack velocity without dramatically increasing its propulsive swimming speed, energy and oxygen consumption. Prey escape speeds and prey densities are likely to be critical in determining the optimum pursuit speed (Wilson *et al.* 2002). Manx shearwaters breeding on

Skomer appear to eat predominantly Clupeid fish around 150 mm in length (Brooke 1990). According to calculations of maximum burst swimming velocity for fish evading predators (5-10 times fish length s^{-1}: Beamish, 1978), their maximum burst velocity should be approximately 1.5 m s^{-1}. It seems likely therefore, that shearwaters should be capable of accelerating beyond this speed in pursuit of prey.

Diving and foraging success

U-shaped dives with time spent at depth and/or undulations in depth may indicate the pursuit of prey during dives (Hanuise *et al.* 2010). In addition, the number of dives made per unit time is likely to be highest where large accessible aggregations of prey are located, while deeper, longer dives are likely to make a larger selection of prey available to a diving bird. Each of these parameters may then be expected to vary with the foraging success of a bird. For a small sample of birds (n=7) we were able to calculate the total mass gain over foraging trips (mass of meal fed to chick plus the net gain by the parent). Total mass gain (g day^{-1}) is not a perfect estimate of the total prey captured, particularly over longer trips where prey ingested early in the trip may be digested, metabolised, and converted to stored lipids by the end of the trip. Nevertheless, birds with higher foraging success ought to make greater mass gains over the foraging trip. While total mass gain increased with dives hr^{-1}, median depth and duration, mean descent and ascent rate, and depth:duration ratio, only the relationship with ascent rate was significant, explaining 85% of the variation in total mass gain $p = 0.033$ (figure 9). The mechanism by which ascent rate may be related to total mass gain in unclear. Possibly, rapid ascents play an important part in the capture of prey, with birds using buoyancy to increase their attack speed. Alternatively, foraging success may increase ascent rates because successful birds have larger fat reserves and thus greater buoyancy. The latter seems unlikely however, since it would predict a negative relationship

between mass gain and descent rate, and there was no significant relationship between body mass and descent or ascent rates (figure 8).

Diving behaviour of males and females

Sex specific differences in diving behaviour (dive frequency, depth and duration) have been found in several species of seabird where there is sexual size dimorphism (Quillfeldt *et al.* 2011; Gomez Laich *et al.* 2012), reversed sexual size dimorphism (Lewis *et al.* 2005; Weimerskirch *et al.* 2006), or where the sexes are similar in size (Lewis *et al.* 2002; Peck & Congdon 2006). Manx shearwaters show little size dimorphism: <1 mm in wing length and bill length, and 1 mm in tarsus length (Brooke 1990) and based on the average dive metrics for individuals, the diving performance of males and females in this study was highly similar.

Spatial and temporal patterns of diving

Plotting the diel patterns of diving behaviour (figure 10) shows that diving was highly constrained to daylight and crepuscular hours, commencing approximately an hour before sunrise and ceasing shortly before sunset. This suggests that the primary mode of foraging during dives was visual pursuit of prey. Similar diel patterns of foraging activity have been shown for Manx shearwaters (Dean *et al.* 2012) and a direct effect of ambient light levels on diving activity has been shown in two species of exclusively diurnal foraging shags (Wanless *et al.* 1999). It is perhaps unsurprising that the diving activity of species predominantly engaging in visual pursuit of prey should be so constrained, since prey detection, pursuit and capture efficiencies are likely to be compromised by low light levels. Yet some species of seabird considered to be visual predators have been recorded diving at night, particularly under bright nocturnal conditions (Regular *et al.* 2011), or where limited daylight hours at high latitudes make it necessary (Gremillet *et al.* 2005). Manx shearwaters breeding on Skomer appear to eat predominantly Clupeid fish (Brooke 1990), which are known to make

diel vertical migrations (DVM) within the water column in response to ambient light levels (Woodhead 1966; Blaxter and Hunter 1982; Giannoulaki *et al.* 1999, Hays 2003). By diving during the crepuscular parts of the day, birds may optimise foraging efficiency by balancing the increased accessibility of prey at shallow depths against decreased prey detection and capture ability under low light conditions. However, diving activity continued throughout the day suggesting that shearwaters are able to access aggregations of prey throughout the day, perhaps by making deeper dives (maximum dive depth was greatest towards the middle of the day, figure 10c), or by taking advantage of the foraging activities of deeper diving predators, which can temporarily force aggregations of prey towards the surface (Evans 1982; Pierotti 1988). Brooke (1990) suggests that while Skomer birds mostly eat fish, mesopelagic squid may make up a significant part of the diet of birds breeding on Rum (NW Scotland). Birds from Rum may then necessarily dive deeper and/or make nocturnal dives in order to capture these prey, but as yet no deployments of TDRs have been made. Diving frequency increased through the day culminating in a peak of diving activity between 17:00 and 18:00 GMT. This may reflect a response to changes in the density, or availability of prey through the day, or may be the result of a strategy to minimise the cost of carrying large payloads of food. Chick-rearing Manx shearwaters frequently return to the colony to feed their chick, but do so nocturnally (Brooke 1990). Those that do not return on a given night, roost out at sea (Dean *et al.* 2012). If the stomach and crop are filled only in the last few hours before returning, the resulting payload only has only to be carried on the return journey to the colony (and not during foraging movements during the day). For birds not returning (perhaps because they do not reach some optimal threshold in payload, or because they need to recover body condition), much of the stomach and crop contents may be digested while roosting overnight at sea, reducing the payload that must be carried the following day.

The co-deployment of GPS and TDRs provided a highly detailed dataset that allowed us to plot diving activity spatially, eliminating the potential problems of interpretation associated from separately collected location and diving data (e.g. Ronconi *et al.* 2010 and see Preston *et al.* 2010). The overall mean rate of diving was around 4 dives hour^{-1} of daylight, but dives typically occurred in bouts of repeated diving activity typically lasting 5-20 minutes (but sometimes longer), during which diving rate could be around 2 dives min^{-1} (figure 3a&b). These bouts were typically separated by longer periods of no, or infrequent dives (figures 2 and 3). Plotting the combined GPS-TDR data revealed that this pattern resulted from periods of high intensity diving activity within spatially restricted areas, separated by periods that were likely to be commuting or searching flight between foraging locations, or periods of rest on the surface of the sea (figure 11). Some brief periods of diving occurred during relatively linear sections of the birds tracks (figure 11) suggesting that birds continue to search for prey during direct flight between foraging areas and engage in diving if prey are located, or perhaps engage in periodic sampling dives to assess conditions. Over larger scales, straight movement may be the most effective method of searching for prey (Zollner & Lima 1999) and there is evidence in other pelagic seabirds that prey may be ingested even during extremely rapid (>100 km h^{-1}) and directed flight (Catry *et al*. 2004). Dean *et al.* (2012) showed that searching flight behaviour, involving area restricted search and repeated take-offs and landings were strongly associated with diving activity, indicating that many of the 'surface intervals' seen in the TDR data are in fact likely to be aerial intervals. If most of the post dive intervals necessarily involve active flight, they may provide little opportunity for recovery from anaerobic dives, which may in part explain why shearwaters appear to largely avoid these.

An understanding of the locations, extents and variability of those areas that are of greatest importance to the foraging success of seabirds is critical to the provision of adequate conservation measures. Furthermore, because Manx shearwaters typically forage in large

dense flocks (King 1974; Jones 1975; Stone *et al.* 1994), those areas recording the highest densities of diving activity are likely to be important for large numbers of birds, comprising (in some areas; Chapter 3) birds from multiple colonies. Our analysis revealed that diving activity was widespread through the Irish and North East Celtic Seas and that the distribution of diving was variable between years (or possibly birds tracked in each year). However, several areas of high density diving activity were consistent between years: in particular, the western Irish Sea and the location of the Western Irish Sea Front (see Chapter 3), coastal areas of south Cardigan Bay, the southwest coast of Anglesey, southwest of the LLyn Peninsular and the waters within 100 km of Skomer.

Conclusions

Here we provide the first detailed information on the diving behaviour of a large sample of Puffinus shearwaters using high-sampling-rate TDRs. More importantly, these data provide the first insights into the diving behaviour of the Manx shearwater. In summary, chick-rearing Manx shearwaters typically made short (<13 s) dives of up to 5-6 m deep, many of which involved some time at depth and undulations in depth, presumably in pursuit of prey-fish. Shearwaters also made much longer, deeper dives. The maximum recorded depth of 55.5 m was similar to allometrically scaled maximum depths recorded for many other Puffinus shearwaters and those predicted for alcids and penguins. However, few dives exceed about 30 m (which may represent their neutrally buoyant depth), or about 40-60 s duration (which may represent their aerobic dive limit). Male and females demonstrated similar diving abilities. Diving behaviour was highly constrained to the daylight and crepuscular hours as expected for a visual predator making pursuit dives. Diving activity continued through the day, but peaked during the evening, possibly reflecting a foraging strategy that minimises the cost of carrying large payloads of food. Foraging success (mass gain over a foraging trip) was related to mean ascent rate, which may reflect the use of

rapid buoyant ascents in prey capture. Diving activity was widespread throughout the Irish and North Eastern Celtic Sea and the recorded distribution was variable between years. Nevertheless, several areas of consistent high-density diving activity were apparent and these are likely to be of high conservation importance. Further detailed analysis of the individual TDR data may reveal subtle changes in diving rate, or differences in dive profiles that might tell us something about the quality, density, or accessibility of prey resources. Analysis of the temporal sequences of diving behaviour in conjunction with corresponding movement data may allow us to better understand the process of diving bouts: how prey are discovered, how bouts of pursuit diving are initiated, why bouts of diving eventually cease (depletion or escape of prey, or satiation or exhaustion of foragers), and how seabirds decide to move from one prey patch to another, or to return to the colony.

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Supplementary Material

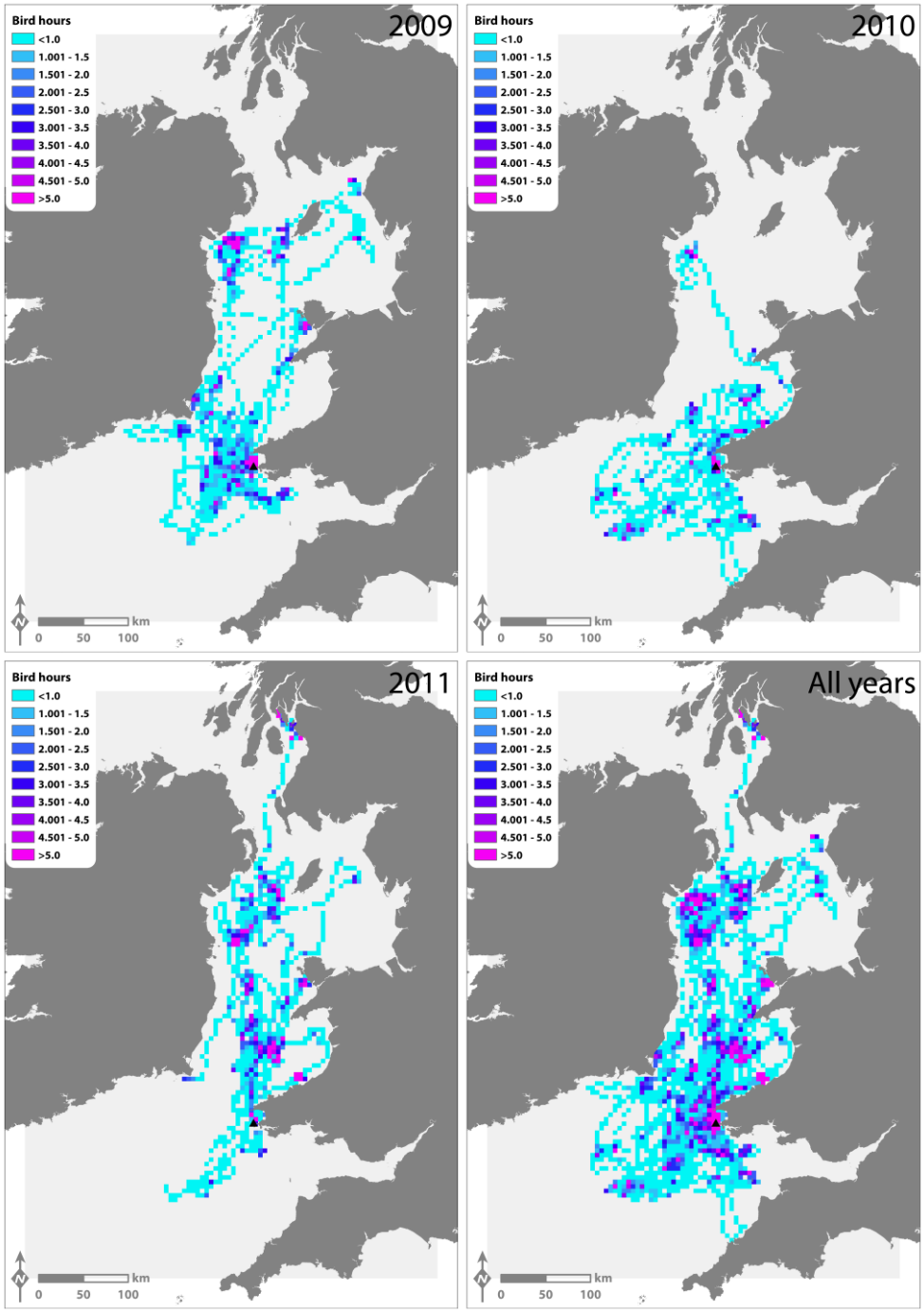

Figure S1. The total number of recorded hours of bird presence in the Irish and Celtic Seas in 2009, 2010, 2011 and overall. 5 km^2 grid cells are coloured from blue (low) to purple (high). The location of the colony on Skomer is indicated by a black triangle.

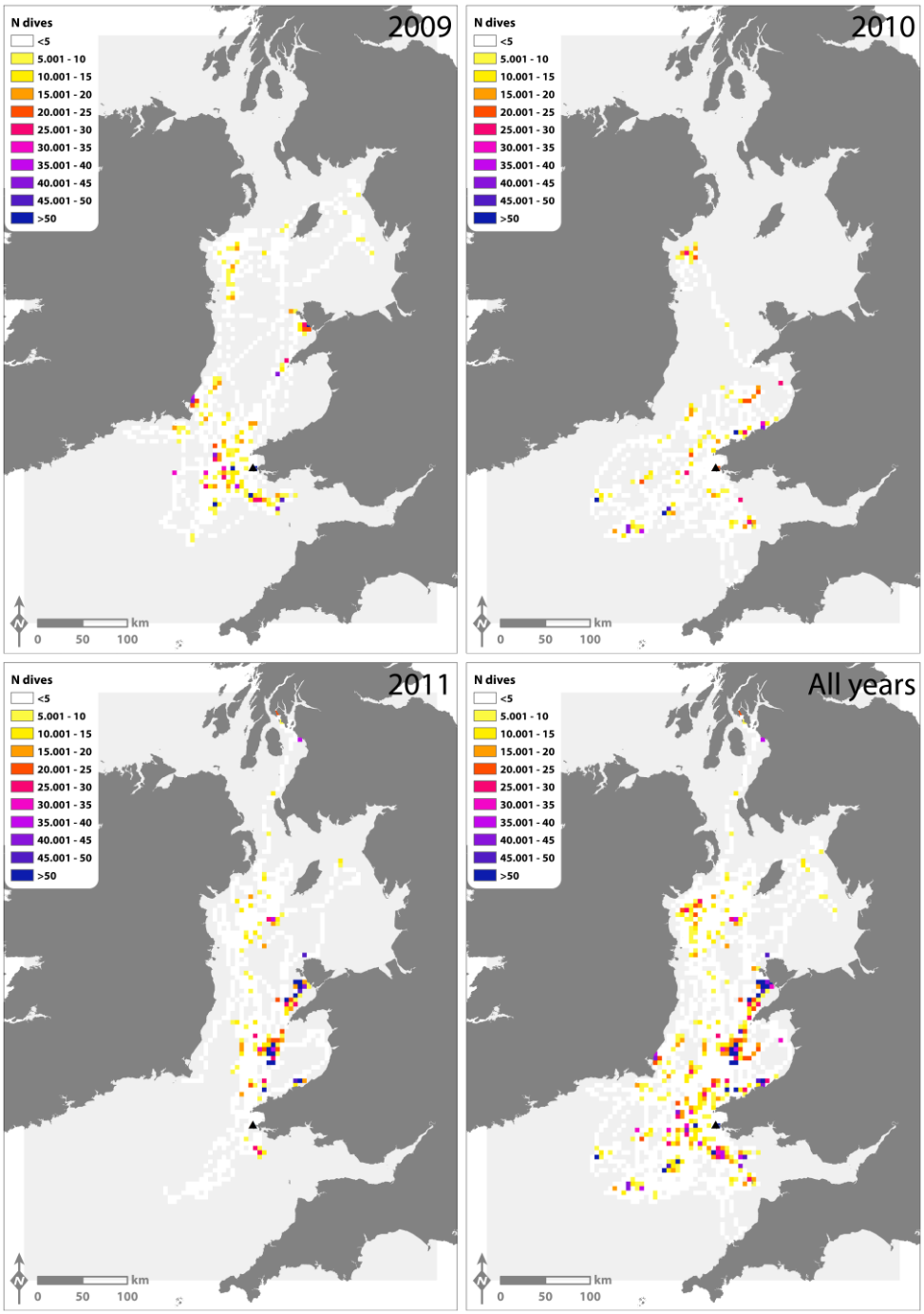

Figure S2. The total number of recorded dives in the Irish and Celtic Seas in 2009, 2010, 2011 and overall. 5 km^2 grid cells are coloured from yellow (low) to blue (high). The location of the colony on Skomer is indicated by a black triangle.

Chapter 5

Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour

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Abstract

The use of miniature data loggers is rapidly increasing our understanding of the movements and habitat preferences of pelagic seabirds. However, objectively interpreting behavioural information from the large volumes of highly-detailed data collected by such devices can be challenging. We combined three bio-logging technologies - GPS, saltwater immersion and time-depth recorders - to build a detailed picture of the at-sea behaviour of the Manx shearwater (*Puffinus puffinus*) during the breeding season. We used a hidden Markov model to explore discrete states within the combined GPS and immersion data and found that behaviour could be organized into three principal activities representing: (1) sustained direct flight, (2) sitting on the sea surface, and (3) foraging, comprising tortuous flight interspersed with periods of immersion. The additional logger data verified that the foraging activity corresponded well to the occurrence of diving. Applying this approach to a large tracking dataset revealed that birds from two different colonies foraged in local waters that were exclusive, but overlapped in one key area: the Irish Sea Front (ISF). We show that the allocation of time to each activity differed between colonies, with birds breeding furthest from the ISF spending the greatest proportion of time engaged in direct flight and the smallest proportion of time engaged in foraging activity. This type of analysis has considerable potential for application in future bio-logging studies and in other taxa.

Introduction

Understanding the at-sea behaviour of pelagic seabirds is both difficult, because of their elusive life-styles, and important, because of their vulnerability to changes in the marine environment and their status as indicators of ocean health (Einoder 2009). Advances in miniature telemetry and data logging systems continue to revolutionise the remote observation of long-distance movements in these and other elusive species (Guilford *et al.* 2008; Egevang *et al.* 2010; Kotzerka *et al.* 2010; Yorio *et al.* 2010; Quintana *et al.* 2010; Votier *et al.* 2011), but such systems can be expensive, impactful (especially on smaller species), and the resulting data are often under-utilised. Many tracking studies use recorded locations to examine movement and habitat use only in broad terms (Egevang *et al.* 2010; Kotzerka *et al.* 2010; Yorio *et al.* 2010; Quintana *et al.* 2010), leaving key questions about where and when animals engage in specific behaviours unanswered. However, behaviour may be inferred by characterising patterns of movement based solely on the geometry or complexity of an animal's path using techniques such as tortuosity (Dicke & Burrough 1988; Benhamou 2004), positional entropy (Roberts *et al.* 2004; Guilford *et al.* 2004), or first-passage time (Fauchald, P. & Tveraa, T. 2003). In addition, modelling approaches such as Gaussian mixtures have been used to classify animal tracking data into discrete modes of movement (Guilford *et al.* 2008; Freeman *et al.* 2010), while state-space models including hidden Markov models (Roberts *et al.* 2004; Jonsen *et al.* 2005; Patterson *et al.* 2008; Franke *et al.* 2006; Patterson *et al.* 2009; Hart *et al.* 2010; Pedersen *et al.* 2011) have been used to identify different modes of movement and the dynamics of switching between them.

Hidden Markov models (HMMs) assume that a sequence of observations (e.g. tracking data) is generated by an underlying unobserved sequence of discrete states (modes of movement, or different behaviours) and that the state occupied at each step in the hidden sequence depends only on the state occupied in the preceding step (Rabiner 1989). This approach is well suited to uncovering hidden patterns of behaviour in animal tracking data since it is consistent with the

fact that behaviour is never directly observed, makes use of the inherent temporal dynamics within the data, and utilises the non-independence of sequential data points. Where these methods have been applied solely to animal tracking data they have offered important insights into behaviour. However, enriching tracking data by concurrent deployment of additional devices that record activity (Weimerskirch *et al.* 2005) may provide both increased power to resolve behavioural states, and the information required to validate and interpret those states as specific behaviours.

The aims of this study were to: identify the principal types of behaviour in which a volant, pelagic, diving seabird engages while at sea; to segment GPS tracks based on those behaviours; and to explore their spatiotemporal distribution. We studied the Manx shearwater, a 400 g procellariiform seabird that breeds predominantly in colonies at remote locations off the west coasts of Britain and Ireland. Females lay a single egg in an underground nest and during the incubation period, both parents alternate stints of 5-7 days at the nest with long foraging trips (Guilford *et al.* 2008) on which they recover body condition. During the chick-rearing period, both parents make repeated, shorter duration foraging trips to sea (Guilford *et al.* 2008; Gray & Hamer 2001), returning at night to provision the chick. See (Brooke 1990) for a detailed description of the breeding behaviour. While marine surveys (Stone *et al.* 1994) and GPS tracking (Guilford *et al.* 2008) have provided valuable insights into the routes and destinations of these foraging trips, little is known about individual and colony based patterns of behaviour at sea.

Our approach applied a HMM to data from two independent, but simultaneously deployed loggers (GPS and saltwater immersion) to categorise at-sea activity into discrete behavioural states. We subsequently interpreted and validated the HMM classification using path tortuosity and data from a third independent device (time-depth recorder) deployed concurrently. We were then able to segment individual GPS tracks into the most likely sequence of behavioural

states. By training and validating the HMM on a detailed multi-sensor dataset and applying it to a much larger, but less detailed tracking dataset, we were able to map the spatial distribution of behaviours and explore where, when and for how long birds from different colonies engaged in each activity, during different stages of the breeding season, over three years.

Materials and Methods

Data Loggers

Loggers were deployed on breeding birds from two colonies in the Irish Sea, during the incubation (May-June) and chick-rearing (July-August) periods of the 2009, 2010 and 2011 breeding seasons: Skomer Island, Wales (Southern Irish Sea: 51°44'N, 5°17'W), and Lighthouse Island in the Copelands group, Northern Ireland (Northern Irish Sea: 54°41'N, 5°31'W). As far as practicable, deployments were carried out simultaneously on both islands to minimise any effects of temporal changes in environmental conditions. Breeding adults were taken from their burrows by hand through a purpose built inspection hatch and weighed prior to device deployment. A total of 168 deployments were made on 117 individuals (table 1). All birds were fitted with at least two data logging devices: a global positioning system (GPS) logger (modified i-gotU GT-120: Mobile Action) and a British Antarctic Survey geolocator-immersion logger (Mk13, 14, or 18L). Twenty five of the birds tracked from Skomer (table 1) were additionally fitted with a CEFAS G5 time-depth recorder (TDR).

Table 1. Number of birds tracked from each colony during the incubation (Inc.) and chick-rearing (Rear.) periods of each year. All birds were tracked using GPS and geolocator-immersion loggers. Birds marked * also carried TDRs. Some individuals were tracked during the same period in two or more years: Incubation Skomer 5 birds, Copeland 8 birds; Rearing Skomer 5 birds, Copeland 9 birds.

	2009		**2010**		**2011**	
	Inc.	**Rear.**	**Inc.**	**Rear.**	**Inc.**	**Rear.**
Copeland	11	13	11	20	11	17
Skomer	9	16*	9	16+9*	11	15

GPS loggers were configured to record location once every 5 or 10 minutes and were attached dorsally using thin strips of tesa marine cloth tape underlying a small number of contour feathers (Guilford *et al.* 2008). Geolocator-immersion loggers test for saltwater immersion every 3 seconds and record the proportion of samples immersed in each 10 minute interval. Immersion loggers were attached by two lightweight cable ties to a metal leg ring, so as to be immersed when sitting on the sea surface. TDRs were configured to record pressure every 1 second and were attached to the central four tail feathers using thin strips of tesa tape (similar to Wilson *et al.* 2009). GPS weighed 15 g in dual device deployments and 10.5-11.3 g (smaller battery) in triple device deployments. Geolocator-immersion loggers weighed 1.5-1.9 g and TDRs 2.7 g. The total mass of devices was approximately 18 g for all deployments. On return, birds were recaptured from the burrow, reweighed, and devices removed. Capture and deployment took <15 minutes, removal <10 minutes. During 2010 and 2011 we weighed the chicks of tracked adults, to determine the size of meals delivered during nest visits. The effect of carrying devices was tested on birds tracked from Skomer in 2009 by comparison of hatching success, chick growth rate and fledging success with a group of unmanipulated control nests.

