At-sea behaviour in marine birds: a life-history perspective

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Thesis submitted for the degree of Doctor of Philosophy
Michaelmas Term 2014

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Abstract

Recent bio-logging technology and associated techniques have uncovered the distribution, behaviour, and phenology of marine predators at remote locations, providing us with insights of not only scientific merit, but also in terms of conservation and management. This thesis explores the at-sea behaviour of marine birds using field studies and ethoinformatic approaches by using multiple data loggers, focusing on four species of free-ranging seabirds breeding in the UK. Key findings and conclusions are:

1. Extending travel distance in central place foragers in the wild is associated with higher prey quality as estimated by an indirect method based on dive profiles. This result is consistent with a prediction of optimal foraging theory, but my results show empirically that seabirds are able to increase reward with distance at the extended scale of the marine environment.

2. Razorbills *Alca torda* are capable of adjusting their foraging behaviour in response to proximate environmental conditions. The potential mechanisms underlying this adaptive behaviour are independent of breeding stage, but the magnitude of flight orientation is scale-dependent. These results suggest that Razorbills are capable of optimising their foraging adaptively, possibly reading cues from the environment or conspecifics.

3. Diving behaviour in sympatric Atlantic Puffins *Fratercula arctica* and Razorbills is very similar, in contrast to the predictions of the competitive exclusion principle. They are likely to be near carrying capacity for the location and this may explain why Skomer’s Razorbill population is declining while its puffin population is stable.

4. Differences in foraging trip duration of chick-rearing Manx Shearwaters *Puffinus puffinus* reflect differences in resource allocation between provisioning offspring and self-feeding. I developed a model based on patch quality and travel time to show that birds should use bimodal foraging trip durations to optimise feeding rates for their offspring.

5. Individual reproductive performance in Manx Shearwaters can be predicted from previous breeding phenology and is linked to differences in overwintering behaviour patterns. This carry-over effect reveals the existence of a trade-off between current parental investment and future reproductive performance.

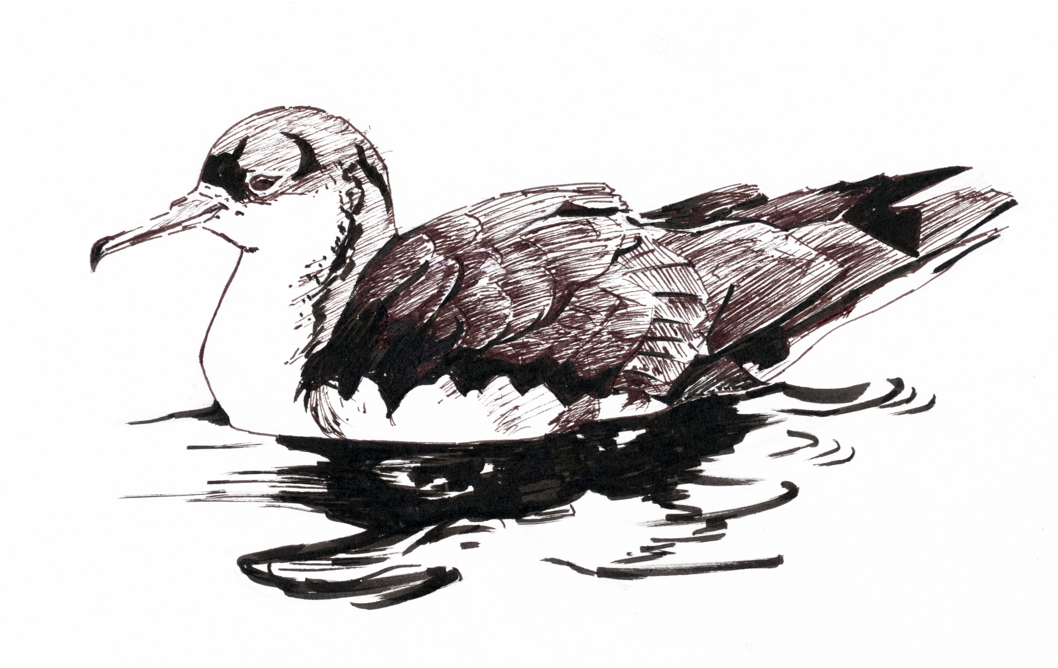
Acknowledgements

I was privileged to receive scholarship support from the Japan Student Services Organisation (JASSO) and Merton College. I also received research support from the Royal Society for the Protection of Birds, the American Animal Behavior Society, the Department of Zoology and Merton College. I also received financial support via the Department of Zoology and Merton College (supplementary travel grant) to visit Stéphane Aris-Brosou at the University of Ottawa and Katherine Wynne-Edward at University of Calgary in Canada.