Hidden Markov Model

Hidden Markov modelling is a temporal pattern recognition method that identifies discrete states and time dependent state changes within time series data. For example, flight and rest might result in distinctly different patterns of movement (fast versus negligible speeds), each constituting a discrete state. The method is well suited to revealing the sequence of such states in animal tracking data where behaviour itself is never directly observed and sequential data points are usually non-independent. A full description of HMM methods is presented by Rabiner (1989). Here, we assumed that at-sea behaviour can be described as a Markov process such that it is composed of an unknown but discrete number of distinct states equating to the birds' principal activities. Foraging trips are segmented into discrete time steps (logger sampling intervals) and in each time step a bird is engaged in one activity. Between time steps the bird can switch from the current state (activity) to a new state, or remain in the same state according to a set of state transition probabilities. The sequence of states is hidden, since we cannot directly observe the bird, but at each time step we make observations in the form of logger data according to a set of emission probabilities, which might be given by Gaussian components for continuous variables or by conditional probability tables for discrete variables. By learning the state transition and emission probabilities we can estimate the probability of the observations recorded at each time step belonging to a particular state.

Model Data

Two data series were used to train the HMM: saltwater immersion and ground speed (figure 1). Because immersion was recorded at regular 10 minute intervals, average speed values were calculated over the same intervals as follows: GPS locations were interpolated to 1-minute frequency using piecewise cubic hermite polynomials as in Tremblay *et al.* (2006). Mean ground speed was then calculated between those interpolated locations falling within each 10-minute interval. In validation tests (Supplementary Material), this interpolation gave a better

representation of speed within 10-minute intervals than the original recorded locations, especially where acceleration or deceleration occurred between intervals. Speed data were log(+1) transformed and immersion data (a proportion) were mapped to the whole real line (-∞, ∞) using a logit transform with a small value ε (the minimum non-zero proportion) added as in (Warton & Hui 2011). Data collected within 1 km of the colony were omitted to exclude colony based behaviours, such as sitting or moving on the ground.

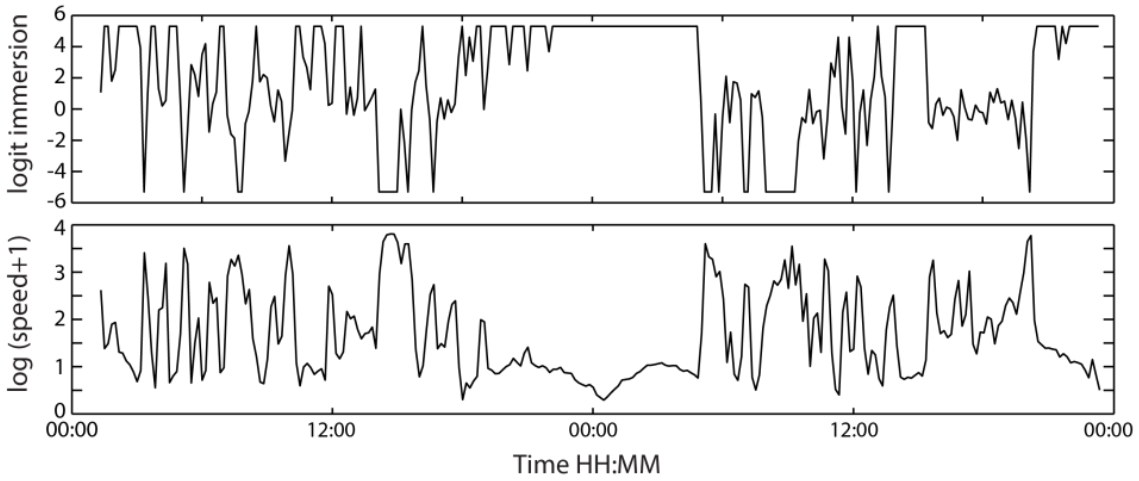

Figure 1. Example speed and saltwater-immersion data used to train the model. Proportion of ten-minute intervals spent immersed (logit transformed) is shown in the top window, average speed (m s-1) over the same intervals (log transformed) is shown in the lower window.

Model Training

We trained the HMM on data from the 25 birds from Skomer fitted with all three logger types using the HMM Toolbox (Murphy 1998) in MATLAB® (The MathWorks™, Natick, Mass., USA). In this implementation we were constrained to the assumption that the emission probabilities were given by Gaussian components in the observed data. For the log-transformed speed data this assumption was valid. The logit transformed immersion data contained a peak of low values, a peak of high values, and a range of values between. As such, the assumption of Gaussian

emission distributions was not ideal for the immersion data, but provided a pragmatic solution to the partitioning of distinct groups within the data.

HMMs can be simple (few states), but have large error around them, or complicated to the extreme case of one state per observation and zero error. As a model selection exercise, we trained a series of candidate HMMs with an increasing number of putative states (2-10). The iterative addition of states (each explaining fewer observations with less error) increased log-likelihood monotonically, favouring over-fitting of complex (many state) models. However, the increase in log-likelihood was greatest between the two and three state models, resulting in a distinct knee point (Zhao *et al.* 2008) (figure 2). We therefore chose a three-state HMM as a trade-off between model accuracy and complexity.

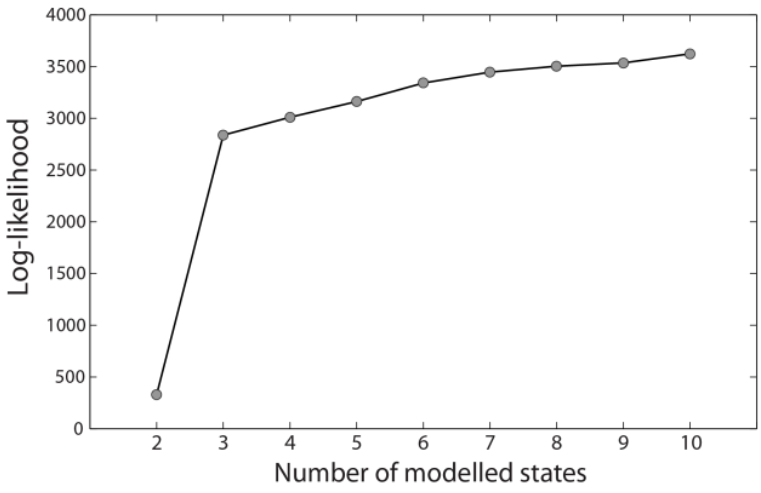

Figure 2. Log-likelihood calculated for candidate models with an increasing number of states. The increase in log-likelihood was greatest between the two and three state models, resulting in a distinct knee point.

HMM parameters were initialised using k-means clustering (MacQueen 1967) and improved through unsupervised training using the Baum-Welch algorithm (Rabiner 1989) which, given a sequence of observations, iteratively adjusts the model parameters to maximise the probability

of obtaining those observations. We then applied the trained final HMM to each individual track in the training data, using the Viterbi algorithm, which calculates the sequence of hidden states that best explains a sequence of observations (Rabiner 1989). We interpreted the nature of the behaviour that was characteristic of each of the emergent states, based on the typical values for immersion and speed, as well as track straightness (Batschelet 1981) (calculated as the ratio between the straight-line distance and the track-line distance over a moving 100 minute section of the interpolated GPS track) and time submerged (recorded by the TDRs).

Mapping behaviour

By linking the HMM classification to the corresponding GPS locations we were able to plot the sequence of activities undertaken during the course of individual foraging trips, showing where, when, and for how long each bird engaged in each of the activities. Finally, we applied the HMM trained and interpreted on the subset of deployments in which all three devices were used, to the whole dataset including a further 143 deployments on birds tracked only with GPS and geolocator-immersion loggers. We used the Viterbi algorithm to classify the most likely behaviour at each 10-minute time-step along each GPS track. This enabled us to plot the sequence and spatial distribution of behaviours and to calculate the time spent engaged in each activity. To explore the spatial distribution of activities for birds from different colonies, during different periods of the breeding season, we calculated kernel density distributions for each activity over 1 km2 grid cells in ArcGIS, using a bandwidth (*h*) of 17km, selected using least-squares cross validation, and which produced contiguous cores without over-smoothing.

Results

Trip metrics and impact of loggers

A total of 168 successful deployments were made on 117 individuals, simultaneously recording location and immersion data during 315 foraging trips mainly within the Irish and Celtic Sea

(table 1). An additional four very long range offshore trips into the Atlantic were excluded from the analysis as extreme outliers.

The median duration of deployments was 8 days (maximum 15) during incubation and 5 days (maximum 13) during chick-rearing. Overall, incubation deployments recorded 1.1 foraging trips and chick-rearing deployments recorded 2.4 trips. The departure weights of birds tracked during incubation and the minimum recorded weights for birds tracked during chick-rearing are the best approximation of a bird's minimum body mass without food in the stomach, or large fat deposits, in each period. These were similar (407 and 412 g respectively) (Supplementary Material, table S1), two sample t-test: t (167) = 1.06, p = 0.31, as were the weights of birds from different colonies: Copeland incubation 407 g, Skomer incubation 406 g, two sample t-test: t (60) = 0.12, p = 0.90; Copeland rearing 415 g, Skomer rearing 409 g, two sample t-test: t (105) = 1.01, p = 0.32. The overall mean minimum weight was 410 ± 30 g, so the combined device weight (18 g) comprised 4.1-4.7% of minimum body weight. During incubation trips, birds from Copeland increased their mass by slightly more (32 g) than birds from Skomer (24 g), two sample t-test: t (51) = 1.07, p=0.29. Following chick-rearing trips, birds from Copeland and Skomer delivered similar size meals: 44 g and 45 g respectively, two sample t-test: t (142) = 0.31, p = 0.75. Median trip duration was longer during incubation (8 days) than during chick-rearing (1 day) (Supplementary Material, table S1), Wilcoxon Rank-sum: z (283) = 10.09, p < 0.001. During incubation, median trip duration was slightly shorter for birds from Copeland (7 days) than from Skomer (8 days), Wilcoxon Rank-sum: z (47) = 0.99, p = 0.32. During chick-rearing, median trip duration was slightly longer from Copeland (2 days) than from Skomer (1 day), Wilcoxon Rank-sum: z (234) = 1.47, p = 0.142. During incubation trips, birds from Skomer covered greater distances overall and per day (24 hours), and reached greater maximum distances from the colony than birds from Copeland, Wilcoxon Rank-sum: z (47) = 2.13, 2.89, 4.85; p = 0.033, 0.004, <0.001 respectively. During chick-rearing trips, birds from Skomer covered greater distances overall and per day, and reached greater maximum distances from the colony than birds from

Copeland, Wilcoxon Rank-sum: z (234) = 1.89, 6.87, 5.50; p = 0.059, <0.001, <0.001 respectively. For the nine nests from which adults were tracked on Skomer during incubation 2009, hatching success was 77.7% compared to 82.4% in the 17 control nests. For the ten nests from which adults were tracked on Skomer during chick-rearing 2009, fledging success was 100% compared to 93% in the 15 remaining control nests. The mean growth rate of chicks whose parents carried tracking devices (8.7± 1.2 g day-1) was not significantly different to that of chicks in the control nests (9.3 ± 1.0 g day-1), two sample t-test: t (24) = 1.34, p = 0.19. There were no differences in trip duration between triple instrumented birds (1.5 days, IQR 1-2) and dual-instrumented birds tracked in the same period from the same colony (1 day IQR 1-2 days), Wilcoxon Rank-sum, z (59) = 0.76, p=0.45.

Interpreting behavioural states

Of the candidate models trained with 2-10 states, the increase in log-likelihood was greatest between the two and three state models (figure 2) suggesting that the at-sea behaviour of Manx shearwaters was most parsimoniously described by three principal activities. Although information on diving and track straightness were not used to train the HMM, these differed significantly between the three states: proportion of time submerged Kruskal-Wallis $\chi^2(2, 72) = 58.37$, $p < 0.001$; and track straightness ratio $\chi^2(2, 72) = 28.68$, $p < 0.001$. This suggests that these states, identified purely on the basis of temporal patterns in combined immersion and ground speed data, represent three distinct activities.

The first activity was consistent with sustained direct flight. First, it was characterised by high speed movement (median speed = 8.9 m s^{-1}), within the theoretical flight speed range for the species (Pennycuick 1969). Second, there was little or no contact with the sea surface (median proportion of time immersed = 0). Third, track straightness was high (median straightness ratio = 0.83 compared to the recorded maximum of 0.87 in this study) indicating directed movement. Fourth, the HMM state transition probabilities (figure 3) indicated that this state was stable over

time and likely to be followed by the same state (p = 0.68). Finally, only a very small proportion of the total time spent diving occurred during this state (median proportion = 0.01).

The second activity was consistent with sitting and drifting on the sea surface. First, it was characterised by slow movement (median speed = 0.65 m s^{-1}), slower than the 0.85 m s^{-1} previously calculated for drifting birds (Guilford *et al.* 2008). Second, there was high to constant contact with the sea surface (median proportion of time immersed = 1). Third, there was high track straightness (median ratio = 0.86). Fourth, the transition probabilities indicated that this state was highly stable and likely to be followed by the same state (p = 0.81). Only a small proportion of the total time spent diving occurred during this state (median proportion = 0.03).

We propose that the third activity is consistent with foraging, incorporating convoluted search flight and periods of immersion in pursuit of prey. First, speed was intermediate (median speed = 2.01 m s^{-1}), slightly slower than the separation between drifting and flying speeds calculated by (Guilford *et al.* 2008). Second, there was intermediate contact with the sea (median proportion of time immersed = 0.63). Third, track straightness was low (median straightness ratio = 0.62 compared to the recorded minimum of 0.49 in this study) suggesting tortuous movements within restricted areas. Fourth, the transition probabilities indicated that this state was stable over time and likely to be followed by further periods of foraging (p = 0.69). Finally, diving was very strongly associated with this activity, with a median proportion of 0.96 of total dive time occurring within this state.

Maps of individual bird tracks classified by the HMM (figure 4) reveal the spatial distribution and sequential patterns of activity, and further support our proposal that the discovered activities represent sustained direct flight, sitting and drifting, and foraging. In particular, by mapping the locations of diving activity along with the HMM classification, we visually demonstrate the high level of agreement between foraging activity and diving.

State at time t \ State at time t+1	fly	sit	forage
fly	0.684	0.002	0.314
sit	0.001	0.812	0.187
forage	0.149	0.159	0.692

Figure 3. State transition probability matrix learned for the final three-state HMM. Given that a particular state is occupied at time t, the matrix shows the probabilities of switching to each of the other states, or remaining in the same state at time t +1.

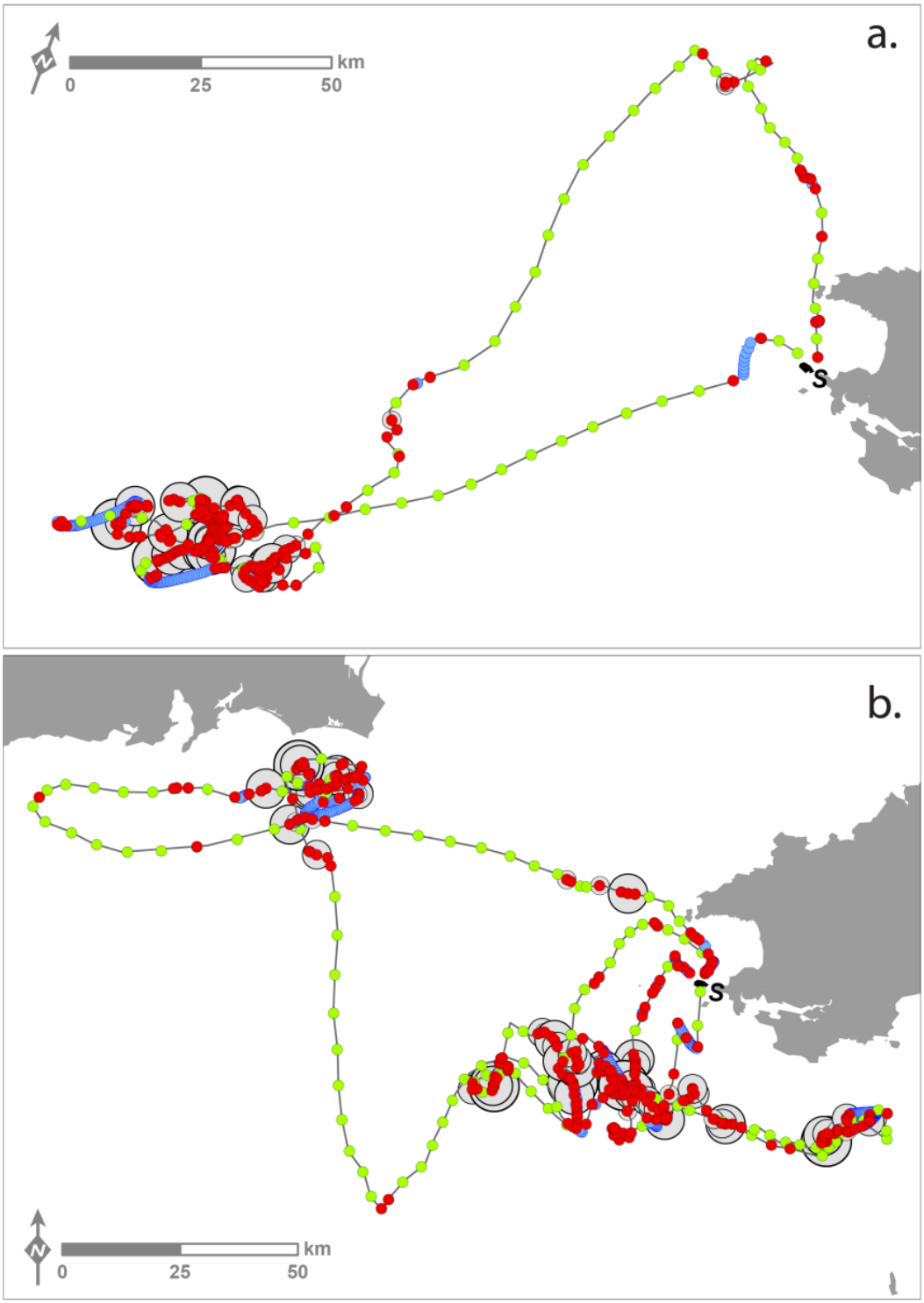

Figure 4. Three day (a) and five day (b) foraging trips from Skomer (S), classified according to activity using the HMM. Ten-minute intervals classified as direct flight are mapped as green circles, foraging as red and sitting as blue. Intervals where diving occurred are mapped as grey circles, scaled in proportion to total time submerged.

Timing of activities

During both incubation and chick-rearing, the majority of sitting activity occurred during the evening and hours of darkness (figure 5), as birds roosted on the sea surface. Direct flight and foraging activities typically increased during the hour preceding sunrise, with a morning peak in flight activity just after sunrise, followed by a lull around midday coincident with an increase in sitting. Flight then peaked again prior to sunset and decreased rapidly as darkness fell. Foraging activity was highly constrained to the hours of daylight and twilight (figure 5), which were shorter during chick-rearing than during incubation.

The percentage of daylight hours engaged in direct flight and foraging activity differed between incubation and chick-rearing, Wilcoxon Rank-sums: (flight) z (167) = 5.35, p< 0.001, (siting) z (167) = 0.25, p<0.79, (foraging) z (167) = 4.23, p<0.001. On average, an incubation trip comprised 10% direct flight, 28% sitting and 63% foraging, whereas a chick-rearing trip comprised 15% direct flight, 28% sitting and 57% foraging (figure 6). During both periods, birds from Skomer spent a greater percentage of daylight hours engaged in direct flight and a smaller proportion engaged in foraging activity than birds from Copeland (figure 6). During incubation trips, birds from Skomer spent a median of 12% of the day in direct flight and 60% engaged in foraging, compared to 6% and 64% for birds from Copeland, Wilcoxon Rank-sum: z (61) = 4.00, p<0.001 and z = 1.74, p 0.08). Birds from both colonies spent 27% of the day sitting, Wilcoxon Rank-sum: z (61) = 0.85, p < 0.39). During chick-rearing trips, birds from Skomer spent 19% of the day in direct flight and 54% engaged in foraging, compared to 12% and 60% for birds from Copeland, Wilcoxon Rank-sum: z (105) = 5.04, p < 0.001; and z = 2.74, p <0.01). Birds from both colonies spent a similar percentage of the day sitting: Skomer 27% and Copeland 28%, Wilcoxon Rank-sum: z (105) = 0.64, p < 0.52).

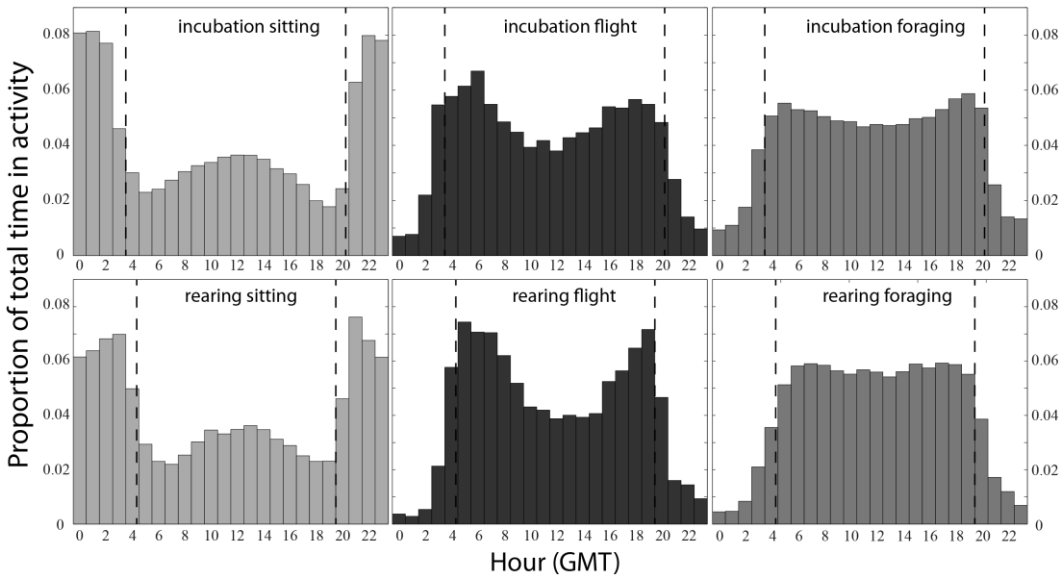

Figure 5. Overall daily activity patterns for all birds during incubation and chick-rearing. The distributions are normalized to sum to unity. Timing (GMT) of sunrise and sunset at the centre of the Irish Sea (53º0'N, 5 º13'W) are shown as dashed lines.

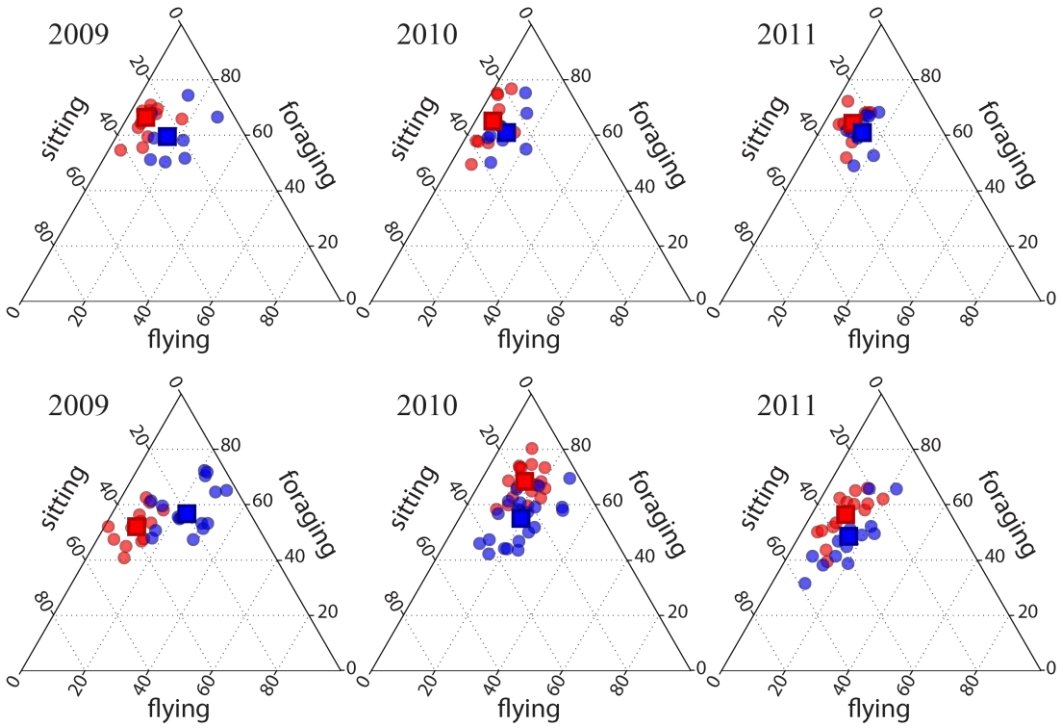

Figure 6. Ternary plots showing the percentage of daylight hours spent in each activity by birds from Copeland (red circles) and Skomer (blue circles) during incubation (top row) and chick-rearing (bottom row). Large squares indicate corresponding median values.

Spatial distribution of activities

The distribution of each activity for birds tracked from both colonies, in both periods of the breeding season and in each year are shown in (example) figure 7 and (all) supplementary materials (Supplementary Material, figures S1-S4). These highlight discrete areas where birds engaged in foraging activity, show the important routes between foraging areas, where birds engaged in direct flight activity and indicate that sitting activity (most of which was nocturnal roosting) generally occurred within foraging areas or close to the colony. Those birds not visiting the nest usually spent the night roosting on the sea away from the colony, while birds that did visit the nest on a given night tended to roost within 20 km from the colony prior to landfall and resume roosting following their visit (figure 8). During both incubation (figure 9) and chick-rearing (figure 10), birds from Copeland typically foraged within relatively discrete, local areas, within 100-120 km of the colony. Birds from Skomer showed a more varied and dispersed foraging distribution. During incubation, few birds foraged locally, most commuting 200 km or more to the south Irish coast or to the area south west of the Isle of Man, where Copeland birds were foraging locally (figure 9). During the chick-rearing period, birds from Skomer foraged locally much more frequently, but continued to commute 200 km or more to the area south west of the Isle of Man (figure 10).

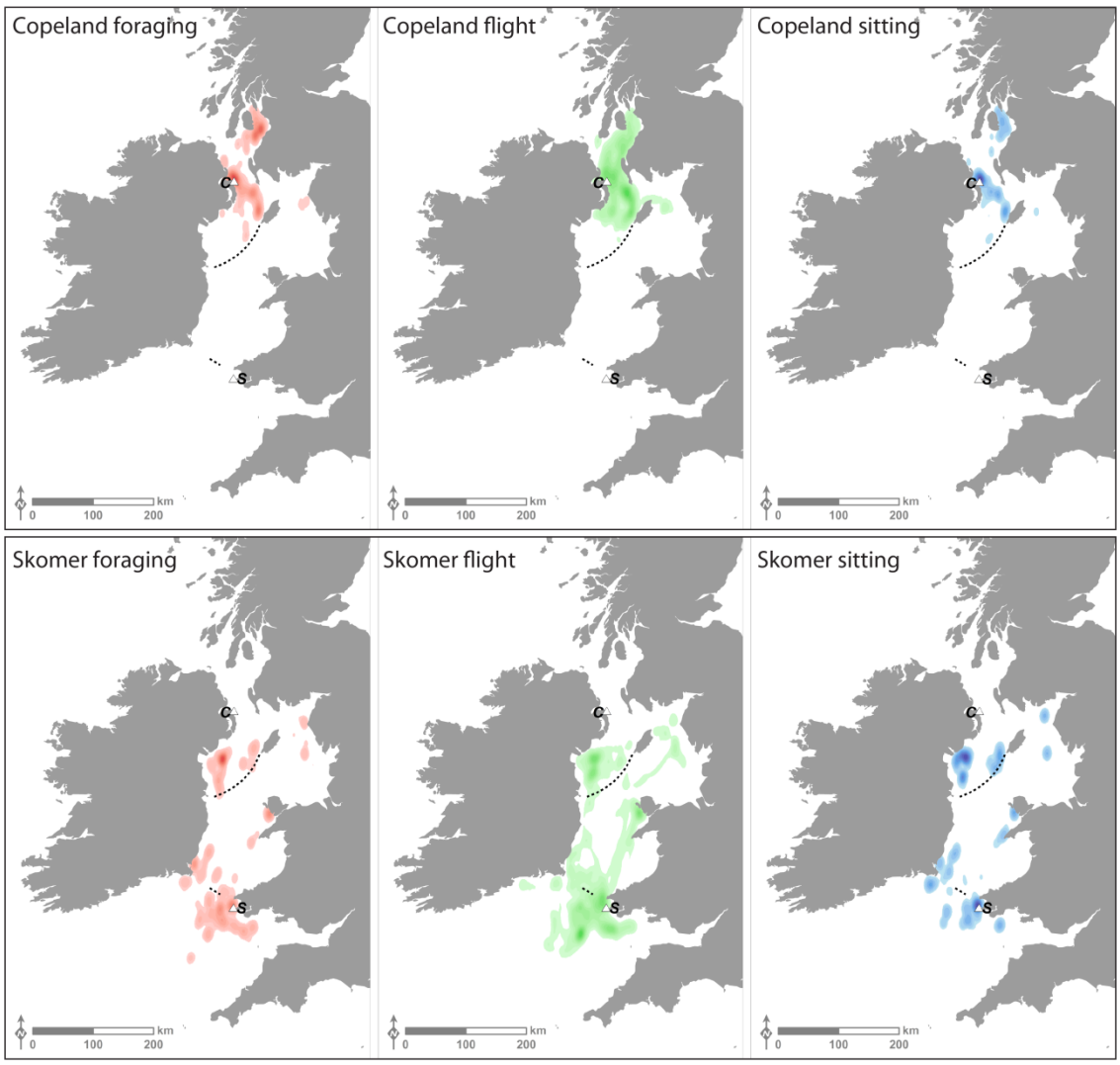

Figure 7. Example kernel density distributions of each activity for birds from Copeland and Skomer during the 2009 chick-rearing period: foraging (red), direct flight (green), sitting (blue). Densities are shaded from the lightest (95% occupancy) to the darkest (10% occupancy). Locations of Copeland (C) and Skomer (S) and the approximate positions of the Irish Sea Front (curved line) and Celtic Sea Front (short line) are shown.

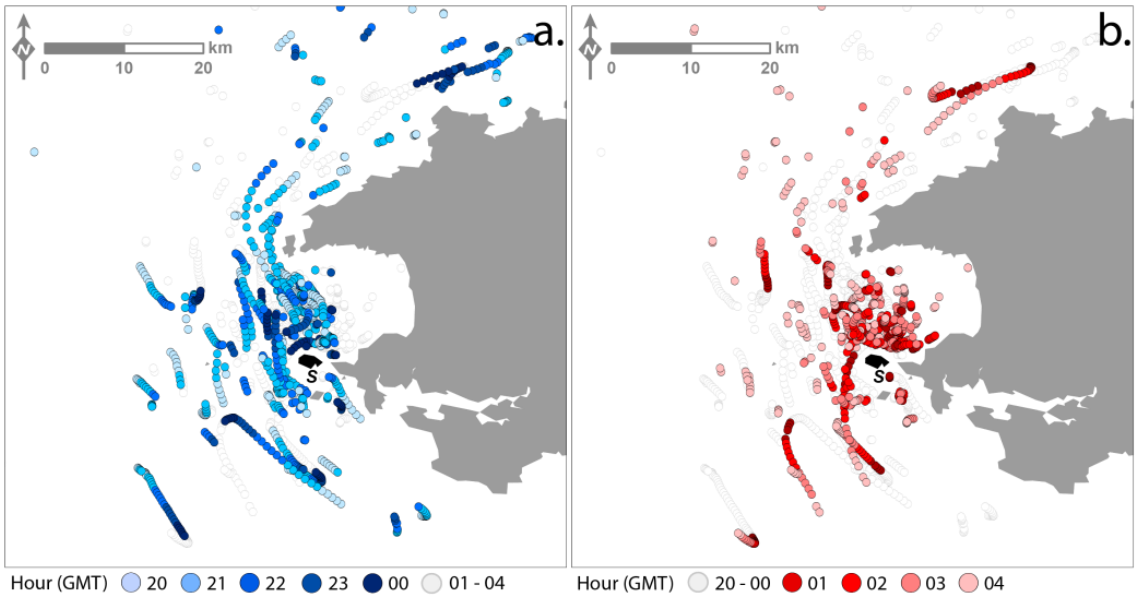

Figure 8. Nocturnal locations classified as sitting (roosting) around Skomer (S): (a) prior to most birds visiting the colony and (b) after most birds have left the colony. Locations are coloured by hour (GMT).

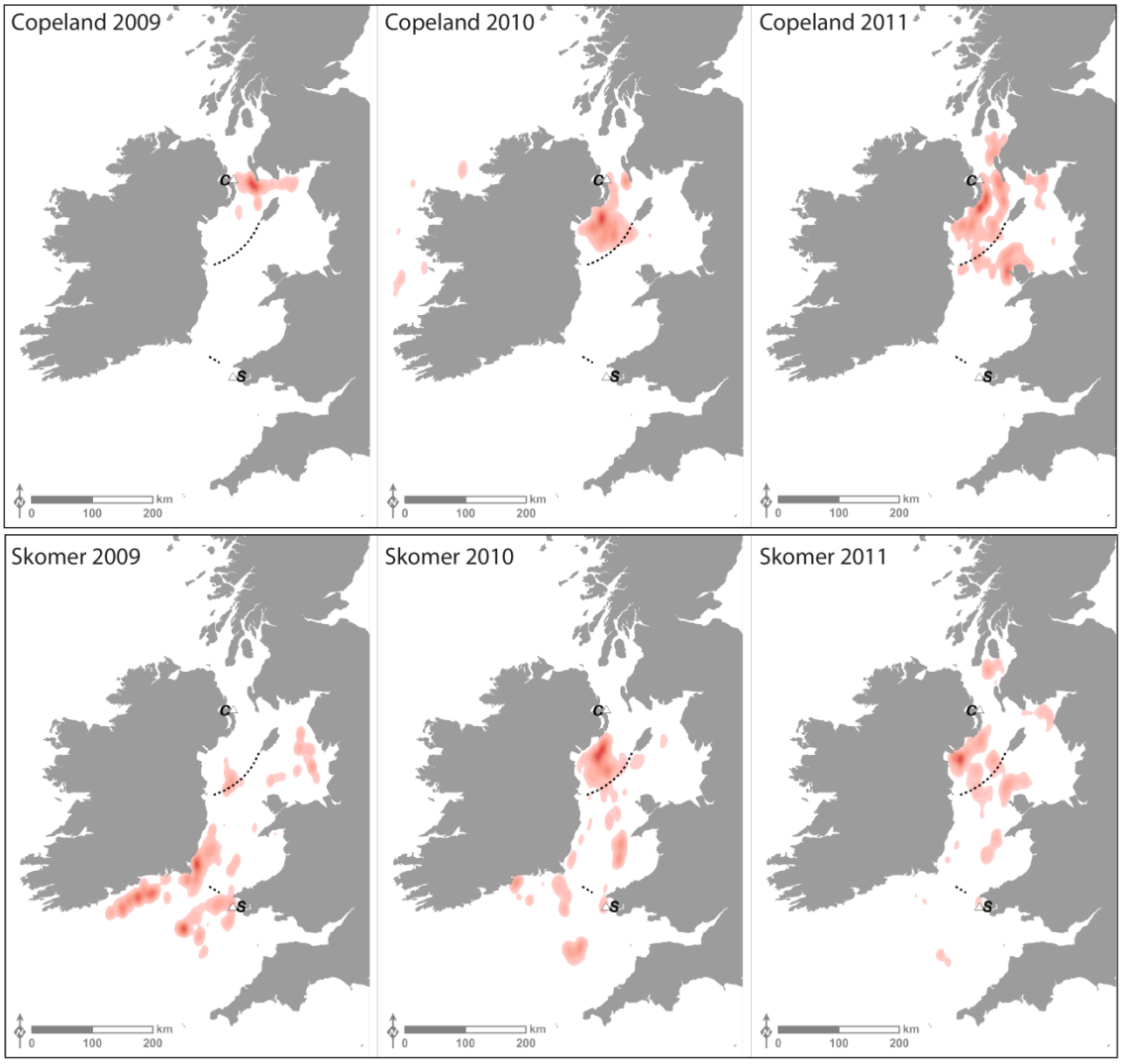

Figure 9. Kernel density foraging distributions of birds from Copeland and Skomer during the 2009, 2010, and 2011 incubation periods. Densities are shaded from the lightest (95% occupancy) to the darkest (10% occupancy). Approximate positions of the ISF (curved line) and CSF (short line) are shown.

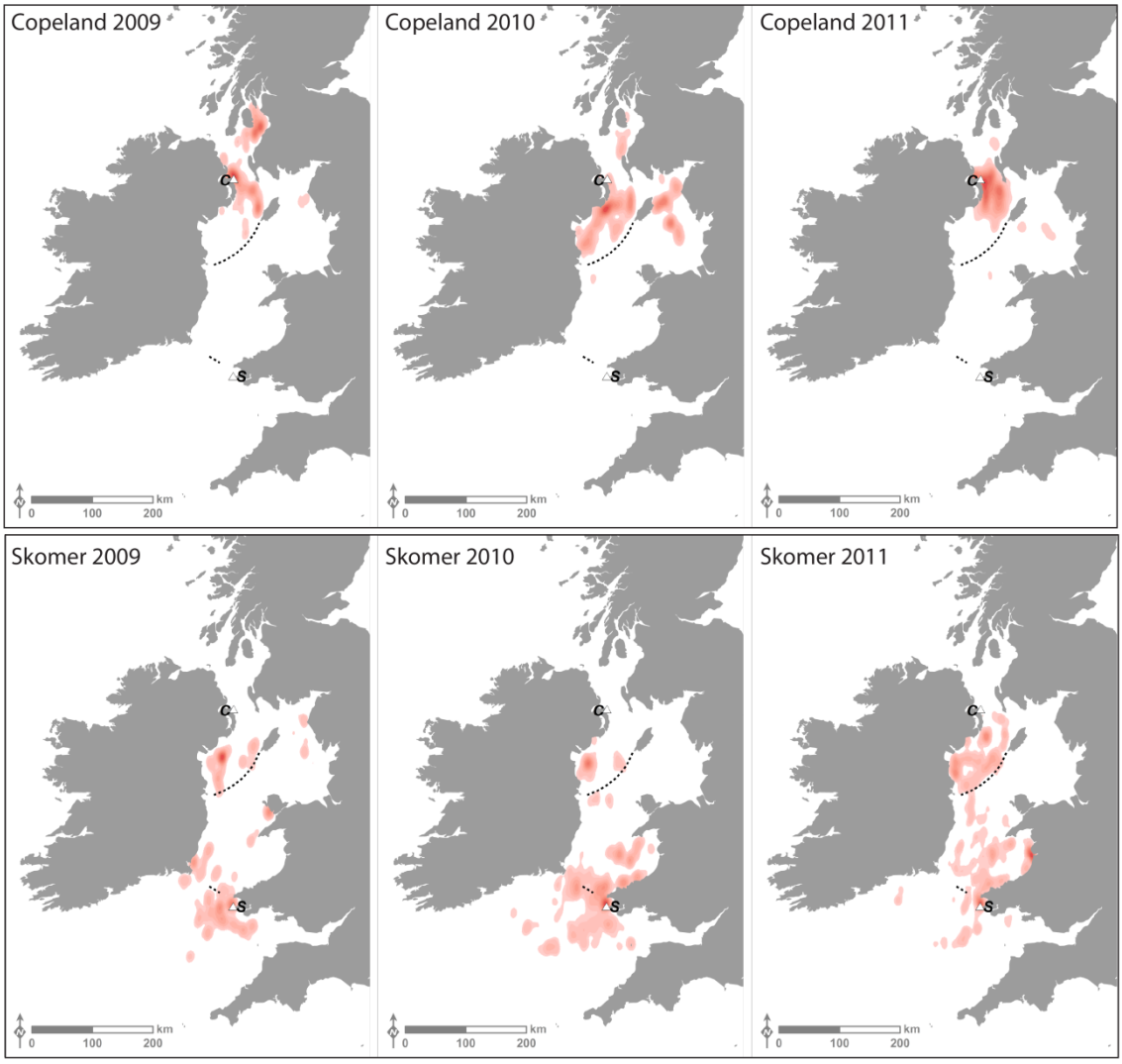

Figure 10. Kernel density foraging distributions of birds from Copeland and Skomer during the 2009, 2010, and 2011 chick-rearing periods. Densities are shaded from the lightest (95% occupancy) to the darkest (10% occupancy). Approximate positions of the ISF (curved line) and CSF (short line) are shown.

Discussion

Impacts of Tracking

Combined deployment of GPS, immersion loggers and TDRs provided highly detailed data on the at-sea movements and behaviour of individual Manx shearwaters. A previous meta-analysis of procellariiform tracking studies (Phillips *et al.* 2003) found negative impacts (nest desertion and increased trip duration) on a range of species carrying devices comprising 0.6–5.5% of body weight, although many of those deployments were of longer duration than here. Our control test suggests that our devices did not have detectable medium-term (breeding season) effects on reproductive success. We did not test for an effect of devices on trip duration, but the median incubation trip duration from Skomer in this study (8 days) was slightly longer than that previously reported for untagged birds from Skomer (5.4-6.9 days) (Brooke 1990), and mean trip duration from Skomer during chick-rearing (1.9 days) was similar to that previously reported for birds from Skomer carrying 2g tags (1.8 days) (Gray & Hamer 2001). It is possible that the devices had some effects on behaviour; however, our results suggest these would have been minor given the relatively short deployment durations.

At-sea Behaviour

The combination of data from multiple loggers (GPS, geolocator-immersion and TDR) and the application of a HMM allowed us to identify, interpret and explore three discrete states in the at-sea behaviour of a pelagic seabird during foraging trips away from the colonies. These three activities were stable over time, generally persisting for many consecutive time-steps within individual tracks. Our use of a HMM offered an integrated approach to identifying hidden states within the immersion and speed data, without requiring prior categorisation of the data into discrete groups of observations, while the deployment of multiple loggers provided additional data for interpretation and validation. The assumption of Gaussian emission distributions for logit transformed immersion data may introduce a small bias. Each of the states roughly

corresponded to a partitioning into low-immersion, high-immersion, and intermediate values. Gaussians fitted to the high and low peaks were likely to be skewed slightly towards the centre of the distribution, increasing the probability that some intermediate values would be categorised as low immersion, or high immersion. This may slightly underestimate the occurrence of the intermediate (foraging) state consistently across all birds, but otherwise we do not believe it significantly affects the findings.

Because of some irregularity in GPS signal acquisition, occasional missing locations, and the need to calculate speed within discrete intervals, we found it necessary to interpolate regular locations prior to implementing the HMM. We used a curvilinear interpolation, which typically produces more realistic estimates of animal movements than linear interpolation (Tremblay *et al.* 2006) and is less prone to underestimating path length and speed. Our tests indicated that it performed well in recreating GPS data recorded at a higher resolution (in Supplementary Material). For some behaviours, interpolation may not represent a realistic model of complex fine-scale movement between sampled locations. An alternative approach would have been to estimate location and behavioural state simultaneously within an integrated state-space framework (e.g. Jonsen *et al.* 2005; Pedersen *et al.* 2011), incorporating models of individual movement such as random walks, correlated random walks, or Lévy walks. Whilst such approaches may offer some advantages they can be computationally more complex, and their performance may depend on the choice of appropriate movement models and their parameters.

Sustained direct flight was characterised by little or no saltwater immersion, low path tortuosity, and an average movement speed of 8.9 m s^{-1}. Assuming that the movement speeds calculated here from the GPS (which include wind velocity) are reasonably representative of flight speeds (which exclude wind velocity), this is within the theoretical flight speed range previously calculated for Manx shearwaters (Pennycuick 1969), but slightly slower than that calculated from previous GPS tracking (11 m s^{-1}) using devices of similar mass (Guilford *et al.* 2008). For

long distance movements, birds may be expected to fly close to their maximum range velocity (c. 14 m s^{-1}, Pennycuick 1969). Here it seems that birds were flying closer to their minimum power velocity (c. 7.5 m s^{-1}, Pennycuick 1969), suggesting some exploitation of non-powered flight such as shear-soaring (Pavia *et al.* 2010a). Flight activity typically persisted over long periods and occurred where birds travelled long distances, often via relatively direct routes (figure 4). The post-sunrise and pre-sunset peaks in direct flight activity (figure 5) are likely to represent the majority of outbound flights from the vicinity of the colony to foraging areas, and return flights to the vicinity of the colony prior to visiting the nest. These peaks are more pronounced during chick-rearing than incubation, as would be expected given the much higher frequency of nest visits during this period. A small amount of diving (1%) occurred during a few of the intervals classified as flight. There is evidence in other pelagic seabirds that prey may be ingested even during extremely rapid (>100 km h^{-1}) and directed flight (Catry *et al.* 2004); hence, it may be impossible to classify behaviour unequivocally in every instance (especially short lived ones) based on 10 minute intervals of movement and immersion data.

Sitting on the sea was characterised by very slow movement and high or continuous immersion, typically persisting over short periods during daylight hours and long periods at night. Sitting on the water at night was apparent as long series of consecutive time steps forming straight or curvilinear series of locations (figure 8). Movement speeds during sitting activity (0.65 m s^{-1}) were consistent with tidal drifting speeds previously estimated for shearwaters from GPS data (0.85 m s^{-1}) (Guilford *et al.* 2008). The virtual absence of diving (3%) during sitting suggests that this activity may largely represent resting behaviour. Much sitting on the surface occurred close to the colonies during the evening and early hours of darkness: as with many procellariids, Manx shearwaters form dense roosting flocks on the sea adjacent to colonies prior to nest visits (Brooke 1990) (figure 8a). Our analysis showed that nocturnal at-sea roosting adjacent to the colony continued after 01:00, when most birds had already visited their burrow (figure 8b). After departing the colony, birds resumed roosting on the sea until first light, while others spent

nights adjacent to the colony without visiting their burrow. Wilson *et al*. (2009) used the locations of radio-tracked birds, assumed to be in nocturnal roosting flocks, to estimate the extent of those flocks around several colonies as a tool to define marine protected areas. For Skomer they estimated a 95% kernel density core that extended 4 km from the colony, suggesting that this area would encompass most roosting birds. Our analysis suggests that nocturnal roosting may routinely occur at much greater distances from the colony.

Foraging activity was characterised by intermediate movement speeds around 2 m s^{-1} and by intermediate levels of immersion which, combined with the relatively high probability (0.69) of persisting over several consecutive 10 minute intervals (figure 3), suggests repeated transitions between the air and the sea surface/submersion. The majority (96%) of diving occurred during this activity, reflecting the majority of attempts at prey capture. Foraging typically occurred within restricted areas (figure 4), reflected by a significantly higher track tortuosity than during either direct flight or sitting. This is consistent with a pattern of foraging involving attraction movements between sparse, locally dynamic prey patches, convoluted search flight (area restricted search), frequent landings and take-offs from the surface, and dives in pursuit of prey. Many intervals classified as foraging did not involve diving, suggesting that our third activity class includes search behaviour as well as prey pursuit, and that birds may often engage in unsuccessful searches without locating prey. A strong visual component to searching and prey capture is suggested by the timing of foraging activity, which appeared to be constrained to the hours of daylight and twilight (figure 5). Thus we tentatively infer that the primary foraging mode of Manx shearwaters involves local-scale area-restricted search involving frequent landings, perhaps to sample or view prey, and then, if conditions are suitable, attempted prey pursuit and capture.

However, the search behaviours associated with foraging are likely to be multi-scaled phenomena (Weimerskirch *et al.* 2007; Nevitt *et al.* 2008; Pavia *et al.* 2010b). Over larger scales,

where the distance between prey patches exceeds the perceptual range of the predator, straight movement may be the most effective method of searching for prey (Zollner & Lima 1999). In our analysis, large-scale straight-line search without significant periods of immersion would be categorised as sustained direct flight. Birds often made sustained flights more or less directly to a restricted area and then engaged in foraging (figure 4). The state transition probabilities (figure 3) support this: intervals classed as flight were most likely to be followed by further intervals of flight ($p = 0.68$), foraging was more likely to follow a period of sustained flight than of sitting ($p = 0.31$ versus 0.19) and flight was more likely to lead to foraging than sitting ($p = 0.31$ versus 0.002). It is possible, then, that shearwaters also searched for food over larger scales using long, relatively direct flights away from the colony, switching to area restricted search only where conditions were perceived as suitable. Nevertheless, the direct nature of some track segments and the consistency of some distant foraging locations also suggest that many larger scale direct movements were informed by previous experience (or the following of other birds informed by previous experience), with shearwaters commuting directly to known profitable areas, and then engaging in local search and pursuit behaviour. This would imply an important role for learning and the building of a large-scale memorised map of foraging areas. The nature of the cues, or representations involved in searching and map learning have yet to be investigated, but almost certainly include a strong social element, with the location of prey patches signalled by the activities of conspecifics or other foragers (Stone *et al.* 1994; King 1974; Jones 1975; Sakamoto *et al.* 2009). Shearwaters are typically recorded feeding in large flocks at sea (Stone *et al.* 1994; King 1974) where there is likely to be a strong element of social enhancement of individual foraging success (Götmark *et al.* 1986).

Colony differences

During both incubation and chick-rearing, birds breeding on Skomer made trips of longer range and covered greater distances per day than birds breeding on Copeland. The results of the HMM

confirm that birds from Skomer spent a greater percentage of daylight hours engaged in direct flight and consequently less time engaged in foraging activity than birds from Copeland. Taken together, this suggests that it may be more difficult for birds breeding on Skomer to locate and reach the prey resources necessary during the breeding season.

Mapping these behaviours reveals that birds breeding on Skomer typically foraged in more distant and dispersed locations than birds from Copeland. The foraging distributions of birds from both colonies consistently overlapped in the area south west of the Isle of Man which corresponds with the location of the western Irish Sea Front (ISF) (Simpson & Hunter 1974) and in particular, the stratified waters to the north and west (figures 8 and 9). The aggregation of seabirds at frontal systems is well documented (Schneider 1990; Stone *et al.* 1994; Begg & Reid 1997; Vlietstra *et al.* 2005) and the ISF is likely to provide profitable feeding opportunities as increased phytoplankton growth (Savidge 1976; Beardall *et al.* 1982) attracts high densities of zooplankton and fish (Scrope-Howe & Jones 1985; Fernandes 1993). During chick-rearing trips, Skomer birds foraged locally (within 100km of the colony) more frequently than during incubation trips, but continued to make longer range trips to the area around the ISF. The increase in local foraging is likely to reflect the requirement to return more frequently to the nest to provision the chick. This requirement may (to some extent) be facilitated by increasing opportunities to forage locally as the summer progresses and variable local fronts such as the Celtic Sea Front (CSF) (Simpson & Hunter 1974) (figure 10) become established.

Differences in the percentage of time engaged in direct flight and foraging activities support the proposal (Guilford *et al.* 2008) that Copeland breeders benefit from reduced travel costs because of the colony's proximity to the ISF. During incubation, the median trip duration from Copeland was slightly shorter (7 versus 8 days) and the mean increase in mass slightly (though not significantly) greater (32 versus 24g) than for birds from Skomer. During chick-rearing, birds from both colonies delivered similar sized meals to their chicks (45 versus 44g), but birds from

Skomer spent more time engaged in direct flight (covering greater distances per day and overall) and less time engaged in foraging activity than birds from Copeland. This suggests that birds breeding on Skomer must work harder to locate prey, presumably at a greater cost to their own body condition (minimum weights of birds from Copeland during chick-rearing were heavier, though not significantly, than those from Skomer: 415 versus 409 g).