Logistical support was supplied by Tim Guilford and Chris Perrins, and by Chris Taylor, Birgitta Büche, Edward Stubbings (Skomer wardens), Kerry Leonard, Shane Wolsey, Julian Greenwood, Neville McKee, David Gabrailth, Philip McNamara (Copeland Bird Observatory), Derren Fox (Lundy warden), Steffen Oppel, Ellie Owen, Mark Bolton, Kyle Elliott, Rhiannon Meier and most thankfully by Annette Fayet. I benefited from help in the field by an amazing group of assistants and colleagues: Annette Fayet, Dave Boyle, Tim Guilford, Holly Kirk, Luke McClean, Phil Collins, Jenni Roberts, Oliver Padget, Robin Freeman, Andrea Flack, Daniel Burke, Igor Boczarow, Mate Nagy, William Whittington, James Roden, Nia Stevens, Lewis Yates, Maria Mak, Dave and Sonia Gadd. Katherine Wynne-Edwards and Lea Bond helped in the lab.

I am particularly grateful to my supervisor, Tim Guilford for providing me with an opportunity to work on this project and for guidance, advice and encouragements. I am also indebted to Chris Perrins for his ideas, discussions and support throughout my PhD. I profoundly thank Alex Kacelnik, Ben Sheldon and Emiel van Loon for rescuing me on several occasions when I was completely stuck in ideas. I am grateful to Theresa Burt de Perera, Ben Sheldon and Chris Perrins for being on my thesis advisory committee and for their invaluable help and kind support. This thesis benefited from helpful discussions with OxNav and ABRG members, including Andrea Flack, Benj Petitt, Holly Kirk, Annette Fayet, Oliver Padget, Ignacio Juarez Martinez, Ben Dean, Rob Holbrook, Anya Nesterova, Dora

Biro, Vicki Davis, Izzy Watts, Takao Sasaki, Robin Freeman, Steve Barlow, Lucy Taylor and Rhiannon Meier. Many of inside and outside of the Department provided me productive and enjoyable work environment in Oxford, particularly my office room mates: Ignacio Juarez Martinez, Oliver Padget, Izzy Watt, Vicki Davies, Andrea Flack, Benj Betitt, Francesco Montiaro, Miguel Gonzalez dos Santos, Nick Golding and Holly Kirk for her unfailling support throughout my time in the UK as well as Igor Boczarow and Dmitry Kondratiuk for being a fantastic company. Special thanks go to Stéphane Aris-Brosou, Kyle Elliott and Tony Gaston for their practical and insightful suggestions and on-going support throughout my studies.



A memory of miserable rainiy nights when we were waiting for LED-decorated shearwaters in the middle of the colony at Lundy Island in 2012. Drawn by I. Boczarow.

Author Contributions

All work in this thesis is primarily my own.

This thesis is structured as a set of independent chapters in the syle of scientific journal articles with a general introduction and a final conclusion chapters linking them, as approved by the Director of Graduate Studies in the Department of Zoology, University of Oxford.

The following people co-authored one or more of these articles and their contributions are as follow:

Tim Guilford and Chris Perrins contributed their ideas and feedback for all chapters.

Stéphane Aris-Brosou participated in data analyses and contributed his ideas and feedback during manuscript preparation of Chapter 2, 3, 5 and 7.

Kyle Elliott participated in data analysis of Chapter 4 and contributed his ideas and feedback during manuscript preparation of Chapter 4 and 6.

Antica Culina participated in data analyses of Chapter 7.

Annette Fayet participated in data collection of Chapter 2 (2011), 3 (2011), 4 (puffin) and 7. Dave Boyle participated in data collection of Chapter 2, 3, 4 (Razorbill) and 7 (Isthmus colony). Holly Kirk and Ben Dean participated in data collection of Chapter 2 (2011), 3 (2011) and 7 (2009-2011). Oliver Padget participated in data collection of Chapter 5 and 7 (2014). Ignacio Juarez Martinez participated in data collection of Chapter 7 (2014). Ellie Owen, Mark Bolton and Robin Freeman contributed their feedback during manuscript preparation of Chapter 2 and 3. Luke McClean, Julian Greenwood and Kerry Leonard participated in data collection of Chapter 6. Co-authors provided me with feedback during manuscript preparation.

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Chapter 1

General Introduction

Introduction

This thesis contributes to our understanding of at-sea behaviour in free-ranging animals, principally via bio-logging techniques based on field studies of a range of colonial seabirds: Manx Shearwaters (*Puffinus puffinus*), Razorbills (*Alca torda*), Atlantic Puffins (*Fratercula arctica*) breeding at Skomer Island, Wales, and Black Guillemots (*Cepphus grille*) breeding at Bangor Harbour and Lighthouse Island in Northern Ireland (Table 1; Fig 1).

In this introduction chapter, I first present backgrounds of the questions that the thesis addresses, and at-sea behaviour as a subject of study. Second, I describe the novelty of the study systems in the context of proposed research. Third, I consider the potential impacts of handling and device deployment on the study animals. Lastly, I outline the specific aims and structure of the following chapters.

Table 1. Summary of the key life-history features in the four study species.