Conclusions

Here we have demonstrated an approach that makes full use of a large, new, multiple sensor bio-logging dataset, applying a HMM to reveal patterns of behaviour and segment foraging trips according to the activities undertaken. We used this technique to identify the principal at-sea activities of the Manx shearwater, to explore the spatiotemporal variation in those activities, and to map those areas that were important for different types of behaviour. We have shown important differences in foraging trip behaviour which may have significant energetic consequences for birds breeding on different colonies and have highlighted the importance of one key foraging area in the Irish Sea, the ISF. This type of analysis has considerable potential for application in future bio-logging studies and in other taxa, to examine behaviour at a range of temporal and spatial scales. For example, analyses of the spatiotemporal structure of activity sequences and transitions between behavioural states in relation to the location of prey may improve our understanding of how animals respond to prey distributions and the decisions they make when searching. While at large scales, this type of behavioural mapping has high value for conservation planning, allowing better identification of the key areas and habitats where animals engage in specific types of behaviour. This type of information could greatly improve assessments of the degree of interaction between particular threats and those behaviours that increase risk: for example foraging and fisheries, commuting flight and wind turbines, or roosting and surface pollution.

Acknowledgements

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Supplementary Material

Table S1. Mean (±SD) bird mass, mass changes (incubation), chick-meal sizes (chick-rearing), and median (+IQR) trip metrics for incubation (Inc.) and chick-rearing (Rear.) trips made by birds from Copeland (Cp.) and Skomer (Sk.).

Colony	Period	Dep./min. mass (g)	Mass change/ meal (g)	Trip dur. (days)	Max. Range (km)	T. dist. (km)	km day^{-1}
Both	**Inc.**	406.9 ± 26.6	+27.8 ± 28.0	8 (5-10)	150.2 (118-239)	1191.2 (737-1608)	163.4 (127-184)
Both	**Rear.**	411.8 ± 31.7	44.8 ± 17.5	1 (1-3)	70.5 (47-115)	284.3 (175-594)	192.4 (148-239)
Cp.	**Inc.**	407.3 ± 22.7	+32.2 ± 29.2	7 (5-9)	119.2 (87-150)	1058.5 (459-1543)	136.8 (116-171)
Sk.	**Inc.**	406.4 ± 32.5	+23.9 ± 26.8	8 (6.5-11)	247.6 (176-290)	1432.4 (910-1861)	179.1 (163-201)
Cp.	**Rear.**	415.0 ± 32.5	44.3 ± 17.4	2 (1-3)	56.3 (29-97)	262.4 (145-560)	171.5 (127-206)
Sk.	**Rear.**	408.8 ± 31.2	45.2 ± 17.6	1 (1-2)	88.3 (63-141)	305.2 (210-599)	223 (187-266)

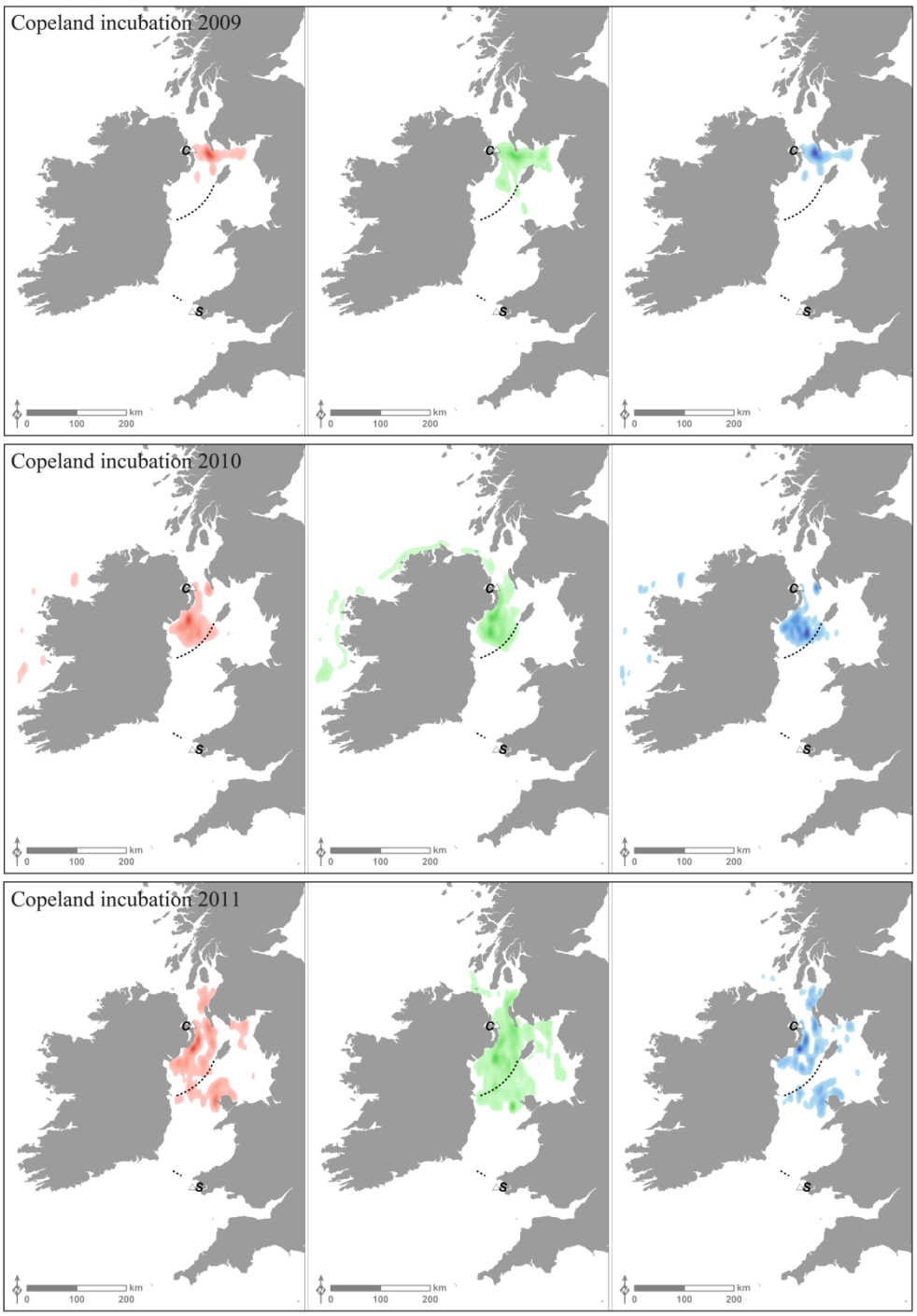

Figure S1. Kernel density maps showing the distribution of each activity for birds from Copeland during incubation: foraging (red), direct flight (green), and sitting (blue). Densities are shaded from the lightest (95 % occupancy) to the darkest (10 % occupancy). Locations of Copeland (C) and Skomer (S) and the approximate positions of the Irish Sea Front (curved line) and Celtic Sea Front (short line) are shown.

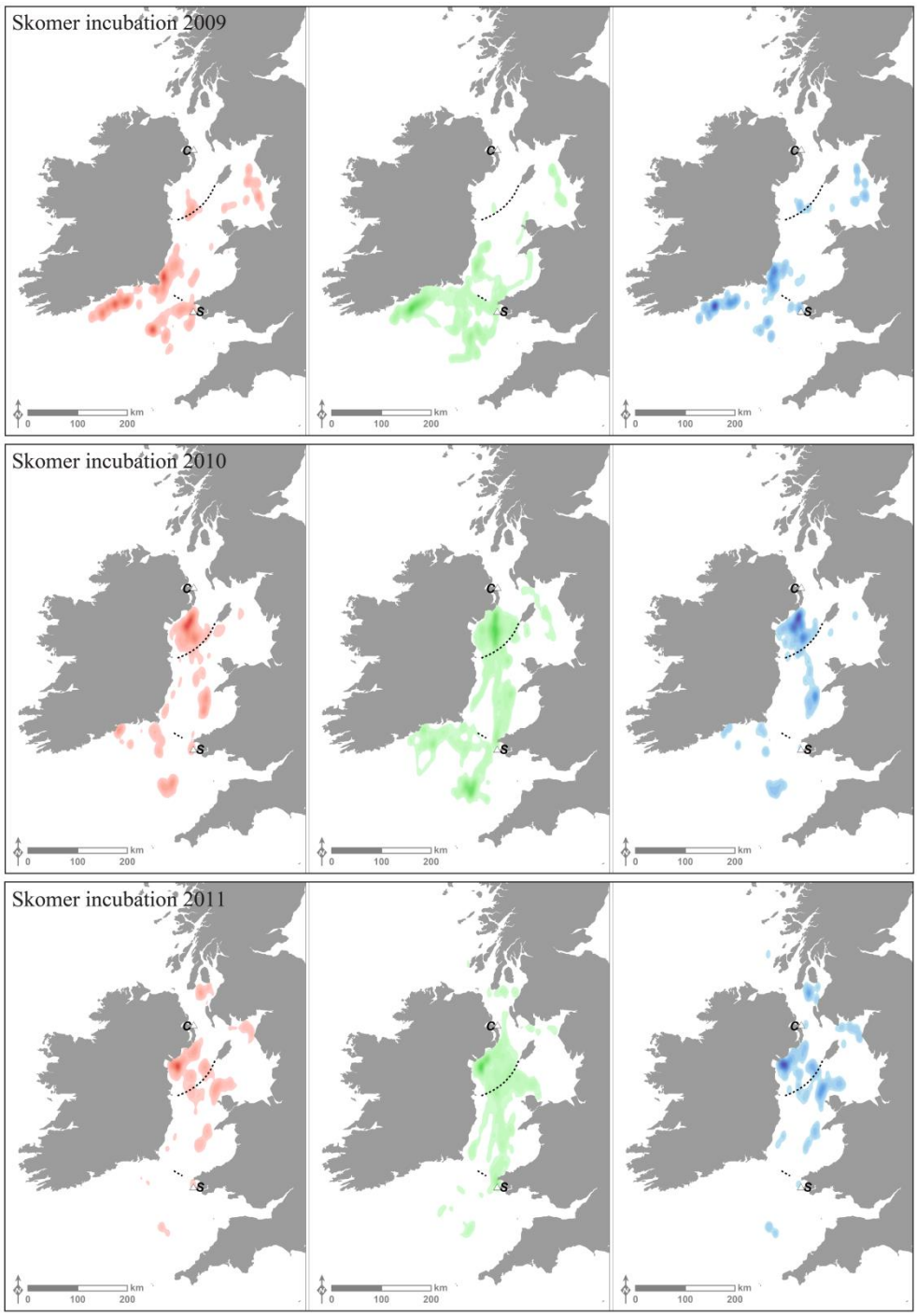

Figure S2. Kernel density maps showing the distribution of each activity for birds from Skomer during incubation: foraging (red), direct flight (green), and sitting (blue). Densities are shaded from the lightest (95 % occupancy) to the darkest (10 % occupancy). Locations of Copeland (C) and Skomer (S) and the approximate positions of the Irish Sea Front (curved line) and Celtic Sea Front (short line) are shown.

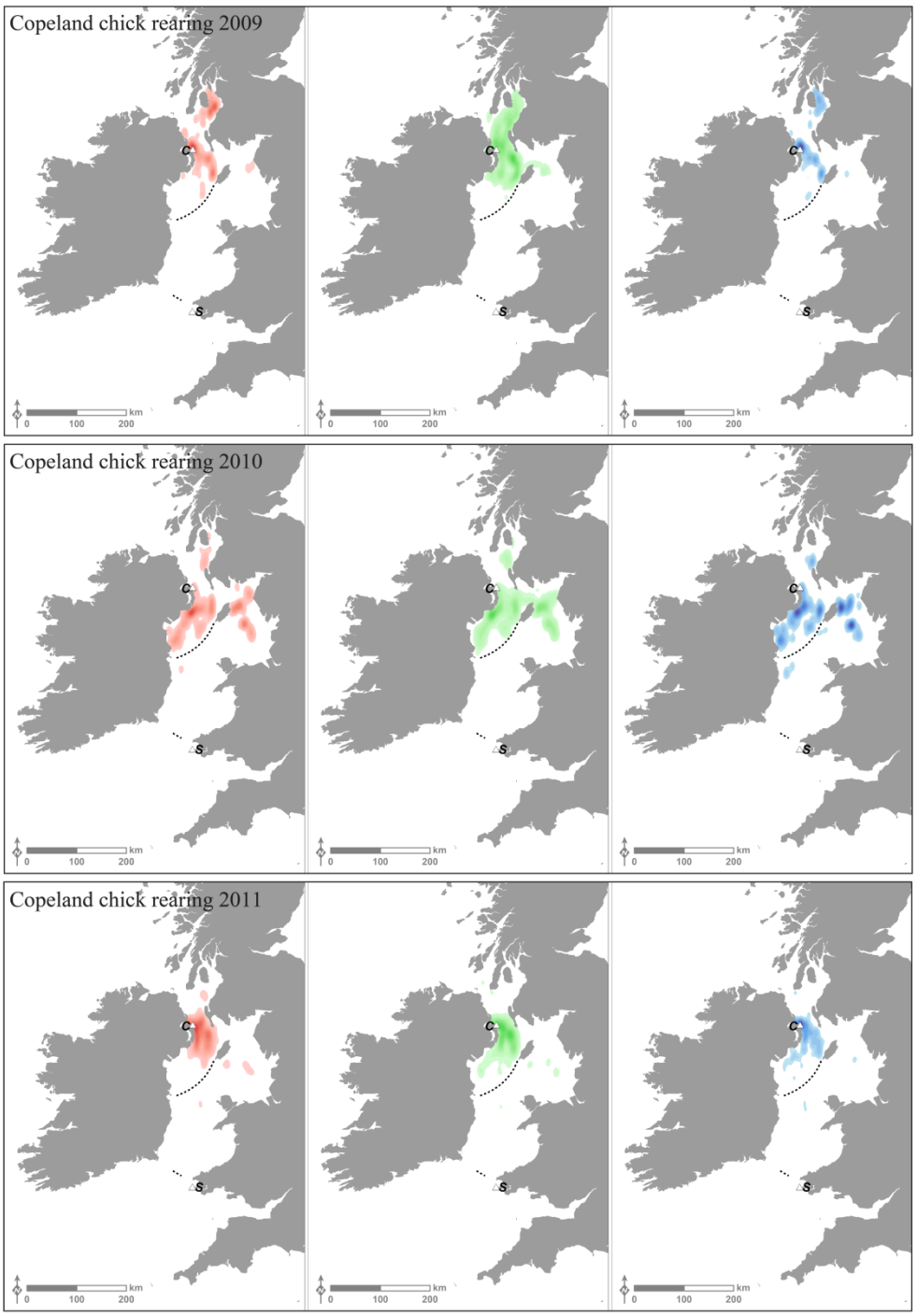

Figure S3. Kernel density maps showing the distribution of each activity for birds from Copeland during chick rearing: foraging (red), direct flight (green), and sitting (blue). Densities are shaded from the lightest (95 % occupancy) to the darkest (10 % occupancy). Locations of Copeland (C) and Skomer (S) and the approximate positions of the Irish Sea Front (curved line) and Celtic Sea Front (short line) are shown.

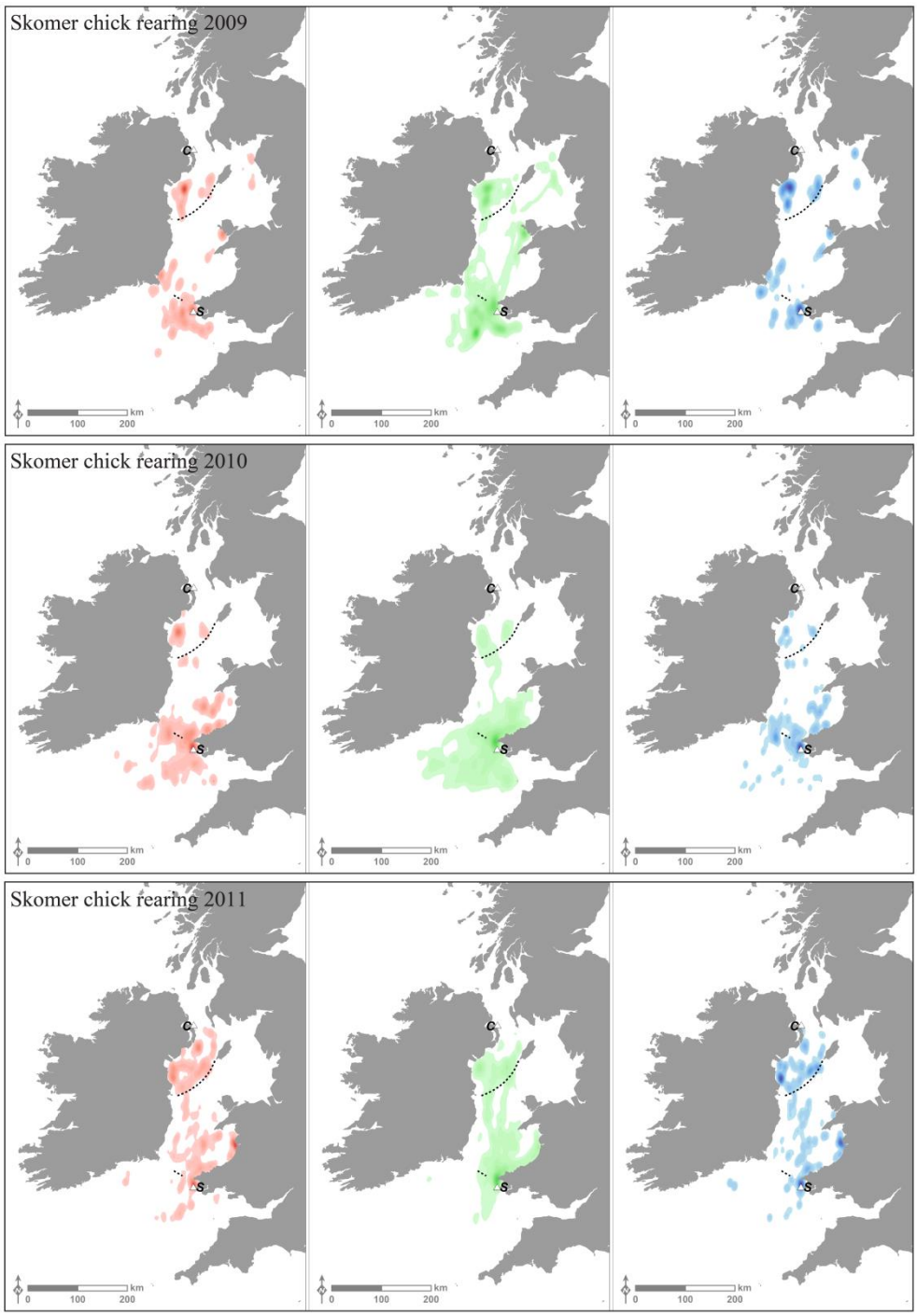

Figure S4. Kernel density maps showing the distribution of each activity for birds from Skomer during chick rearing: foraging (red), direct flight (green), and sitting (blue). Densities are shaded from the lightest (95 % occupancy) to the darkest (10 % occupancy). Locations of Copeland (C) and Skomer (S) and the approximate positions of the Irish Sea Front (curved line) and Celtic Sea Front (short line) are shown.

Validation of our interpolation for speed calculations

The GPS loggers used in this study (modified i-gotU GT-120: Mobile Action) make an on-board calculation and log their movement speed each time they record a location. However, these values appear to be based upon almost instantaneous on-board estimation of speed at the point of acquiring and logging the location. The value recorded by the device therefore is not necessarily representative of the average speed over the whole interval between GPS fixes. For example, if a bird spends most of a 5 minute period resting on the sea surface, but then takes off and accelerates just before the GPS takes a fix, the recorded speed would be unrepresentative of the bird's overall behaviour. We did not use these data.

We calculated speed as the straight-line distance divided by time between sequential locations. Because the recording intervals of the GPS and immersion loggers were not in sync and because the GPS recording interval was not precisely regular (due to slightly variable satellite acquisition times) it was difficult to make appropriate speed calculations using the raw data. As an example, in figure S5, 5-minute resolution GPS points (1-8) fall within 10-minute periods of immersion data (A-D). Red parts of the track indicate fast movement, blue parts indicate slower movement. A mean speed value for the ten minute period B-C could be calculated between GPS locations 3 and 4. But this would not represent all of the movement during the period, in particular the faster movement as the bird decelerates at the start of the period B-C would not be represented, resulting in an underestimate of mean speed. An alternative would be to calculate the mean speed between GPS locations 2, 3 and 4, but this would include additional fast movement prior to period B-C, resulting in an overestimate of mean speed. This is a particular problem where speed changes quickly and frequently.

To overcome this we interpolated 1-minute resolution GPS locations from the recorded GPS locations using piecewise cubic hermite polynomials following Tremblay *et al*. (2006). In figure S6 the mean speed for the 10-minute period B-C can be calculated using all interpolated

locations between 3 and 4 inclusive. This better represents all movement within the period B-C including the faster movement during the initial deceleration, without including movement from the previous or following periods. In this study, mean movement speed was calculated over the ten interpolated locations within each 10-minute interval in the immersion data.

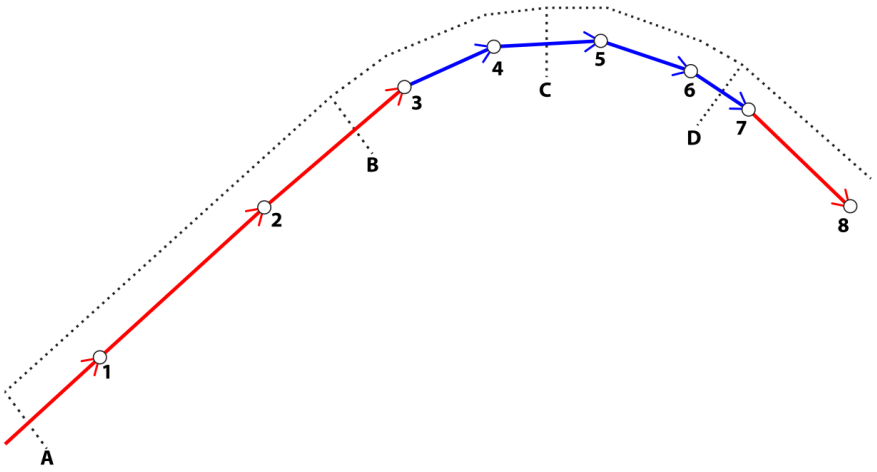

Figure S5. Schematic of the calculation of mean speed corresponding to 10-minute samples in the immersion data, based on 5-minute resolution GPS locations.

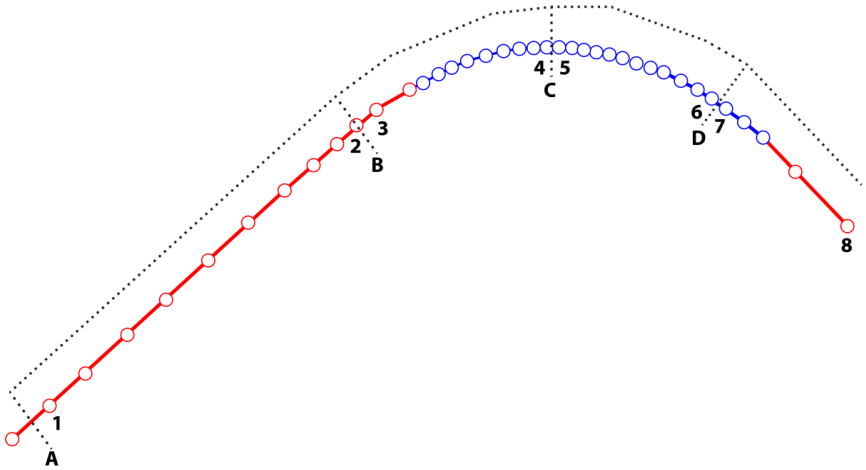

Figure S6. Schematic of the calculation of mean speed corresponding to 10-minute samples in the immersion data, based on 1-minute locations interpolated from 5-minute resolution GPS locations.

Calculating speed in this way gave a better representation of movement over each entire 10-minute interval than the more sparsely recorded raw locations. To confirm this assertion and to ensure that the interpolation did not give spurious speed values we analysed a small number of additional Manx shearwater GPS tracks that were originally recorded at 1-minute resolution. We sub-sampled the 1-minute resolution GPS tracks to create tracks at 5-minute resolution. We then interpolated 1-minute resolution GPS locations from the sub-sampled 5-minute locations using the same method as in this study. We therefore had three sets of the same tracks (i) recorded at 1-minute resolution, (ii) subsampled to 5-minute resolution and (iii) interpolated from 5-minute to 1-minute resolution. We then calculated average speed and location over ten-minute periods (as in this study) for each of the 3 sets and compared results. The interpolated data showed no bias and better represented the original 1-minute data (Pearson correlation between the 1-minute recorded and 1-minute interpolated mean speed values $r=0.99$, $P<0.001$) than did the sub-sampled 5-minute data (figure S7). Previous tests of this method Tremblay *et al*. (2006) indicated that the average accuracy of interpolated locations was always within the precision of the tracking technique used.

In addition, tracks plotted using the averaged locations from the interpolated data better represented spatially the tracks plotted using the averaged locations from the original 1-minute data than did those plotted using 5-minute sub-sampled data (figure S8). In summary, the use of interpolation here better represents high resolution recording of movement over the 10- minute intervals in the immersion data than more sparsely recorded 5-minute GPS locations, without introducing significant bias to the estimation of speed and location.

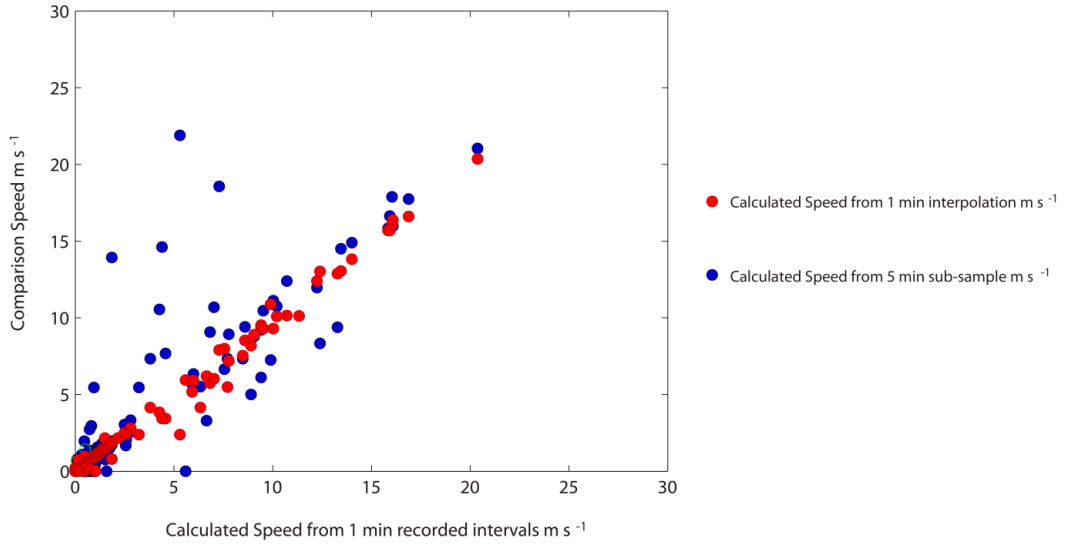

Figure S7. (Red points) Comparison of calculated mean speed values for recorded 1-minute GPS locations and 1-minute positions interpolated from sub-sampled 5-minute GPS locations. (Blue points) Comparison of calculated mean speed values for recorded 1-minute GPS locations and sub-sampled 5-minute GPS locations.

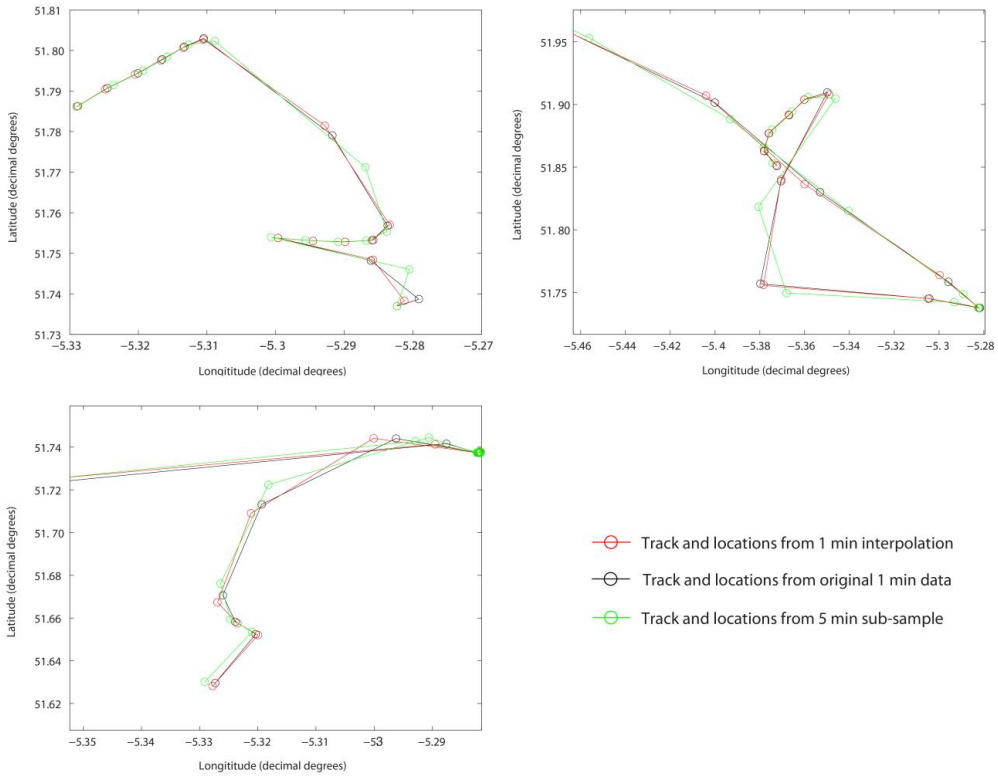

Figure 4. Comparison of GPS tracks for averaged locations from the original 1-minute tracks (black), interpolated tracks (red) and 5-minute sub-sampled tracks (green).

Chapter 6

The effect of reduced provisioning requirement on the provisioning and foraging behaviour of Manx shearwater parents

Dean, B.J., Fayet, A., Freeman, R., Perrins, C.M. & Guilford, T.C.

Unpublished Manuscript

Abstract

Procellariiform nestlings accumulate large quantities of fat during the nestling period. This accumulation appears to be regulated in many species, potentially allowing the fat reserves of chicks and parental provisioning to be optimized; maximising the survival of the chick up to and beyond fledging, and minimizing foraging effort by the parents. Foraging trip duration and hence provisioning rate provides a potential mechanism by which parents may regulate provisioning effort. The parents of well-fed chicks have been shown to make fewer nest visits and hence a greater proportion of longer duration (self-feeding) foraging trips. However, the role of foraging ranges, destinations and at-sea foraging behaviour of parents in this flexible provisioning response is unknown.

We provided a high-energy supplemental diet to Manx shearwater chicks, then monitored the provisioning behaviour and tracked the at-sea behaviour of their parents and the parents of control chicks. We found that the parents of supplemented chicks did not reduce the frequency of their nest visits, but did not deliver detectable meals in the majority of visits. The lack of an expected decrease in provisioning rate in favour of longer-duration foraging trips probably results from a large positive knock-on effect of the supplemental feeding on the body condition of the parents, negating the requirement for long self-feeding trips. The lack of detectable meals fed to supplemented chicks probably resulted from chicks being unable to ingest further meals from their parents, but there was also some evidence of a responsive reduction in the mass of food brought to the nest by parents.

Despite our large energetic input into the rearing of supplemented chicks and the likely energetic advantage to their parents, we found no significant differences in the routes and destinations of foraging trips compared to those of control parents. Neither did we find any significant differences in foraging behaviour. This suggests that while foraging trip duration has been shown to be flexible in response to chick and adult body condition, the at-sea foraging

behaviour does not appear to form part of this flexible response. At-sea behaviour probably is controlled more by foraging conditions and prey distributions than by the nutritional demands of the chick.

Introduction

Feeding offspring forms a major component of parental effort, particularly for central place foragers such as seabirds whose dependent offspring may remain in the nest for extended periods, far from the best foraging areas. Parents should therefore optimize food delivery so as to balance current and future reproductive output (Martin 1987; Stearns 1992): ensuring that chicks are never chronically underfed (at the expense of current nestling growth and survival), or excessively provisioned (at the expense of parental effort, survival and future reproductive opportunities). To this end, parental provisioning rates may be regulated by a cycle of sequential events comprising the nutritional status of the chick, solicitation for food by the chick, parental foraging effort, parental body condition, and delivery of food to the chick (Harper 1986, Hussell 1988). However, all procellariiform nestlings accumulate large quantities of fat/lipid during the nestling period (Warham 1990), much of which is metabolized prior to fledging during a period of reduced (or absent) parental provisioning. In conjunction with a protracted period of development, the accumulation of fat has been viewed as an adaptation that provides insurance against periods of reduced food delivery resulting either from sparse, patchy and unpredictable prey distributions (Lack 1968, Ashmole 1971), from reduced feeding rates during bright moonlit periods (Riou & Hamer 2008), or from chance variability in the foraging success of individual parents (Ricklefs & Schew 1994; Hamer *et al.* 2000; Phillips & Hamer 2000). Alternatively, the primary functional role of stored lipids may be to fuel the final stages of development during the period of reduced parental provisioning prior to fledging (Riou & Hamer 2010), or during the initial critical period following fledging (Phillips & Hamer 1999).

But while accumulation of large lipid reserves by the chick has several potential advantages in terms of chick development and survival, excessive lipid accumulation also may have negative effects on the survival of the chick if it necessitates an extended period of fasting that delays fledging (Perrins *et al.* 1973; Cherel *et al.* 1988). More importantly for the parent where provisioning is excessive, such accumulation is likely to be wasteful of parental foraging effort, with potential negative effects on parental survival. Procellariiforms rear one chick at a time and may breed many times in their long lives (Warham 1990). Life-history theory predicts that parents should therefore limit their provisioning effort during a given breeding attempt to optimize the balance between current and future reproductive output (Martin 1987; Stearns 1992; Sæther *et al.* 1993; Mauck & Grubb 1995). The fat reserves of chicks and parental provisioning rates should therefore be optimized to maximise the survival of the chick up to and beyond fledging, and minimize foraging effort by the parents (Ricklefs & Schew 1994; Lorentsen 1996). Responsive regulation of provisioning effort requires chicks to signal their nutritional status though begging (Quilfeldt *et al.* 2004; Quillfeldt & Masello 2004; Hamer *et al.* 2005; Quillfeldt *et al.* 2007; Gladbach *et al.* 2009; Quillfeldt *et al.* 2010) or an inability to accept further food (Weimerskirch *et al.* 1997a; Hamer *et al.* 1999a). Parents must then be capable of perceiving those signals and regulating their subsequent provisioning effort in response (Bolton 1995; Hamer *et al.* 1998; Hamer *et al.* 1999b; Quilfeldt *et al.* 2004; Quillfeldt & Masello 2004; Hamer *et al.* 2005; Quillfeldt *et al.* 2010; Weimerskirch *et al.* 1995; Weimerskirch *et al.* 1997a; Hamer & Hill 1997; Hamer & Thomson 1997; Granadeiro *et al.* 1999; Baduini 2002).

Foraging trip duration and hence provisioning rate provides a potential mechanism by which parents may regulate provisioning effort. Many procellariiform parents mix short duration and longer duration foraging trips during chick-rearing (Chaurand & Weimerskirch 1994; Weimerskirch *et al.* 1994; Weimerskirch *et al.* 1997b; Weimerskirch *et al.* 1998; Weimerskirch *et al.* 2003; Magalhães *et al.* 2008), although it may not be the rule (Phillips *et al.* 2009). Such a strategy is thought to allow parents to optimize reproductive effort by combining short trips to

local areas (which maximise food delivery rate to the chick at a net energetic cost to themselves) with longer trips to more distant productive areas (which result in a lower rate of food delivery to the chick, but which allow parents to recover body condition lost on short trips). Longer duration foraging trips also may be advantageous by allowing birds to make exploratory forays, providing new information about potential foraging opportunities, and may reduce the cumulative risk of mortality associated with frequently returning to the colony (Riou & Hamer 2008). Several studies have demonstrated that the decision to embark on longer duration foraging trips may be controlled by the parent's body condition (Weimerskirch 1998; Weimerskirch & Cherel 1998), and/or the chick's nutritional status (Weimerskirch *et al.* 1997a; Hamer *et al.* 2005). The mass of meals delivered to (or accepted by) chicks provides a second mechanism by which provisioning rate may be regulated (Weimerskirch *et al.* 1997a; Quilfeldt *et al.* 2004; Hamer *et al.* 2005). While adjustment of trip duration (and hence provisioning frequency) is likely to be controlled by parents adjusting provisioning in response to both the chick and their own body condition, the mass of meals may largely be controlled by the assimilatory capacity of the chick (Weimerskirch *et al.* 1997a). Parents may however, subsequently adjust the mass of meals brought to the nest (e.g. Sæther *et al.* 1993). In the case of reduced meals this could allow parents to increase their own body condition without affecting wing-loading (Pennycuik 1982).

While the ability to regulate provisioning appears to be a feature of the breeding behaviour of many species, the effect on the at-sea foraging behaviour of parents and the extent to which this is flexible is largely unknown. Previous studies of the provisioning responses of parents have examined the effect of manipulations of chicks' nutritional status on the at-nest provisioning behaviour (e.g. Bolton 1995; Weimerskirch *et al.* 1995; Weimerskirch *et al.* 1997a; Hamer *et al.* 1998; Hamer *et al.* 2005), or have linked at-sea behaviour with natural variation in the nutritional state of the chick and parents (e.g. Weimerskirch & Cherel 1998), but have not directly examined the effects of manipulated chick condition on the at-sea behaviour of parents.

We studied the foraging and provisioning behaviour of the Manx shearwater *Puffinus puffinus*. Chick rearing Manx shearwaters make foraging trips of 1-7 days (Gray & Hamer 2001a), with short trips tending to maximise food delivery to the chick at the expense of parental body condition and longer trips tending to maximise improvement in parental condition at the expense of reduced food delivery to the chick (Chapter 3). During foraging trips they exploit areas within the Celtic and Irish seas (Guilford *et al.* 2008; Dean *et al.* 2012; Chapter 3), returning nocturnally to feed the chick at an average interval of 1.8 nights (Gray & Hamer 2001a). Males have been shown to feed their chick on a greater proportion of nights than females, delivering food to chicks at a higher rate, and making a greater contribution to overall food provisioning than females (Gray & Hamer 2001a). Both chicks and parents have been shown to influence the rate of food provisioning (Hamer *et al.* 1999b; Gray & Hamer 2001b). Chicks convey honest information about their condition in begging calls (Quillfeldt *et al.* 2004) to which parents are capable of responding through short term adjustment of provisioning effort, either by increasing provisioning rate (but not meal sizes) to underfed chicks (Hamer & Hill 1997), or by decreasing provisioning rate and meal sizes to well fed chicks (Hamer *et al.* 1998; Hamer *et al.* 2005). Both sexes appear to be able to regulate provisioning effort (Hamer *et al.* 2005), although females may be more responsive to begging intensity by the chick (Quillfeldt *et al.* 2004).

However, although the parents of well-fed (experimentally supplemented) chicks make fewer nest visits and hence longer duration foraging trips (Hamer *et al.* 2005), their maximum recorded trip duration was unchanged, suggesting that the foraging ranges, destinations and overall foraging behaviour of parents may not be altered as part of the flexible provisioning response. To address this question we experimentally decreased the nutritional requirements of Manx shearwater chicks (and consequently the provisioning requirements on the parents) using supplemental feeding of a high energy diet. We then examined the subsequent at-nest provisioning (provisioning rate and meal sizes) and at-sea foraging behaviour (routes, destinations and foraging) of their parents, compared to the parents of a control group of un-

manipulated chicks. Based on previous studies, we predicted several outcomes for the supplemented group: (i) with respect to provisioning behaviour at the nest, we expected the parents of supplemented chicks to decrease provisioning effort, as compared to the control parents, either making fewer nest visits and/or delivering smaller meals; (ii) with respect to foraging behaviour at sea, if parents of supplemented chicks reduced their provisioning rate we expected them to make more long-duration and longer-range (self feeding) foraging trips; and (iii) since their overall energy requirements should be lower, we expected parents of the supplemented chicks to show a reduced foraging effort at sea.

Materials and Methods

The study was carried out during the chick-rearing period (July-August) of the 2011 breeding season on Skomer Island, Wales (Southern Irish Sea: 51°44'N, 5°17'W). Twenty-five nests were selected for the experiment. Each nest was accessible via an access hatch (fitted at the beginning of the season) and contained a single chick, being reared by a pair of birds, identified by a metal leg ring and previously sexed by a combination of cloacal inspection and vocalisations. Chick age was estimated by wing measurements as in Brooke (1990). The study nests were split into an experimental (12 nests) and a control group (13 nests) such that each group contained nests spread across the study area and contained chicks of similar mass and age.

Supplemental feeding

Between the 17 July and the 8 August 2011 (23 days), the 12 chicks in the experimental group received supplemental food every day, while the 13 chicks in the control group received food only from their parents. The 12 experimental chicks were fed at approximately 21:00 GMT each evening of the experiment, so that returning parents would always encounter a recently fed chick. Experimental chicks were removed from their burrows, weighed, fed, and reweighed.

Control chicks were also removed from their burrows and weighed each evening, shortly before, or after feeding the experimental chicks.

We gradually introduced chicks to supplemental feeding during the first five days: chicks received an increasing amount of food starting at approximately 15 g on the 17 July and reaching approximately 40 g by the 21 July. Chicks then received approximately 40 g each night until 8 August. This was less mass than the mean daily food delivery for chicks in this age range (55 g in Hamer & Hill 1997; 53 g in Gray & Hamer 2001a), slightly smaller than the mean individual meal mass (49 g in Hamer & Hill 1997; 56 g in Gray & Hamer 2001a) and approximately half of the mean mass of double meals (both parents visit in one night: (98 g in Hamer & Hill 1997; 71 g in Gray & Hamer 2001a).

The supplemental diet was based on that described in Miskelly *et al*. (2009): un-drained tinned sardines (*Clupea spp*) in sunflower oil (~60%), homogenized to a smooth fluid paste with additional sunflower oil (~10%) and cooled boiled water (~30%). This diet has been successfully tested on a wide range of Procellariiforms including two Puffinus species: Fluttering shearwater (*Puffinus gavia*) and Hutton's shearwater (*Puffinus huttoni*) (Miskelly *et al*. 2009). While the daily mass of supplemental meals was lower than normal parental delivery, the energy content was much higher approximately 517 KJ day^{-1} compared to approximately 364 KJ day^{-1} (assuming 55g of raw Atlantic herring *Clupea harengus,* USDA Nutrient Database). The estimated nutritional composition of the diet is shown in (Supplementary Material table S1).

Batches of food were prepared daily approximately 6 hours prior to feeding and kept cool until needed. Prior to feeding, the mixture was warmed in a water bath to 30–35 °C. Supplemental meals were administered to chicks by intubation from plastic syringes into the proventriculus via flexible crop tubes, following the method of Miskelly *et al*. (2009). Chicks appeared to accept the meals comfortably and were never observed to regurgitate their supplemental meals. Supplemental feeding ceased on the 8 August, which we expected to allow sufficient time for

the normal pattern of parental provisioning to resume before the point at which it typically ceases around 10 days prior to fledging (Brooke 1990). Care was taken to maintain high levels of hygiene. Between feeds, crop tubes, syringes and preparation containers were immersed in boiled water to remove particulate matter, then immersed in Benzalkonium Chloride disinfectant solution (Ark-Klens) and finally rinsed in boiled water. The health and growth rate of all chicks was carefully monitored daily.

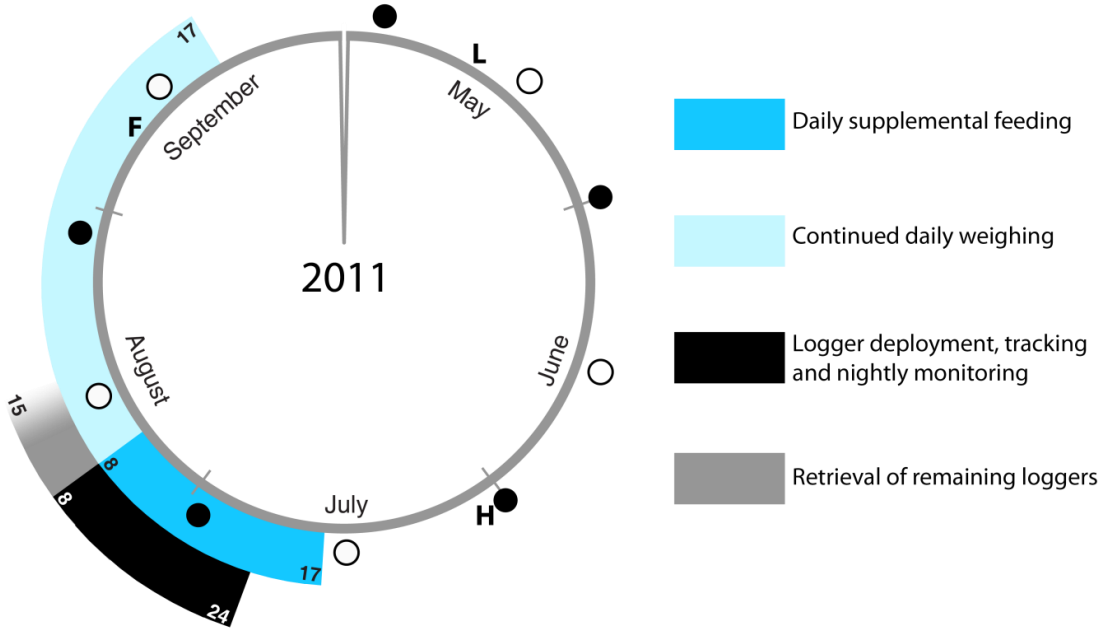

Figure 1. The experiment schedule in relation to the breeding season of the Manx shearwater: clockwise May-September. Median dates of laying (L), hatching (H) and fledging (F) are shown for all study nests on Skomer. Daily supplemental feeding (17 July-8 August) and continued daily weighing of chicks (9 August-17 September) are shown in orange and yellow. Nocturnal activities are shown in black: deployment of loggers and nightly monitoring of parent activity (24 July-8 August), total tracking period (24 July-15 August). Full (○) and new moon (●) phases are also shown.

Monitoring parental provisioning

Between the 24 July and 8 August we monitored the attendance and mass changes of parents visiting the experimental and control nests along with changes in chick mass throughout each night. Control and experimental group chicks were weighed daily at around 21:00 GMT (before parents returned) and the following day at around 12:00 GMT. Each burrow entrance was set with small bamboo pegs that were disturbed by birds entering or leaving the burrow. Between sunset and sunrise every night, we made regular checks (at 20 minute intervals) of the entrance to each burrow. When disturbed pegs were encountered the nest was checked using the access hatch and the chick was reweighed. If an adult was present the entrance was temporarily blocked (approximately 10 minutes) to allow the parent to feed the chick undisturbed without allowing it to escape. The adult was then removed, weighed and returned to the nest and the entrance was unblocked and the pegs reset. Once the adult had left the nest, the chick was reweighed. This protocol allowed us to attribute individual feeds to individual parents. Where weighing the following day indicated that we had missed all or part of a feed (or feeds), we calculated the size of the missed feed(s) based on the rate of mass loss by ten chicks weighed every three hours between 22 and 24 July 2010 (mean 1.7 ± 0.6 g $hour^{-1}$). Nightly monitoring ended following the night 15-16 August, after which we continued to monitor and weigh all chicks daily until the 16 September. To compare the nutritional status of chicks in each group prior to and following supplementary feeding, we calculated an index of body condition (body mass corrected for age) by regressing body mass upon age and expressing the residuals as a proportion of the predicted value in each case (as in Hamer & Hill 1993). Rates of mass gain by the chicks were calculated as the slope of linear regressions of day on mass.

Tracking at sea behaviour

Between 24 July and 5 August we deployed data loggers on a sample of parents from both sets of nests to track their movements and behaviour at sea. Deployments were made on 14 parents

from each group and as far as possible were deployed alternately on birds from each group. Birds were fitted with three data logging devices: a global positioning system (GPS) logger (modified i-gotU GT-120: Mobile Action), a British Antarctic Survey geolocator-immersion logger (Mk19) and a CEFAS G5 time-depth recorder (TDR). Two parents in the control group and one in the supplemented group were fitted only with GPS and geolocator-immersion loggers. GPS loggers were configured to record location once every 20 minutes and were attached dorsally using thin strips of TESA marine cloth tape underlying a small number of contour feathers (Guilford *et al.* 2008). Geolocator-immersion loggers tested for saltwater immersion every 3 seconds and recorded each transition between water and air. Immersion loggers were attached by two lightweight cable ties to a Darvik leg ring, so as to be immersed when sitting on the sea surface. TDRs were configured to record pressure every 1 second and were attached to the central four tail feathers using thin strips of TESA tape (similar to Wilson *et al.* 2009). GPS weighed approximately 10.5-11 g, geolocator-immersion loggers weighed 2.5 g and TDRs 2.7 g: total mass approximately 19 g (approximately 16 g for birds with only two devices). On return, parents were allowed to feed the chick before being recaptured from the burrow, reweighed, and devices inspected. If the devices had been deployed less than a week and were still well attached the bird was released, otherwise the devices were removed. Capture and deployment took <15 minutes, removal <10 minutes.

To test whether the routes of foraging trips made by parents from the control and supplemented groups were different, we used a nearest neighbour analysis similar to (Guilford *et al.* 2011). For all pairwise combinations we paired every control track with every supplemented track (between group comparisons). We also paired every track in the control group with every other track in the control group (within control group comparisons) and finally did the same within the supplemented group (within supplemented group comparisons). For each track paring we calculated the distance between each location in one track and the nearest location in the paired track. The mean nearest neighbour distance for each pair was calculated

as a measure of track similarity. Comparison of the between group mean nearest neighbour distances with those for the two within group comparisons was used to determine whether control and supplemented tracks were less similar to each other than were control tracks to other control tracks, or supplemented tracks to other supplemented tracks. To show the density of at-sea activity for birds in each group, we calculated kernel density contours in ArcGIS using all GPS locations and only those locations where diving occurred. The kernel bandwidth (21 km) was selected using Least-squares Cross-validation (Worton 1995).

Results

Logger deployments in this study were relatively short: mean 7.6 ± 4.3 days in the control group and 7.1 ± 4.2 days in the supplemented group. At deployment the mean mass of birds in the control group was lower (398 ± 20 g) than in the supplemental group (420 ± 20 g): t test t (26) = 2.88, p = 0.008. As a result the deployed loggers comprised a slightly larger percentage of body weight: control mean (4.7 ± 0.19 %), supplemented mean (4.5 ± 0.22), Wilcoxon rank-sum z (26) = 2.3, p = 0.019. Disturbance at the nest presented a second source of impact, but all birds continued to visit and feed their chicks, with the exception of one chick in the supplemented group. It was visited throughout the supplemental feeding periods, but probably fed only twice after supplemental feeding ceased. It probably fledged at around 76 days old, but was very light. One control burrow collapsed during the study. It was repaired, but removed from the experiment. In another control burrow we initially missed visits due to the presence of a second entrance: data from this burrow are included following the entrance's discovery. Over the 16 nights of nest monitoring we recorded 285 parental visits to nests for which we could attribute changes in chick mass (or lack of) to individual parents. On a further nine occasions where both parents were simultaneously discovered in the nest, we split the total mass increment between the two parents. In addition, weighing chicks the following day indicated that we probably missed 19 feeds in the control burrows that could not be attributed to an individual parent.

Because of the meal sizes delivered in supplemented burrow (see below) we could not rely on this secondary detection of missed visits to supplemented nests and so the few records of secondary detections were omitted from the analysis. We recorded 23 foraging trips by 14 birds in the control group and 28 trips from 12 birds in the supplemented group (table 1). Most tracks gave complete foraging trips: control group 74%, supplemented group 82%. In only two trips did the GPS fail before the bird had reached its likely maximum range. These tracks were excluded from calculations of trip range.

Table 1. Loggers retrieved with data intact. One GPS was lost, one recovered waterlogged. One TDR was lost, six TDRs failed or data were corrupted. Three immersion loggers failed.

		GPS	GLS	TDRs	N. Trips	N Trips Complete
Control	**All birds**	14	13	7	23	17
	Males	9	9	6	16	13
	Females	5	4	1	7	5
Supplemented	**All birds**	12	10	8	28	23
	Males	8	6	6	19	16
	Females	4	4	2	9	7

Chick mass growth

At the beginning of the experiment (17 July) the chicks in each group were of a similar age, although the supplemented group were slightly older and larger on average (control median 15.5 days, IQR 11.5-24.5; supplemented median 18 days, IQR 15-24; Wilcoxon rank-sum z (22) = 1.04, p = 0.30) and mass (control mean 245.5 ± 80.6 g; supplemental mean 290.4 ± 111.9 g; Wilcoxon rank-sum z (22) = 1.18, p = 0.24). Body condition (age corrected mass) was also similar

between groups (control mean -0.034 ± 0.15 g; supplemental mean -0.035 ± 0.24 g); Wilcoxon rank-sum *z* (22) = 0.26, p = 0.80. During the supplemental feeding period, chick mass gains were qualitatively different between the two groups (figure 2), with supplemented mass growth being much less variable than the controls. Linear regressions of day versus chick mass were used to provide rates of mass gain between 24 July and 8 August (Supplementary Material). The mean rate of mass gain was higher in the supplemented chicks (10.03 ± 3.3 g day^{-1}) than in the control chicks (8.02 ± 5.1 g day^{-1}), but the difference between the groups was not significant: Wilcoxon rank-sum *z* (22) = 0.95, p = 0.34. The day after the last supplemental feed (9 August) chicks in the supplemented group were significantly heavier (560.8 ± 41.7 g) with higher body condition indices (0.084 ± 0.06) than those in the control group (449.3 ± 64.3 g and -0.123 ± 0.14), Wilcoxon rank-sum *z* (22) = 3.61 and 3.61, both p < 0.001. Following the end of the experimental feeding period, a normal pattern of parental feeding appeared to resume within 2-3 days in all but one supplemented nest (figure 2). Eleven out of 12 chicks had received at least one meal after 3 days. All control chicks continued to be fed following the supplemental feeding period.

Fledging is difficult to determine with certainty as nestlings become very mobile prior to fledging (Brooke 1990) and their absence from the burrow could indicate fledging, predation, or that they have entered an adjacent burrow. All chicks in the study probably fledged: disappearing from their burrow at approximately the right age (65-81 days, Brooke 1990) and stage of development (having lost almost all of their down). Chicks disappeared from the burrow at a median estimated age of 70 days (IQR 69-73) and a mean (±SD) final recorded mass of 453.3 ± 61 g. One supplemented chick was fed only twice after supplemental feeding stopped. It disappeared from its burrow at approximately 76 days old, but was very light. One supplemented chick moved out of reach within its burrow and so fledging could not be determined. There was no difference in estimated age of disappearance from the burrow between supplemented (71 days IQR 67-72) and control chicks (70 days IQR 70-73 days): Wilcoxon rank-sum *z* (21) = 0.56, p = 0.59. Neither was there a difference in final recorded mass

prior to disappearance from the burrow between supplemented (450.2 ± 76 g) and control chicks (456.2 ± 46 g): Wilcoxon rank-sum *z* (21) = 0.43, p = 0.66. Excluding the chick that was not subsequently fed by its parents, supplemented chicks still fledged at a similar mass (471.8 ± 26 g) to controls; Wilcoxon rank-sum *z* (20) = 0.86, p = 0.39.

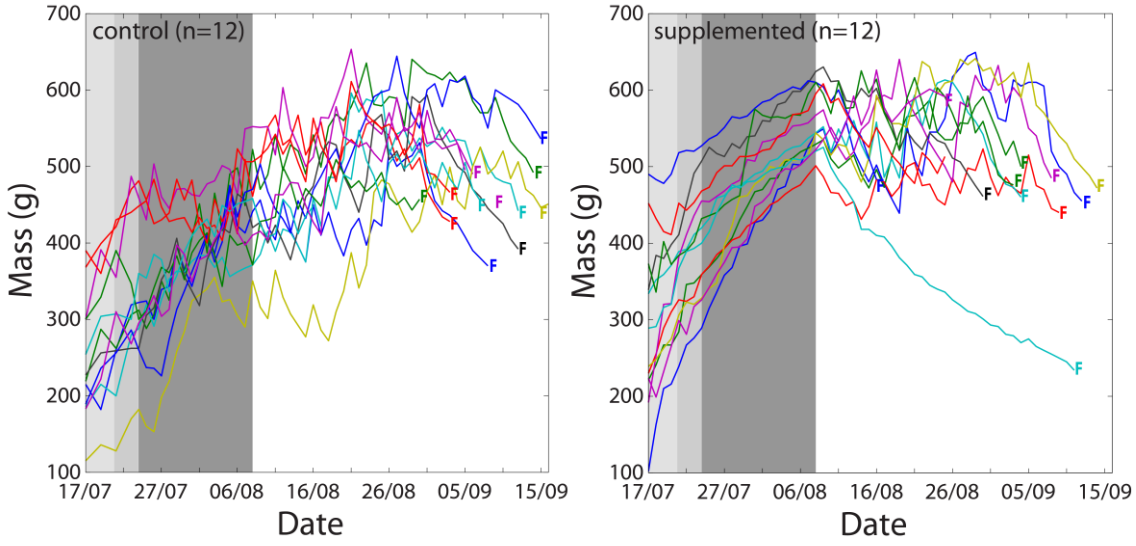

Figure 2. Changes in mass of each of the control (left) and supplemented (right) chicks from the beginning of the experiment until fledging (F). The duration of the supplemental feeding period is indicated in grey: initial incremental feeding (light grey), main supplemental feeding (mid and dark grey), nightly monitoring and tracking (dark grey). One chick in the supplemented group probably was fed by its parents only twice following the supplemental feeding period.

Nest visits

There was no difference between control and supplemented nests in the proportion of nights on which chicks received a visit from one or both parents: control median 0.63 (IQR 0.56-0.75), supplemented median 0.69 (IQR 0.50-0.78), Wilcoxon rank-sum *z* (22) = 0.15, p = 0.88 (figure 3). Similarly, there was no difference in the number of individual parental visits per night: control median 0.75 (IQR 0.69-0.83), supplemented median 0.84 (IQR 0.61-0.97), Wilcoxon rank-sum *z* (22) = 0.58, p = 0.56. There was no difference in the visit rates of either sex between the control

and supplemented groups: males Wilcoxon rank-sum *z* (22) = 1.37, p = 0.17, females Wilcoxon rank-sum *z* (22) = 0.35, p = 0.73 (figure 3). Within the control group, male and female parents visited the nest with similar frequencies: males 0.38 (IQR 0.31-0.44), females 0.38 (IQR 0.31-0.42) Paired Wilcoxon test *W* (11) = 32, p = 0.95. Within the supplemented group, male and female parents visited the nest with similar frequencies: males 0.50 (IQR 0.36-0.58), females 0.44 (IQR 0.28-0.47) Paired Wilcoxon test *W* (10) = 18.5, p = 0.22 (figure 3). Out of 276 burrow-days in each group during the 23 days of supplemental feeding we encountered parent remaining in the nest during the day on 9 occasions in the fed group and 3 occasions in the control group.

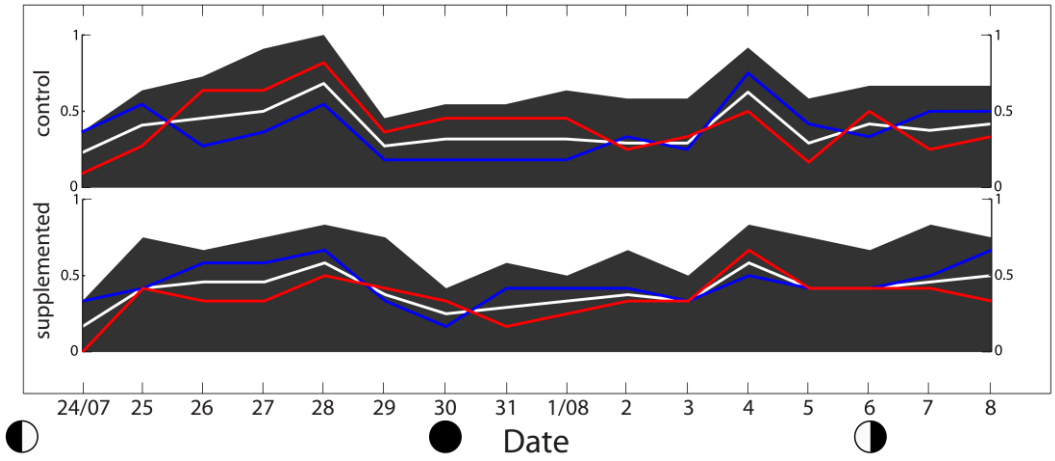

Figure 3. Proportion of nests visited on each night of the monitoring period (in black) in the control and supplemented groups. Proportion of all parents visiting their nest on each night (white line), and proportion of all males (blue) and females (red) visiting their nest on each night. The date in July/August and the moon phase (last quarter, new moon and first quarter) are given at the bottom of the panel.

Meal sizes

Although the frequency of parental visits was similar in both groups, the mass of food delivered to the chick was very different. Parents delivered no detectable meal to the chick in 83.6% of visits to supplemented nests (figure 4), compared to only 4.3% in control nests. Where meals were fed to chicks (excluding visits without feeds), chicks in the control group received significantly larger meals (mean 46.3 ± 9.9 g) than did supplemented chicks (mean 24.5 ± 8.9 g): Wilcoxon rank-sum $z(19) = 3.23$, $p < 0.01$ (figure 5). This led to a mean total parental feeding rate of 39.3 ± 8.6 g day^{-1} in control nests and 3.3 ± 3.4 g day^{-1} in supplemented nests: Wilcoxon rank-sum $z(22) = 4.13$, $p < 0.001$. Within each group there were no differences in meal sizes between the sexes: control males 46.9 ± 11.1 g, control females 47.4 ± 14.9 g, Wilcoxon paired test $W(11) = 38$, $p = 0.68$; and supplemented males 26.1 ± 14.0 g and supplemented females 25.1 ± 10.9 g, Wilcoxon paired test $W(4) = 7$, $p = 1.0$. There were no significant differences in overall provisioning rate between the sexes: control males 16.1 g ± 5.2 day^{-1}, control females 17.2 ± 7.3 g day^{-1} Wilcoxon paired test $W(11) = 38$, $p < 0.97$; and supplemented males 1.6 ± 2.3 g day^{-1}, supplemented females 1.8 ± 1.8 g day^{-1} Wilcoxon paired test $W(11) = 15$, $p < 0.74$.

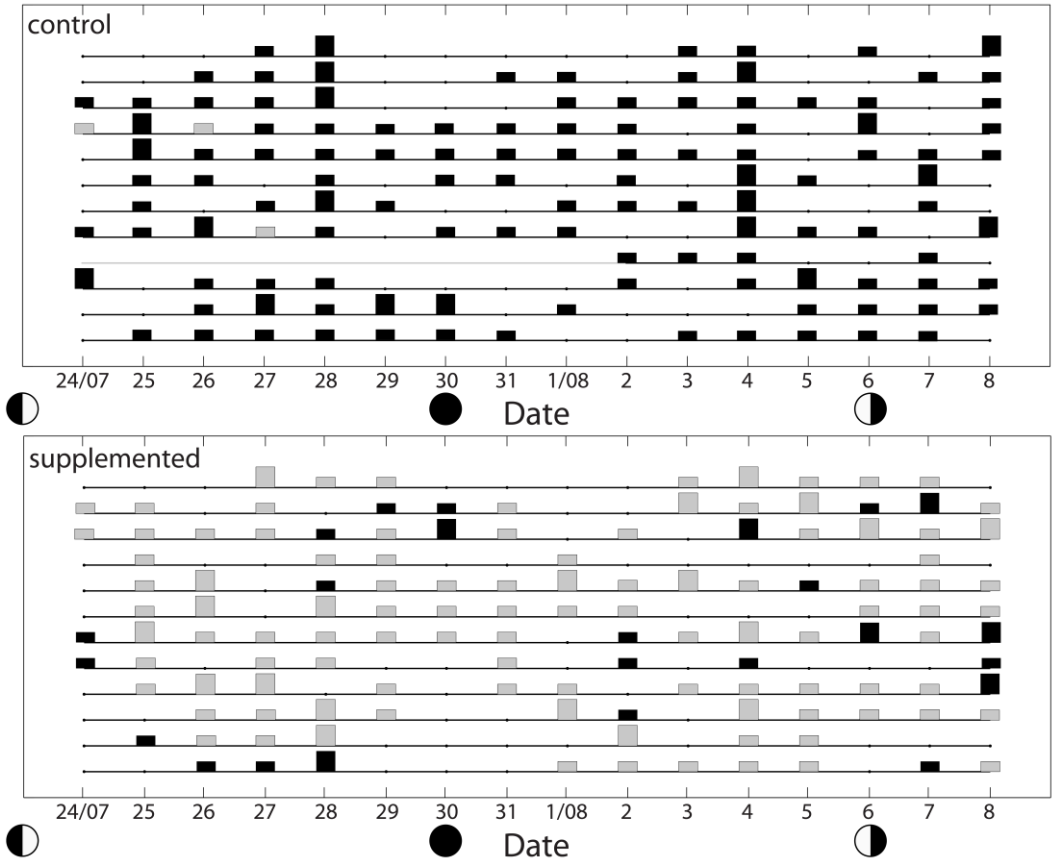

Figure 4. Timelines for each nest (one horizontal line per nest) in the control (top panel) and supplemented (bottom panel) nests during the nightly monitoring period. The date in July and August and moon phase (last quarter, new moon and first quarter) are given at the bottom of each panel. Single parent visits (small bars) and double parent visits (large bars) are shown for each nest on each night. Nights on which chicks received food from one or more parent are coloured black and nights on which no feed occurred are coloured grey.

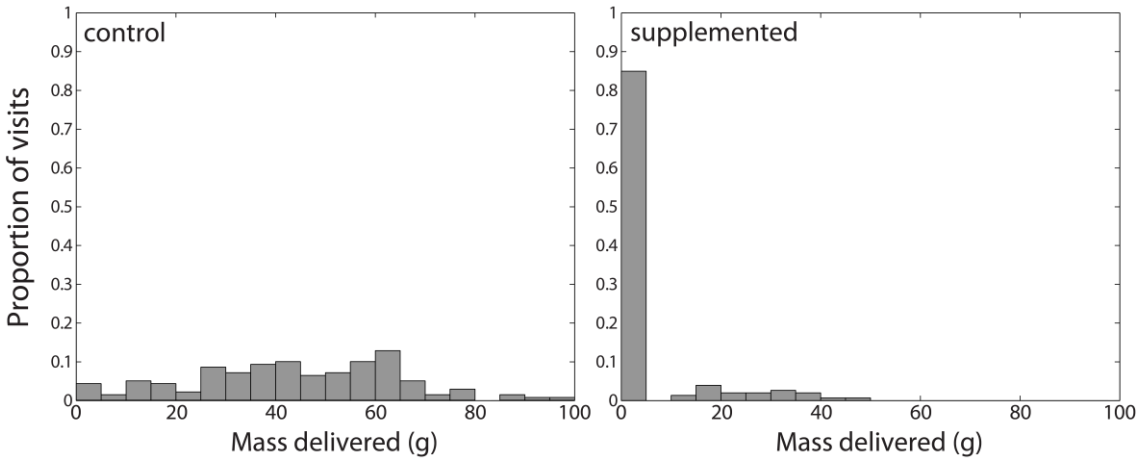

Figure 5. Frequency distributions of the mass of meals delivered on individual parental visits to control and supplemented chicks. 85% of all visits to the supplemented nests did not result in a meal being fed to the chick.

Parental arrival and departure weights

Individual mean arrival weights (prior to feeding the chick) were similar for male (448.8 ± 28 g) and female (443.1 ± 26 g) parents in the control group, Wilcoxon paired test W(10) = 24, p = 0.46 (figure 6a). In the supplemented group, female arrival weights (416.2 ± 30 g) were marginally lighter than male arrival weights (433.8 ± 18 g), although the difference was not significant: Wilcoxon paired test W(10) = 12, p = 0.067. Male arrival weights were similar between the control and supplemented groups (Wilcoxon rank-sum z(21) = 1.23, p = 0.21), but female arrival weights were significantly lighter in the supplemented group (Wilcoxon rank-sum z(21) = 2.37, p = 0.018). Individual mean departure weights (after feeding the chick) were similar for male (404.4 ± 21 g) and female (399.5 ± 17 g) parents in the control group, Wilcoxon paired test W(10) = 27, p = 0.63 (figure 6b). In the supplemented group, female departure weights (409.6 ± 28 g) were lighter than male departure weights (429.9 ± 19 g), Wilcoxon paired test W(10) = 7, p = 0.019. Male departure weights were lighter in the control groups (Wilcoxon rank-sum z(21) =

2.67, p = 0.007), but female departure weights were similar between groups (Wilcoxon rank-sum z(21) = 1.56, p = 0.12).

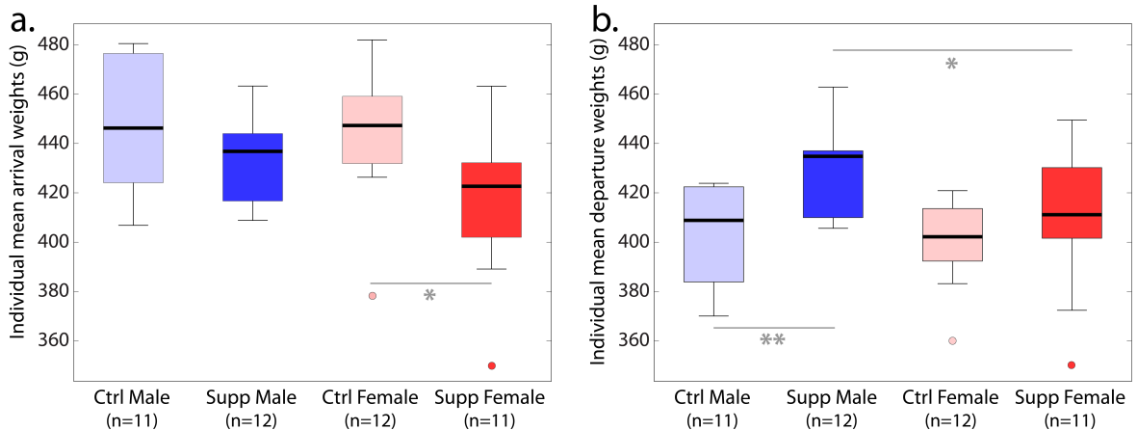

Figure 6. Individual mean arrival weights of male (blues) and female (pink/red) parents in the control (light colours) and supplemented (dark colours) nests. Boxes indicate the group median, and interquartile range, whiskers indicate the range of the data, excluding outliers (indicated by ○). Significant differences are indicated by *<0.05, **<0.01.

Changes in parental mass during foraging trips

For the small number of GPS tracked foraging trips where we could determine both the corresponding net mass change by the parent and the meal size fed to the chick (8 parents in the control group, 9 in the supplemented group), parents in the control group gained more total mass (including the meal fed to the chick) than parents in the supplemented group: control mean (± SD) total mass gain 40.19 ± 29 g, supplemented 4.0 ± 17 g, Wilcoxon rank-sum (15) = 98, p = 0.012. Accounting for the duration of trips, parents in the control group gained total mass at a mean rate of 20.7 ± 22 g day^{-1}, compared to supplemented parents 1.3 ± 12.5 g day^{-1}, Wilcoxon rank-sum (15) = 93, p = 0.046. However, the net mass retained by parents after feeding the chick was more similar between groups: control mean net mass gain 5.0 ± 24 g, supplemented = 2.4 g ± 16 g, Wilcoxon rank-sum (15) = 74, p = 0.91. Parents in each group gained net mass at similar

rates: control mean net mass gain = 5.75 ± 14 g day^{-1}, supplemented = 0.94 ± 12 g day^{-1}, Wilcoxon rank-sum (15) = 77, p = 0.67 (figure 7).

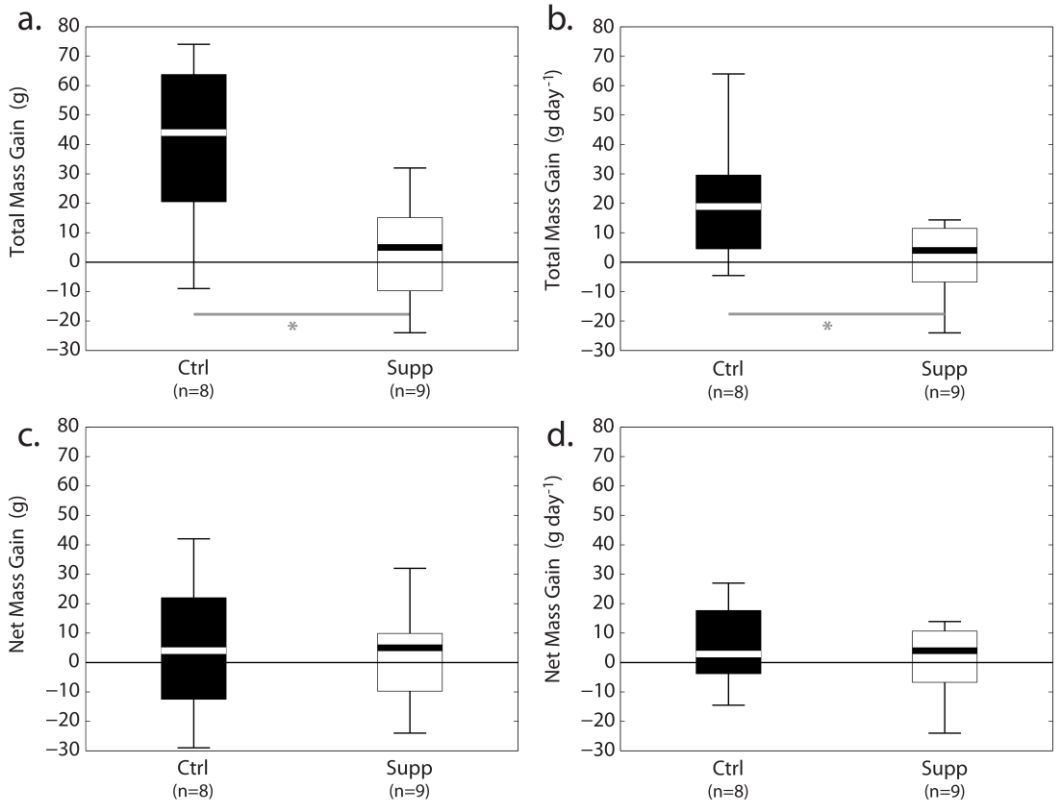

Figure 7. Mean total mass (including the chick's meal) and net mass (retained by parent) gains (g and g day^{-1}) for parents in the control (8 birds) and supplemented group (8 birds). (a) Total mass gain (g) over trip; (b) total mass gain (g day^{-1}) over trip; (c) Net mass gain (g); (d) Net mass gain (g day^{-1}). Boxes indicate the group median and interquartile range, whiskers indicate the range of the data.

Foraging trips and destinations

The routes and destinations of foraging trips were similar for parents in the two groups, as were the locations in which birds dived (figure 8). Mean nearest neighbour distances between control tracks and supplemented tracks were not different to the distances between different control tracks, Wilcoxon rank-sum *z* (895) = 1.05, p = 0.29. Nearest neighbour distances between control tracks and supplemented tracks were larger than between different supplemented tracks,

Wilcoxon rank-sum z (1020) = 3.09, p = 0.002, but nearest neighbour distances between different control tracks and between different supplemented tracks were similar, Wilcoxon rank-sum z (692) = 1.36, p = 0.17 (figure 9). Trip range, duration and distance travelled per day did not differ significantly between the two groups (table 2), although histograms of trip range and duration suggest a slightly greater tendency towards shorter duration, shorter range trips in the supplemented group (figure 10).

The behaviour at sea (as recorded by our loggers) also was highly similar for parents in the two groups. There were no significant differences in the number of take-offs and landings, or the proportion of time spent on or in the water (table 3). Neither were there significant differences in the number of dives made, nor the depth, duration or shape of those dives (table 4). The timing of activity through the day was also similar between the two groups (figure 11).

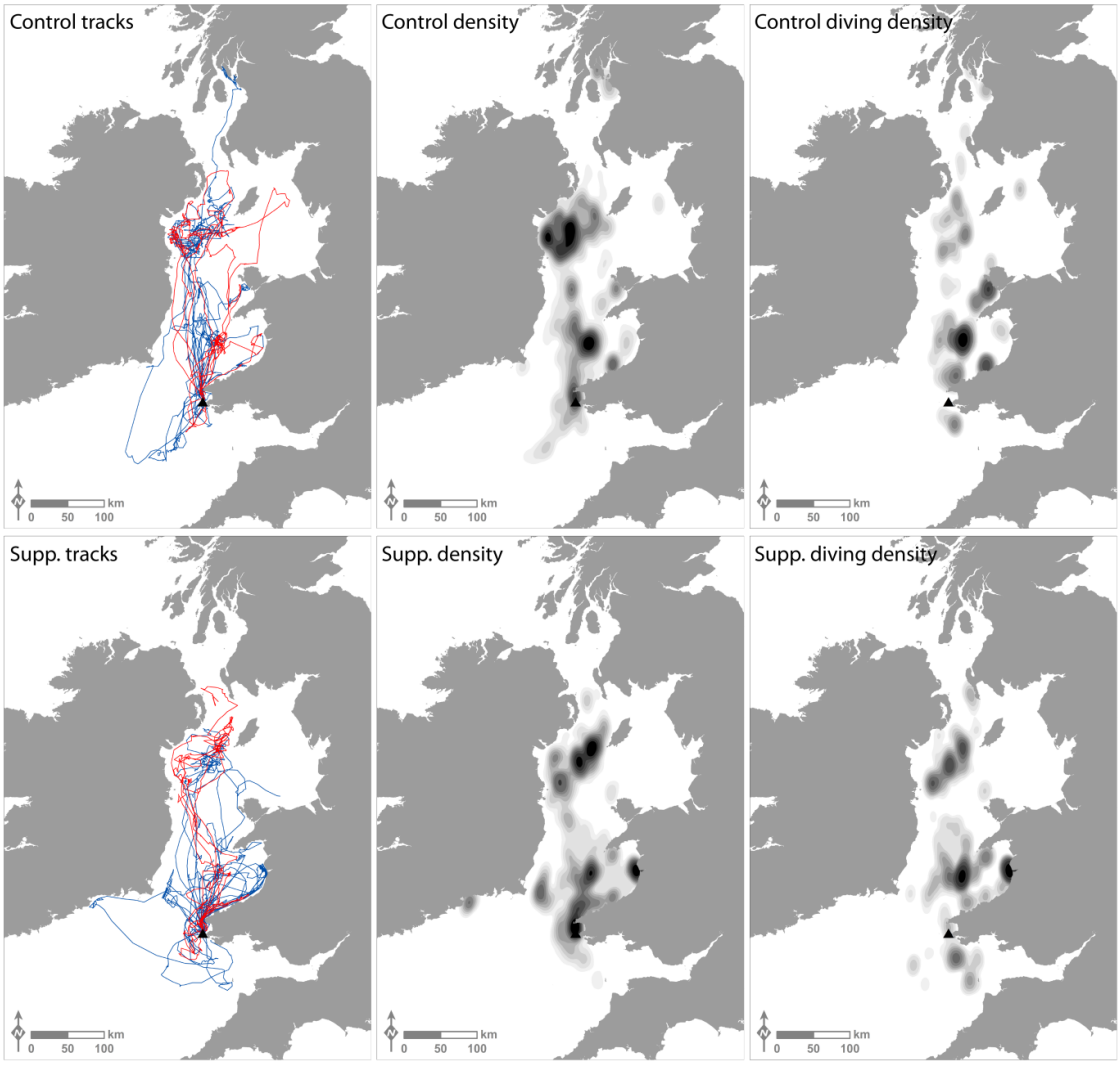

Figure 8. Comparison of at-sea movements and foraging distributions of parents of control (top row) and supplemented (bottom row) chicks. Individual tracks are shown for male (blue) and female (red) parents. Density maps show kernel density of all recorded GPS locations, and dive locations where birds engaged in diving. Density percentiles are indicated by colour density (95% lightest – 10% darkest).

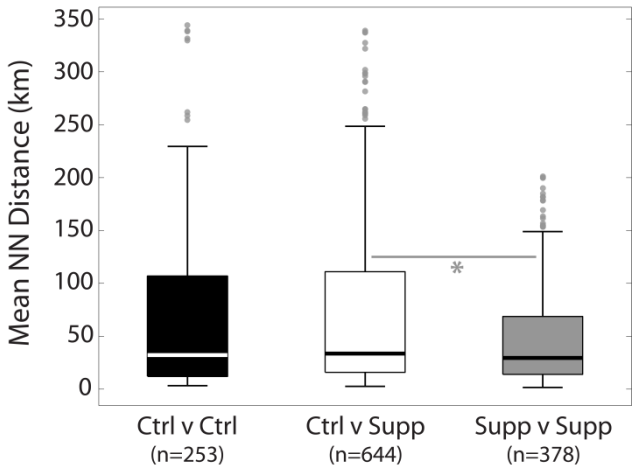

Figure 9. Comparison of mean nearest neighbour distances between all pairwise combinations of control versus control tracks, control versus supplemented tracks, and supplemented versus supplemented tracks. Distances between control and supplemented tracks were as similar as between tracks within each group (a). Boxes indicate the group median, and interquartile range, whiskers indicate the range of the data, excluding outliers (indicated by ○).

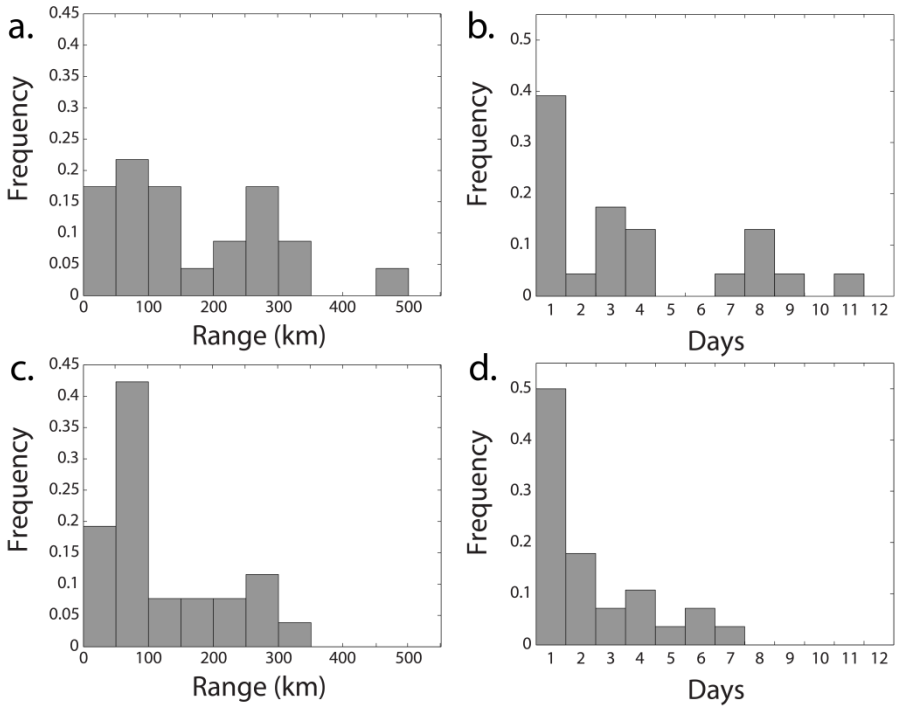

Figure 10. Histograms of foraging trip range (maximum distance from the colony km) and duration (days) for parents on the control (a, b) and supplemented (c, d) groups.

Table 2. Median (and interquartile range) trip metrics (duration, trip range and km travelled per day) for parents from control and supplemented chicks. Superscripts reference the results of Wilcoxon rank-sum tests of difference between the two groups shown at the bottom of the table, none were significant.

		Duration (days)	Range (km)	Km day^{-1}
Control	**Overall**	**3.5** (2.0-5.0) [1]	**174.1** (118-244) [2]	**166.9** (142-195) [3]
	Males	**4.0** (2.0-5.8) [4]	**128.8** (91-242) [5]	**153.6** (141-195) [6]
	Females	**3.0** (2.9-5.4) [7]	**202.8** (152-260) [8]	**181.7** (154-201) [9]
Supplemented	**Overall**	**2.4** (2.0-3.0) [1]	**115.4** (93-154) [2]	**177.6** (150-224) [3]
	Males	**2.4** (2.0-2.8) [4]	**100.1** (94-154) [5]	**176.2** (145-215) [6]
	Females	**2.3** (1.3-3.3) [7]	**137.2** (84-180) [8]	**199.6** (164-230) [9]

[1] $z(24) = 1.89$, $p = 0.058$. [2] $z(24) = 1.62$, $p = 0.11$. [3] $z(24) = 0.90$, $p = 0.37$. [4] rank-sum(15) = 62, $p = 0.35$, [5] rank-sum (15) = 63, $p = 0.42$. [6] rank-sum (15) = 80, $p = 0.48$. [7] rank-sum (7) = 15, $p = 0.29$. [8] rank-sum (7) = 15, $p = 0.29$. [9] rank-sum (7) = 22, $p = 0.73$.

Table 3. Mean (±SD) wet-dry transition metrics from the immersion loggers: number of transitions (take-offs and landings) per hour of daylight; proportion of the day spent on or in the water; the proportion of the day spent off the water. Superscripts reference the results of Wilcoxon rank-sum tests of difference between the two groups shown at the bottom of the table, none were significant.

		Transitions hr^{-1}	P day wet	P day dry
Control	**Overall**	**11.23** ± 3.85 [1]	**0.72** ± 0.09 [2]	**0.28** ± 0.09 [3]
	Males	**10.36** ± 3.35 [4]	**0.72** ± 0.10 [5]	**0.28** ± 0.10 [6]
	Females	**13.19** ± 4.69 [7]	**0.74** ± 0.09 [8]	**0.26** ± 0.09 [9]
Supplemented	**Overall**	**13.95** ± 4.26 [1]	**0.70** ± 0.10 [2]	**0.30** ± 0.10 [3]
	Males	**13.10** ± 4.42 [4]	**0.74** ± 0.10 [5]	**0.26** ± 0.10 [6]
	Females	**15.27** ± 4.25 [7]	**0.67** ± 0.08 [8]	**0.33** ± 0.08 [9]

[1] z (21) = 1.58, p = 0.11; [2 and 3] z (21) = 0.84, p = 0.40; [4] rank-sum (13) = 58, p = 0.27; [5 and 6] rank-sum (13) = 47, p = 0.95; [7] rank-sum (6) = 15, p = 0.49; [8 and 9] rank-sum (13) = 23, p = 0.20.

Table 4. Mean (±SD) dive metrics from the TDRs: number of dives per hour of daylight; median and maximum dive depth; median dive duration; and mean ratio of depth:duration (smaller numbers indicate more U-shaped dives, larger numbers more V-shaped dives). Superscripts reference the results of Wilcoxon rank-sum tests of difference between the two groups shown at the bottom of the table, none were significant.

	Dives hr^{-1}	**Median depth (m)**	**Max. depth (m)**	**Median dur. (s)**	**Dep/dur (m s^{-1})**
Control	**3.56** ±1.37 [1]	**4.94** ±1.36 [2]	**34.39** ±9.01 [3]	**12.57** ±2.70 [4]	**0.438** ±0.022 [5]
Supplemented	**3.82** ±1.34 [1]	**4.38** ±1.39 [2]	**40.54** ±10.56 [3]	**11.25** ±2.96 [4]	**0.449** ±0.052 [5]

[1] rank-sum (13) = 51, p = 0.61. [2] rank-sum (13) = 67, p = 0.23. [3] rank-sum (13) = 48, p = 0.40. [4] rank-sum (13) = 66, p = 0.29. [5] rank-sum (13) = 51, p = 0.59.

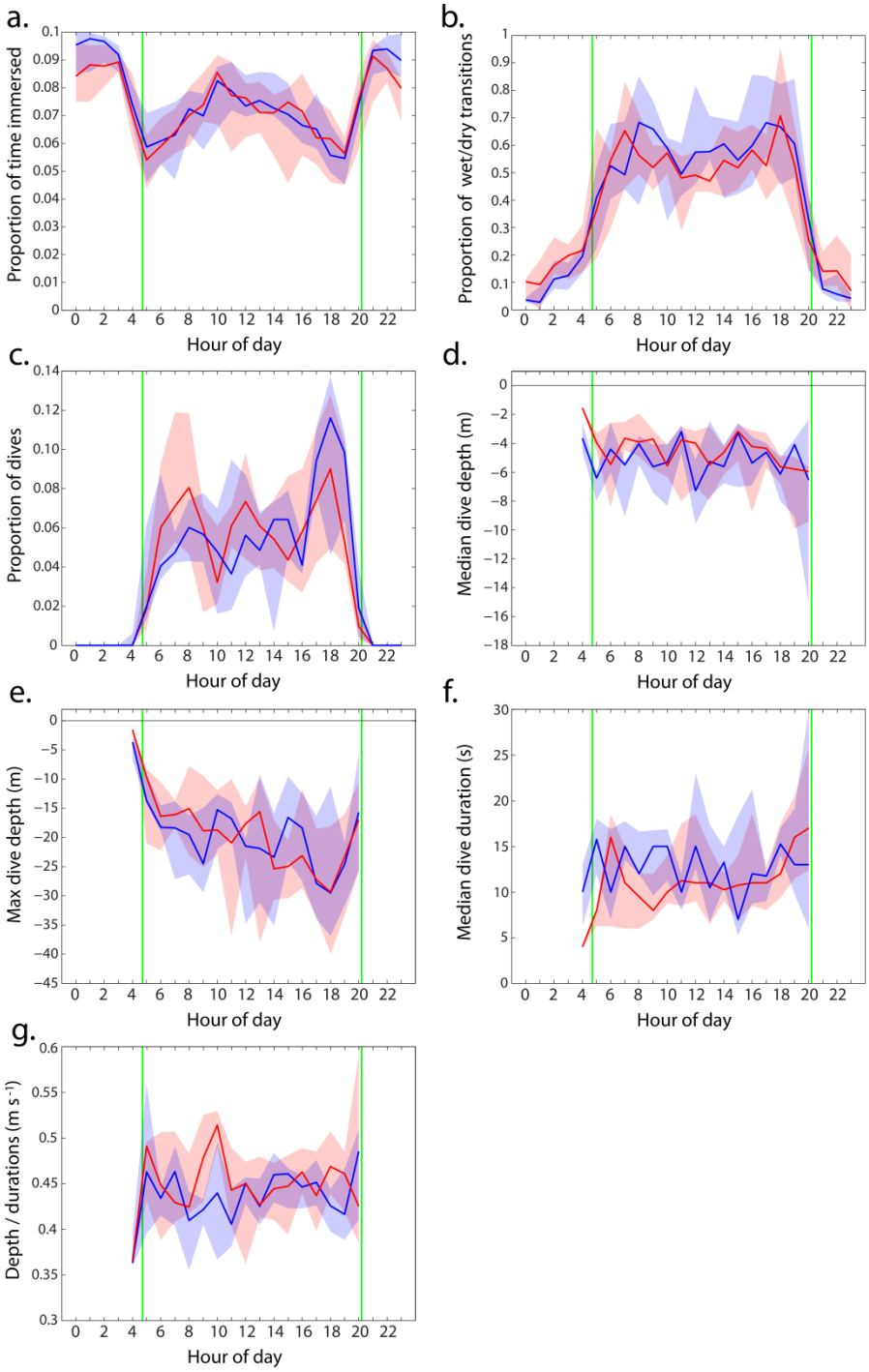

Figure 11. The timing of at-sea activity through the day for control (blue) and supplemented (red) parents: (a) proportion of time on or in the water; (b) proportion of wet/dry transitions; (c) proportion of dives; (d) median dive depth (m); (e) maximum dive depth (m); (f) median dive duration (s); (g) mean ratio of dive depth:duration (m s^{-1}). All lines are medians, shaded areas the inter-quartile range.

Discussion

Impacts

The at-sea behaviour recorded here should be interpreted with the possibility in mind that behaviour may have been affected by the data loggers deployed on birds in the study. However, devices were deployed on the same number of birds in each group and, as far as practicable, such that the same numbers of parents in each group were carrying devices at any one time. Any effects should therefore be balanced between the two groups. At deployment the mean mass of birds in the control group was lower than in the supplemented group and as a result the deployed loggers comprised a slightly larger percentage of body weight. This may have led to slightly different effects of carrying transmitters on the parents in each group, but the difference should have been small. We needed to check nests frequently throughout the night and handle and weigh birds regularly. Disturbance at the nest therefore presented a second source of impact, but one that also should be balanced between the experimental and control group. All birds continued to visit and feed their chicks, with the exception of one chick in the supplemented group that may have been abandoned following supplemental feeding. Other than that, we detected no deleterious effects of the supplemental diet, or feeding procedure. Supplemented chicks did not regurgitate the supplemental food during the procedure and we saw no evidence of subsequent regurgitation within the nests. We are therefore confident that we did not overload the chicks gut capacity. Based on the mass of the supplemental feeds (40 g) compared to the mean daily food delivery for chicks in this age range (53-55 g), the mean individual meal mass (49-56 g) and the mean mass of double meals (71-98 g 71 g) (Hamer & Hill 1997; Gray & Hamer 2001a), chicks ought to have been capable of ingesting further (but limited) meals from their parents. However, while the daily mass of supplemental meals was lower than normal parental delivery, the lipid content probably was much higher than the fresh or partly digested clupeid fish normally fed to chicks (Brooke 1990). If the level of lipid provisioning was

close to the chicks assimilatory capacity, there may have been some accumulation of lipids in the proventriculus that might have further limited the capacity of chicks to accept parental meals (Ricklefs 1992; Hamer & Hill 1994; Roby *et al.* 1997; Hamer *et al.* 1999a).

Provisioning behaviour

During the experimental period, supplemented chicks gained mass at a faster and more constant rate and by the end of the experimental period they were heavier, with a higher body condition (age corrected mass) than control chicks. Previous studies have demonstrated a reduction in visit rate by Manx shearwater parents in response to well-fed chicks (Hamer *et al.* 1998; Quillfeldt *et al.* 2004; Hamer *et al.* 2005). Contrary to our expectations, the parents of supplemented chicks in this experiment did not reduce their nest visitation rate in response to well fed chicks. There was no significant difference between control and supplemented nests either in the proportion of nights on which chicks received a visit from one or both parents, or the number of individual parental visits per night. Although not significant, the nest visit frequencies were actually higher in the supplemented group. There was no difference in the visit rates of either sex between the control and supplemented groups. Within the control group, male and female parents visited the nest with similar frequencies, while within the supplemented group, males visited the nest with a slightly higher frequency than their partners, although the difference was not significant. Although the parents of supplemented chicks continued to visit their chicks, in the vast majority of cases no detectable meal was fed to the chick: the parents of supplemented chicks delivered detectable meals on only 16% of visits, compared to 96% of visits by parents in the control group. Where meals were passed to supplemented chicks, they were significantly smaller than those fed to control chicks. Overall this led to a mean total parental feeding rate of 36.9 g day^{-1} in control nests and 3.03 g day^{-1} in supplemented nests. The amount of food consumed during these visits may have been limited by the chick, by a reduction in begging response (Quilfeldt *et al.* 2004; Quillfeldt & Masello 2004;

Hamer *et al.* 2005; Quillfeldt *et al.* 2007; Gladbach *et al.* 2009; Quillfeldt *et al.* 2010), by refusal of food, or by an inability to consume the food load offered if already full (Ricklefs 1992; Hamer & Hill 1994). The proximate cause of the lack of food passed to chicks in this experiment is unknown.

The supplemented chicks were fed reduced meals on some occasions by parents, indicating that parents continued to bring some food to the nest. However, in response to reduced begging, or refusal of food by chicks, parents may have regulated the amount of food subsequently brought to the nest. The mean arrival weights of parents of control chicks and male parents of supplemented chicks were similar. However, the arrival weights of female parents of supplemented chicks were significantly lower than those of control females, but were similar to the departure masses of control females. This may indicate a degree of responsive reduction in payload by female parents. The departure masses of supplemented females were slightly (but not significantly) heavier than control females, and so it may be that supplemented females actually increased their integrated body mass (condition), while reducing payload mass (chick meal), allowing them to remain at an optimally low mass overall for flight and foraging (Sæther *et al.* 1993). Males did not appear to make such an adjustment since their arrival and departure masses were similar to the arrival masses of control males. It might be that males were unable to respond to the reduced probability that their chick would require feeding and continued to return with a full payload of prey regardless. Previous studies have indicated that in Manx shearwaters, males provide 40–50% more food for chicks than do females (Gray & Hamer 2001a) and that females may be more responsive to the chicks nutritional requirements than males (Quillfeldt *et al.* 2004), or that males respond at different thresholds (Hamer *et al.* 2005). Alternatively, males may have been making a similar responsive reduction in food payload as females, but simultaneously increased their own body condition, the two changes cancelling each other out.

For the birds tracked with GPS, where we can be certain of the duration of trips, the total mass changes (net gain by adult plus meal fed to chick) and mass change per day at sea were greater for parents of control chicks than parents of supplemented chicks. However, the net mass gains (gain by adult after feeding the chick) were similar. In common with the arrival and departure masses, this may also suggest a degree of responsive reduction in payload, since it seems that the parents of supplemented chicks reduced their total prey consumption without affecting their own body condition. this explains the female pattern seen in the arrival and departure masses (reduction in payload without very large increases in body mass), but does not well explain the male pattern (either no reduction in payload with no increase in body mass, or a large reduction in payload and a commensurate increase in body mass), but might explain an intermediate explanation whereby over the course of several trips, males gradually reduce their payload and gradually increase their body mass.

At-sea behaviour

During the experimental period we provided the vast majority of the supplemented chicks' total nutrition, effectively removing the requirement for parents to feed their chicks. Under this scenario we expected the parents of supplemented chicks to reduce their provisioning effort, spending more time at sea on longer-duration, longer-range (self feeding) foraging trips. Although there was no significant difference in the average duration or range of trips between groups, the frequency distributions of trip duration and range were different. Contrary to our expectations (but fitting with the slightly higher nest visit rate), the parents of supplemented chicks made slightly more short-duration, short-range trips and fewer long trips than the control group. The effect of the supplemental diet was of a greater magnitude than we anticipated and this exposed a potential problem with the use of supplemental feeding experiments to study the effect of the chick's nutritional state on the subsequent behaviour of the parent in regulating parental effort with a view to maintaining its own body condition. That is, it is impossible to

supplement the diet of the chick without simultaneously supplementing the diet of the parents, since any food not passed to the chick on return to the nest is retained by the parent and thus contributes to the parent's body condition. This in turn is likely to reduce the requirement for parents to make long duration self-feeding trips. This knock-on effect of supplemental feeding on the parents is likely to be highly dependent on the size and energetic content of the supplemental feeds provided and the duration of the supplemental feeding period. It is not clear however, why parents should continue to visit the nest at a similar rate, especially if visiting the colony entails some risk (Riou & Hamer 2008). Out of 276 burrow-days in each group during the 23 days of supplemental feeding we encountered parents remaining in the nest during the day on 9 occasions in the fed group and 3 occasions in the control group. These days spent in the burrow may have been the result of our disturbance at the nest preventing birds from leaving before dawn. They may however, be further evidence of the increased body condition of the supplemented parents, who on occasions did not need to spend a day foraging at sea.

The routes and foraging destinations did not differ between the groups and (with one exception in the control group) the maximum range was similar. This accords with the view of Hamer *et al.* (2005) that that the foraging ranges and overall foraging and provisioning strategies of parents may not be altered as part of the flexible provisioning response. Further, our results suggest that the at-sea foraging behaviour also may be largely inflexible. Given the likely large energetic advantage to the parents of the supplemented chicks and their lower total mass gains over foraging trips, we would have expected a reduction in foraging effort at sea. However, we found no significant differences between the supplemented and control groups in the distance travelled per day, the number of wet-dry transitions made per daylight hour, the proportion of time spent on (or in) the water, the number of dives made per daylight hour, or the depth and duration of dives made. The lack of a response in foraging effort, as measured by us, is perhaps not surprising. First of all, individual foraging effort is likely to be highly variable. The amount of foraging activity undertaken (wet-dry transitions and dives) is likely to be highly dependent on

chance encounters with aggregations of prey, their accessibility, longevity, and the success of previous encounters. These encounters are in turn likely to be highly dependent on individual experience (Limmer & Becker 2009), searching behaviour (Zollner & Lima 1999; Nevitt *et al.* 2008: Weimerskirch *et al.* 2007), stochastic oceanographic processes (Begg & Reid 1997; Vliestra *et al.* 2005), and the presence of conspecific and heterospecific foragers (Götmark *et al.* 1986; Sakamoto *et al.* 2009). Second, the costs of foraging for parents may not be adequately captured by the measurements we made.

Conclusions

The lack of an apparent reduction in nest visit rate in response to supplemented chicks might suggest a lack of an appropriate regulation response by the parents. However, the very large effect of our supplemental feeding and the likely positive knock-on effect on the parents body condition may account entirely for the lack of an expected response. While we found no response in visit rate, the number and mass of meals fed to supplemented chicks was greatly reduced. Much of this response may have been a result of well-fed chicks refusing parental feeds or failing to solicit them through begging. However, parental mass changes suggest that some degree of responsive reduction in prey payloads brought to the nest may have occurred, without a reduction in net mass gains (adult body condition) and, at least in female parents, this was apparent as a reduction in arrival mass at the nest. Despite our large energetic input into the rearing of supplemented chicks and the likely energetic advantage to their parents, we found no significant differences in the routes and destinations of foraging trips. Neither did we find any significant differences in foraging effort between the parents of supplemented and control chicks. This suggests that while foraging trip duration has been shown in other studies to be flexible in response to chick and adult body condition, the maximum ranges, destinations and daily foraging behaviour do not appear to form part of this flexible response in the Manx

shearwater. At-sea behaviour probably is controlled more by the foraging conditions and prey distributions experienced by the parent than by the nutritional demands of the chick.

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Supplementary Material

Table S1. Approximate nutritional composition of the supplemental diet.

Nutrition	per 100 g	in 40 g feed
Energy kj	1327	517
Energy kcal	321	125
Protein g	10.9	4.2
Carbohydrate g	trace	trace
of which sugars g	trace	trace
Fat g	30.8	12.0
of which saturates g	4.3	1.7
of which poly-unsaturates g	17.7	6.9
of which mono-unsaturates g	5.0	1.9
of which Omega 3 g	0.9	0.4
Fibre g	trace	trace
Sodium g	0.3	0.1
Salt equivalent g	0.7	0.3
Water g	30.0	12.0

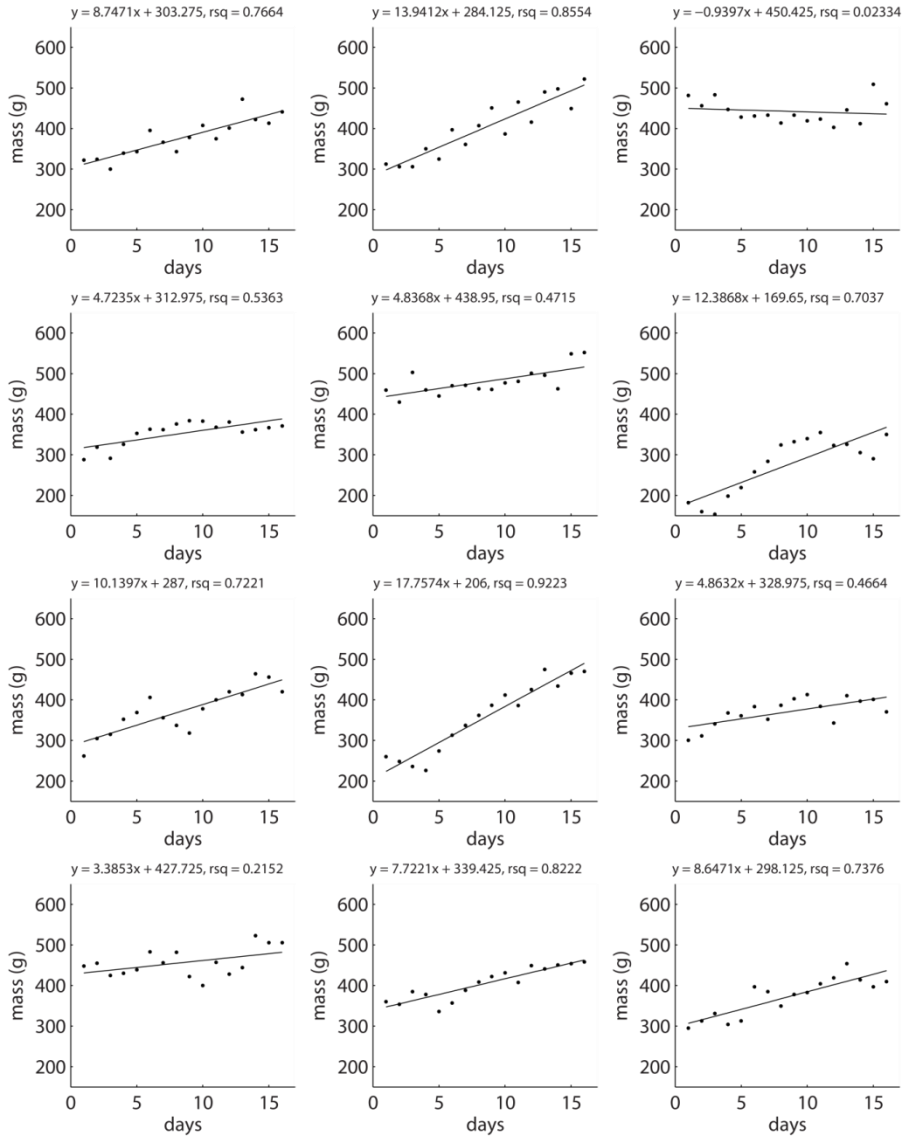

Figure S1. Mass growth rates (slope of linear regression of mass on day) of chicks in control nests over the duration of the nightly monitoring and tracking period (24 July-8 August).

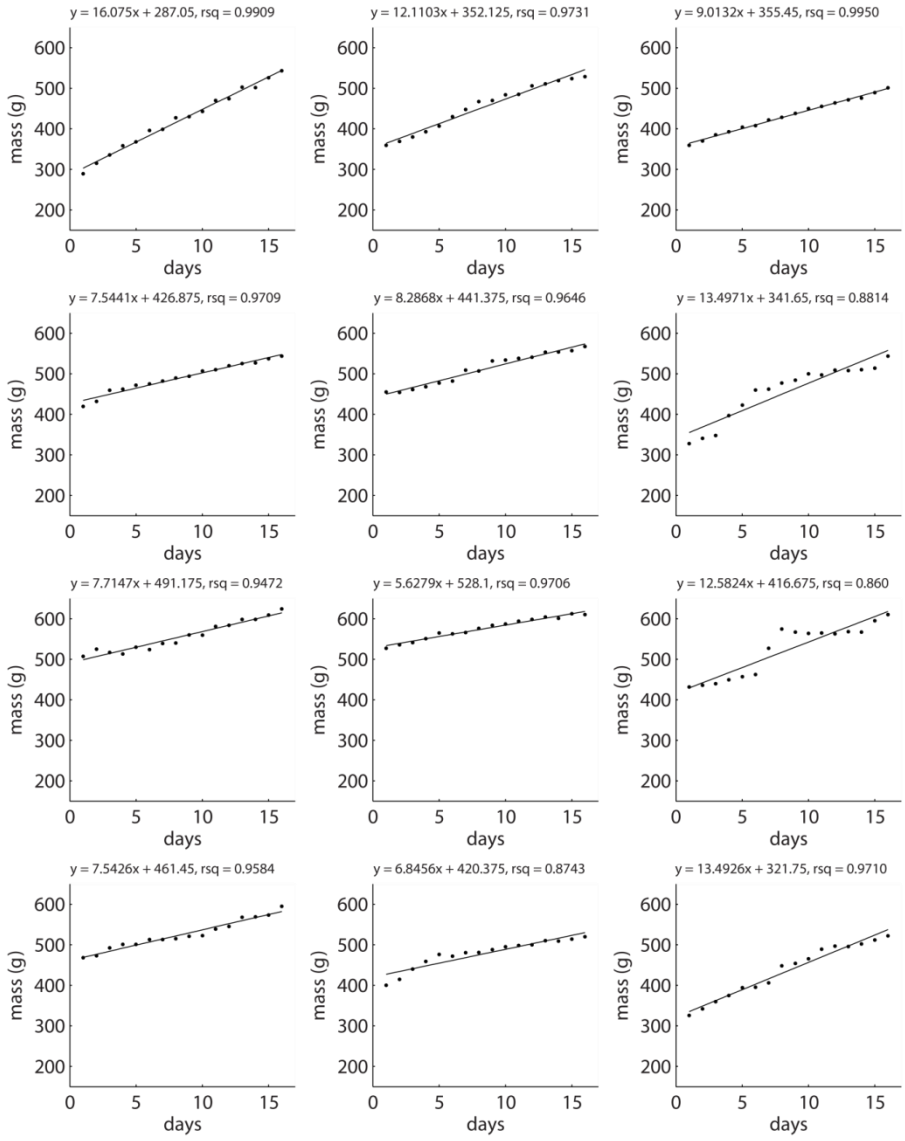

Figure S2. Mass growth rates (slope of linear regression of mass on day) of supplemented chicks over the duration of the nightly monitoring and tracking period (24 July-8 August).

Chapter 7

General Discussion

Introduction

In the opening chapter of this thesis I proposed that the aim of my research was to reveal new insights into the at-sea behaviour of the Manx shearwater. I hope that the intervening chapters have indeed advanced our understanding of the foraging movements and behaviour of the species and provided further insights into the foraging behaviour of seabirds in general. This final chapter provides a brief summary of the thesis findings and discusses some of the many questions that remain for future investigation.

Main findings and further questions

Foraging distributions

A lack of detailed knowledge of the variation in at-sea movements and distributions of seabirds across colonies, sex, age classes and breeding status has presented a substantial challenge to seabird ecology (Lewison *et al*. 2012). We recorded considerable variation in the foraging distributions of birds tracked in this study. The foraging distributions, ranges and trip durations of Manx shearwaters varied between stages of the breeding season (and pre-laying period), between colonies, between years, and - at least during the pre-laying season - between the sexes. Some of this variation may have resulted from of tracking different birds in different years; however, much of the variation is likely to relate to the distribution of accessible prey resources, which may be highly variable between years. This variation highlights the importance of continuing tracking studies over several years.

In addition to foraging distributions, the extent to which birds engaged in different behaviours (such as searching, commuting and resting) also varied between years and stages of the breeding season and pre-laying period. Seabirds such as the Manx shearwater, are vulnerable to a wide range of impacts at sea and an understanding of variability, not just in foraging distributions, but also in foraging behaviour will be increasingly important in designing

appropriate conservation measures, particularly in light of global climate change (Grémillet & Boulinier 2009) and our increasing use of the seas at industrial scales (Halpern *et al*. 2008).

Prior to the work presented in chapter 2, little was known about the movements of male and female Manx shearwaters during the pre-laying period. There was some indication that (like other procellariiforms [Pinet *et al*. 2012; Rayner *et al*. 2012]) males and females might have different foraging distributions (Guilford *et al*. 2009), but no high-precision (GPS) data previously had been collected on the fine-scale movements of individual pre-breeding birds. The movements we recorded were highly variable between years and (in most years) between males and females, being consistent with the different reproductive roles and nutritional demands placed on the two sexes during the pre-laying period. These data are of high value in conservation planning, since they describe highly variable, sex-specific foraging movements during a critical period of the breeding season. In addition they represent a challenge to conservation planning in that the continental shelf-edge area utilised by females is vast and probably unsuitable for protected area based conservation measures. The use of the continental shelf area southwest of Ireland by Manx shearwaters from Skomer Island probably depends greatly on the location of Skomer in relation to the shelf. Further tracking of the pre-laying exodus for birds from northern colonies such as Rum and St Kilda (Outer Hebrides, Scotland) may reveal different patterns of distribution and behaviour during the pre-laying exodus.

A relatively high degree of inter-annual variation in foraging distributions was also apparent during incubation and chick-rearing (chapter 3). Nevertheless, consistent patterns emerged. As expected for central placed foragers constrained to return to the nest frequently (Orians & Pearson 1979), birds from each colony consistently foraged within local waters (within 200 km of the colony). These local foraging distributions overlapped only between birds from colonies on Skomer and Lundy (the closest tracked colonies at only 75km apart), in areas roughly equidistant between the two colonies. Given the distribution of other colonies (so far un-

tracked) it is highly likely that the local foraging distribution of birds from Skomer also overlaps with other colonies, particularly Bardsey Island on the LLyn Peninsular. Density dependent depletion of prey through intense intraspecific competition close to colonies (Ashmole 1963; Furness & Birkhead 1984; Birt *et al.* 1987; Lewis *et al*. 2001) may lead to density dependent foraging ranges (Lewis *et al*. 2001). The distribution of different sized colonies in relation to the distribution of prey resources is therefore a likely mechanism controlling the extent of overlap between the foraging ranges of neighbouring colonies, but this is yet to be tested in these data.

However, birds from all four colonies (and most likely from the majority of Manx shearwater colonies in and around the Irish Sea) also foraged within a single relatively restricted area of the Irish Sea, indicating co-foraging on a shared resource. The key area in which birds from all four colonies foraged was the vicinity of the Irish Sea Front (ISF) and the stratified waters of the Western Irish Sea (WIS) (Simpson & Hunter 1974). This area is likely to experience high productivity (Savidge 1976; Beardall *et al.* 1982; Le Fèvre 1986; Yoder *et al.* 1994) and aggregation of zooplankton and nektonic organisms (Scrope-Howe & Jones 1985; Herman *et al.* 1981; Yoder *et al.* 1994), attracting and retaining high densities of pelagic fish in the associated gyre currents (Hill *et al.* 1994; Laurs *et al.* 1977; Dickey-Collas *et al.* 1997; Alemany *et al.* 2009). Even prior to the first GPS tracking of UK seabirds, this area was well known to support very high densities of foraging Manx shearwaters, as well as many other species of seabird (Stone *et al.* 1994; Begg & Reid 1997; Durazo *et al.* 1998), although the extent to which breeding birds from different colonies utilised this area was not known. Clearly this area is of very high conservation value, but its use by high densities of birds, potentially from many different colonies also raises an interesting question: if, as suggested earlier, intense intraspecific competition in areas of high-density foraging can lead to prey depletion, to the extent that this controls foraging ranges, why should birds from distant colonies travel to forage in an area of presumably high conspecific density (Stone *et al*. 1994)? The frequency of recorded visits to this area declined with increasing distance of the colony, suggesting that the energetic net gain of foraging was significantly

affected by the energetic costs of travelling to it. However the mechanisms by which high foraging densities might affect the foraging success in Manx shearwaters are unknown. This question requires further investigation into the relative levels of foraging effort (energy expenditure) and foraging success (energetic gains) in relation to colony sizes, foraging ranges and specific foraging locations.

Environmental correlates of distribution

The results of our analysis of oceanic conditions in relation to pre-laying foraging distributions were not clear. Nevertheless, it is likely that foraging conditions close to the colony (within the Irish and Celtic Seas) during the pre-laying period have a large impact on the foraging distributions of the two sexes during this period. In particular, the presence of local aggregations of prey and well-formed tidal mixing fronts signalled by dense patches of chlorophyll may be critical in determining the distribution of females (and to a lesser extent males) during this period. Later in the season, during incubation and chick-rearing it is clear that tidal mixing fronts such as the ISF play an important role in determining the foraging movements of Manx shearwaters. However, many foraging areas do not appear to relate to such large-scale features, although they may be predicted by more complex analyses of sea-surface features (e.g. Miller 2009).

The lack of clarity in our analysis of oceanic conditions in relation to pre-laying foraging distributions probably is because remotely sensed chlorophyll densities appear to provide an incomplete predictor for the foraging activity of Manx shearwaters. The same conclusion has been reached previously for other seabird species (e.g. Grémillet *et al.* 2008; Votier *et al.* 2010) and this is likely to be the result of a series of spatial and temporal mismatches across trophic levels between primary production, aggregations of accessible prey-fish, and foraging seabirds (Grémillet *et al.* 2008). Data on the distribution of prey-fish (Karpouzi *et al*. 2007; Fauchald *et al*. 2011), or at least higher trophic level indicators of areas of productivity (e.g. copepods, Votier *et*

al. 2010; Fauchald *et al*. 2011; Fort *et al*. 2012), may provide more powerful predictors of foraging in Manx shearwaters, but for now such data typically are patchy in both spatial and temporal distribution, requiring spatial interpolation and / or averaging over large temporal periods. Further analyses with more appropriate null models (e.g. Wakefield *et al.* 2011) and perhaps more suitable predictor variables may reveal clearer patterns. However, where birds primarily forage on highly mobile resources, that have variable detection probabilities, and are only periodically available at high densities and for short periods of time, (perhaps due to the foraging activities of other pelagic predators; Evans 1982; Pierotti 1988), it is possible that no oceanographic, or prey distribution datasets will consistently predict the presence and absence of foraging behaviour.

Behaviours

In addition to following the movements of seabirds, it is critical to understand the types of behaviour in which they engage when visiting different areas. For this reason, much effort has been put into classifying different types of behaviour from seabird tracking data, particularly with respect to identifying foraging like behaviours from movement data (e.g. Awkerman *et al.* 2005; Pinaud & Weimerskirch 2007; Guilford *et al*. 2008; Votier *et al.* 2010). In chapter 5 we explored the at-sea behaviour of the Manx shearwater using a hidden Markov model (HMM, Rabiner 1989) to identify discrete activities. We found that at-sea behaviour could be organized into three principal activities representing: (1) sustained direct flight, (2) sitting on the sea surface, and (3) foraging, comprising tortuous flight interspersed with periods of immersion. Foraging activity was highly constrained to daylight hours and corresponded well to the occurrence of diving indicating that the primary foraging mode of Manx shearwaters involves local-scale area-restricted search involving frequent landings, perhaps to sample or view prey, and then, if conditions are suitable, attempted prey pursuit and capture. This matches previous observations of Manx shearwaters foraging at sea (King 1974; Jones 1975; Brooke 1990) as well

as recently captured footage from one on-board camera deployed on a breeding Manx shearwater in 2011 (Unpublished Data). Although, the HMM analysis in this thesis may seem relatively complex and requires both GPS and saltwater-immersion data to be collected simultaneously, it has some important advantages over other methods such as first-passage time (FPT), or studies that classify behaviours based on thresholds of speed and path tortuosity. First, it is relatively objective, without the need for identification of (often subjective) thresholds between types of behaviour. Second, methods such as FPT analysis (chapter 3) often fail to identify periods of foraging that do not involve area-restricted search (ARS) and sections of high path tortuosity (e.g. Robinson *et al*. 2007). The HMM method was able to identify short periods of (perhaps exploratory) foraging behaviour that did not involve ARS, but which did involve some landing and diving (and hence immersion). However, there are many seabird species for which this type of method may not be able to distinguish between foraging and resting activity: particularly those, such as auks, which do not have particularly volant modes of foraging.

At large scales, this type of behavioural mapping clearly has high value for conservation planning, allowing better identification of the key areas and habitats where animals engage in specific types of behaviour. In addition, future analyses of the spatiotemporal structure of activity sequences and transitions between behavioural states in relation to oceanic features (Begg & Reid 1997; Miller 2009; Raymond *et al*. 2010), weather conditions (Adams & Flora 2009; Raymond *et al*. 2010) and indicators of prey aggregations (Karpouzi *et al*. 2007; Grémillet *et al*. 2008; Raymond *et al*. 2010; Fauchald *et al*. 2011; Fort *et al*. 2012) may allow us to understand how animals respond to prey distributions and the types of decisions they make when foraging. The three principal activities identified here (commuting, resting and foraging) appear to be a robust set of activities that are sufficiently different from each other to produce distinct differences in speed, track tortuosity, immersion and diving behaviour. Within these broad activity categories there are, of course, more subtle behaviours (different modes of foraging, preening, social behaviours etc.) that cannot easily be differentiated, but which we ought to be

able to identify through more detailed analyses of multiple logger datasets, particularly where simultaneous on-board camera footage is available for validation (e.g. Sakamoto *et al*. 2009; Votier *et al*. 2013; Watanabe & Takahashi 2013).

In chapter 4 we examined a subset of foraging behaviour (which includes searching and diving), specifically diving behaviour, using high-resolution dive loggers. These data provide the first insights into the diving behaviour of Manx shearwaters and the first large dataset providing detailed information on the diving behaviour of any Puffinus shearwater. Approximately 50% of all dives were less than 6 m deep, but all birds routinely dived deeper. The deepest dive recorded was 55.5 m; highly similar (when scaled for body mass) to maximum depths recorded for several other Puffinus shearwaters and similar to the allometric relationship between body mass and maximum dive depth calculated for penguins and alcids (Burger 1991). Our analysis suggests that shearwaters rarely dive beyond 40-60 s, which may represent their aerobic limit, or beyond 30 m depth, which may represent their neutrally buoyant limit. Shearwaters typically made bouts of high intensity diving activity within spatially restricted areas, separated by periods that were likely to be commuting, or searching flight between foraging locations, or periods of rest on the surface of the sea. As suggested by the results of the HMM (chapter 5), diving was highly constrained to daylight and crepuscular hours. Diving typically commenced just prior to sunrise and activity increased through the day, culminating in an evening peak of diving activity. This may reflect a response to changes in the density or availability of prey through the day, or may be the result of a strategy to minimise the cost of carrying large payloads of food. The analysis presented here provides a valuable initial description of the diving behaviour of the Manx shearwater, the details of which previously were unknown. However, these data (recorded at 1Hz) contain a wealth of further detailed information on diving behaviour. In particular, further detailed analysis of the sequence of diving by individual birds (perhaps in conjunction with sequences of activity from state-space models such as the HMM in Chapter 5) may allow us to better understand the process of foraging and diving bouts: how prey are

discovered, how bouts of pursuit diving are initiated, why bouts of diving eventually cease and how seabirds decide to move from one prey patch to another, or to return to the colony.

Foraging, nutrition and provisioning

The duration of exodus recorded in chapter 2 and previous work on yolk development (Astheimer & Grau 1989) suggests that many female Manx shearwaters may in fact initiate yolk development several days prior to departing the colony, possibly mobilising endogenous reserves to do so. Females then appear to meet the majority of the egg's nutritional requirements by foraging during a prolonged absence from the colony (Imber 1976; Warham 1990; Warham 1996); however, the potential for further use of endogenous reserves is suggested once females depart the colony. Oceanic conditions varied between years, as did the distribution and extent of female foraging movements. However, in all but one year (when we probably missed the pre-laying exodus) females were capable of forming an egg during trips of similar duration, suggesting that endogenous reserves may act to buffer the costs of egg formation. This is interesting since, in a long-lived species like the Manx shearwater, females would not be expected to severely compromise their own condition (by using endogenous reserves) to produce an egg (Stearns 1992). Future studies of stable isotopes in body and egg tissues (e.g. Hobson 2006), would be effective in determining the relative contribution of endogenous and exogenous nutrient sources to egg formation.

During incubation, we found no strong relationship between foraging trip duration, location and net mass gain. Incubation trip duration is likely to be controlled by a complex trade-off between the ability of the incoming partner to fast during the following incubation stint and the time needed for the outgoing partner to recover the body condition lost during the previous incubation stint. In addition, the outgoing partner's success during this finite foraging opportunity will be highly dependent on the presence, detectability and accessibility of suitable

prey, which may be unpredictable during the early breeding season, when tidal mixing fronts may not yet be established.

The relationship between foraging trip duration and net mass gain during chick-rearing suggests that in common with many procellariiforms (Chaurand & Weimerskirch 1994; Weimerskirch *et al*. 1994; Weimerskirch *et al*. 1997; Weimerskirch 1998; Gray & Hamer 2001; Magalhães *et al*. 2008), but not all (Phillips *et al*. 2009), the foraging and provisioning strategy of Manx shearwaters may allow parents to regulate reproductive effort by combining short trips to local areas (which maximise food delivery rate to the chick at a net energetic cost to parents) with less frequent, longer trips to more distant productive areas (which result in a lower rate of food delivery to the chick, but which allow parents to recover some of the body condition lost on short trips). In Manx shearwaters (at least those breeding on Skomer) the majority of longer duration trips included visits to the ISF/WIS. For this reason, it is difficult to separate the relative importance of long duration trips in general, and visits to the productive ISF/WIS region specifically, in regulating provisioning and foraging effort.

Foraging trip duration and hence provisioning rate has been shown in several species to provide a potential mechanism by which parents may regulate provisioning effort (Chaurand & Weimerskirch 1994; Weimerskirch *et al*. 1994; Weimerskirch *et al*. 1997; Hamer *et al.* 2005); the parents of well-fed chicks typically making fewer nest visits and hence a greater proportion of longer-duration (self-feeding) foraging trips. However, the role of foraging ranges, destinations and the at-sea foraging behaviour of parents in this flexible provisioning response was unknown. In chapter 6 we attempted to experimentally manipulate the provisioning and foraging behaviour of Manx shearwater parents by supplementing the diet of their chicks. The lack of an expected decrease in provisioning rate probably resulted from a positive knock-on effect of the supplemental feeding, negating the requirement for long self-feeding trips. This important effect

must be present to varying extents in most supplemental feeding studies of provisioning in seabirds, but is rarely (if ever) mentioned.

The lack of detectable meals fed to supplemented chicks probably resulted from chicks being unable to ingest further meals from their parents, but there was also some evidence of a responsive reduction in the mass of meals brought to the nest by parents. However, the most interesting result of this experiment is that despite our large energetic input into rearing the chicks, we found no significant differences in the routes, distributions, or foraging behaviour of parents. This suggests that while nest-visit frequency - and therefore foraging trip duration - may be flexible in response to chick and adult body condition, the at-sea foraging behaviour does not form part of this flexible response and probably is controlled more by foraging conditions and prey distributions than by the nutritional demands of the chick. It may be that in some years, when prey are plentiful, Manx shearwater parents work well below their maximum foraging effort limit while adequately provisioning their chick. Indeed, the results of the HMM (chapter 5) suggest that in some years approximately 30-40% of the day may be spent sitting (apparently resting) on the surface of the water. The extent to which this is true for Manx shearwaters rearing chicks in other years, from other colonies, and for other seabird species merits further investigation.

Individual movement, memory and navigation

Plotting the movements of individual birds tracked during exodus across multiple years indicated that the choice of foraging locations was flexible, with birds of both sexes selecting different strategies in different years. However, the routes of birds travelling to and from the continental shelf were remarkably consistent and direct, with most birds heading directly towards the Porcupine Bight area, and then exploring the continental shelf edge. The direct nature and consistency of these routes suggest that they may be informed by previous experience and / or accurate navigational mechanisms. Despite the variation in foraging distributions of birds

tracked during incubation and chick-rearing, there were relatively high levels of consistency in the use of some foraging locations within and between birds foraging from different colonies, at different stages of breeding, and in different years. Again, the direct nature of some track segments and the consistency of some distant foraging locations suggest that many larger scale direct movements were mediated by accurate navigational mechanisms and informed by previous experience (or the following of other birds informed by previous experience). These details imply an important role for learning and the building of large-scale memorised maps of foraging areas. The nature of the cues, or representations involved in navigation and map learning are beginning to be investigated (e.g. Nevitt 2000; Nevitt & Bonadonna 2005; Dell'Ariccia & Bonadonna 2013) and offer a potentially fascinating and fruitful area of research. Almost certainly, navigation and searching behaviour during foraging trips include a strong social element, with the location of prey patches signalled by the activities of conspecifics or other foragers (Stone *et al.* 1994; King 1974; Jones 1975; Sakamoto *et al.* 2009). Shearwaters are typically recorded feeding in large flocks at sea (Stone *et al.* 1994; King 1974) where there is likely to be a strong element of social enhancement of individual foraging success (Götmark *et al.* 1986).

Final remarks

When I started this thesis much was known about the breeding biology of the Manx shearwater, helpfully collated in one wonderful book – *The Manx shearwater* by Mike Brooke. Conversely, relatively little was known about the at-sea behaviour of the species – a seemingly huge gap in knowledge for a bird that spends the vast majority of its life foraging, roosting and migrating at sea, but unsurprising given the difficulty of following individual birds away from the colony. I hope that this thesis has gone some way to filling in that gap, at the same time opening up intriguing new questions about the at-sea behaviour of the Manx shearwater and seabirds in general. Only through developments in biologging technology, particularly the increasingly

impressive miniaturisation, has the collection of such detailed data become possible. I am certain that future developments in biologging techniques will continue to reveal ever more fascinating details of many pelagic seabirds. In particular the deployment of miniature cameras (e.g. Sakamoto *et al*. 2009; Votier *et al*. 2013; Watanabe & Takahashi 2013) promises to reveal unprecedented levels of detailed data on searching strategies, foraging success, decision making, responses to oceanic and meteorological conditions, interactions with conspecifics and other marine foragers, and many more aspects of seabird behaviour.

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