	Family	Mass (g)	Prey load	Clutch size	Main flight style	Fledging strategy
Manx Shearwater	Procelariiform	450	Regurgitate	1	Gliding	Altricial
Razorbill	Alcid	750	Multi-prey loader	2	Flapping	Intermediate
Atlantic Puffin	Alcid	380	Multi-prey loader	1	Flapping	Altricial
Black Guillemot	Alcid	380	Single-prey loader	2	Flapping	Altricial

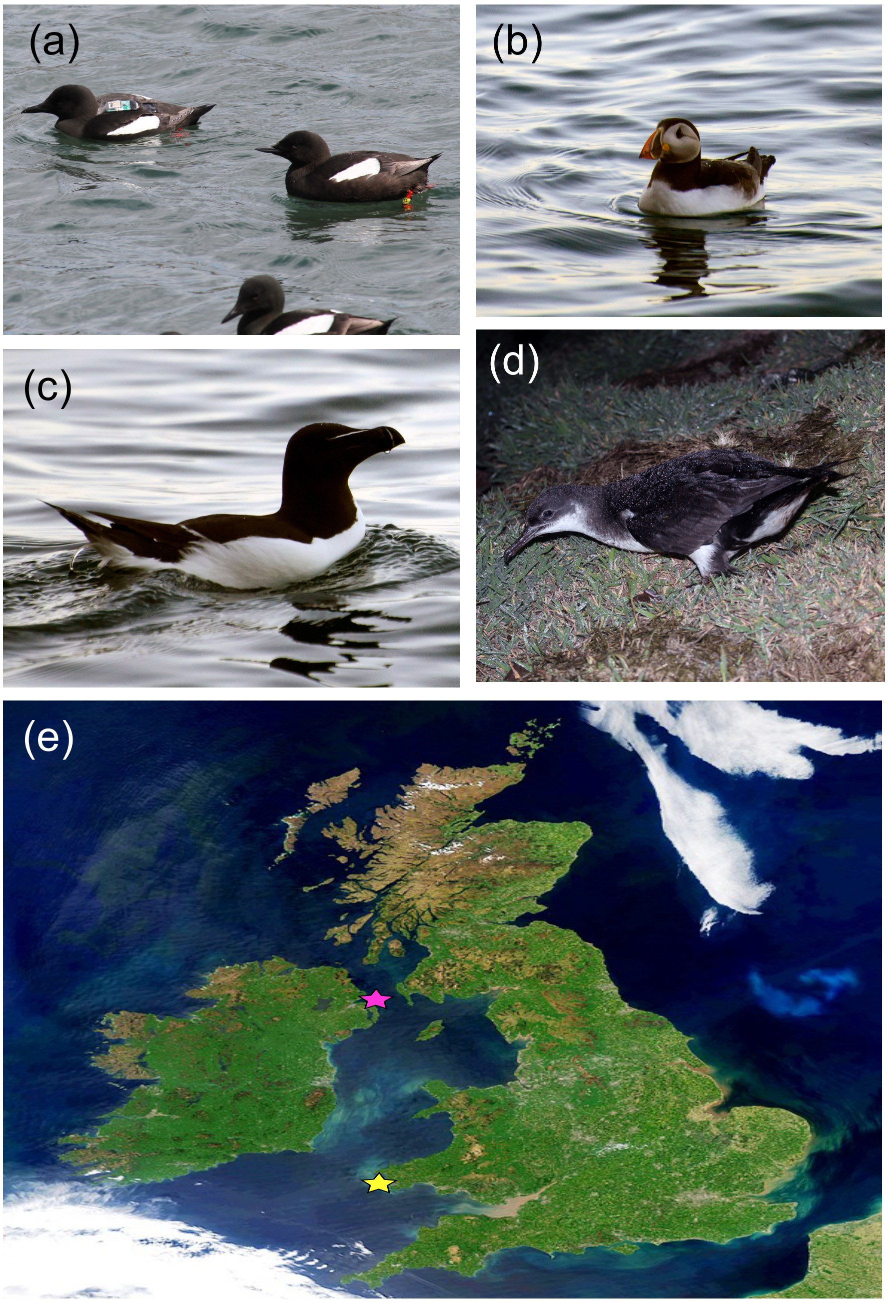

Figure 1. Four seabird species used in this thesis: (a) the Black Guillemot (*Cepphus grylle*: photo A. Shoji) breeding populations of the Bangor harbour and Light house Island (indicated as a pink star) in Northern Ireland; (b) the Atlantic Puffin (*Fratercula arctica*: photo I. Juarez-Martinez), (c) the Razorbill (*Alca torca*: photo I. Juarez-Martinez) and (d) the Manx Shearwater (*Puffinus puffinus*: photo L. McClean) breeding at Skomer, Wales (indicated as a yellow star).

Individual animals continuously face decisions that are linked with their fitness. Decisions on movements are fundamental and are crucial for their survival and reproduction (Jander 1975) and are connected with all types of animal behaviour. For instance, movements are involved in foraging, migration, escaping from predators and reproduction. Therefore, understanding animal movements is a fundamental aspect in animal behaviour research. Amongst movement patterns, foraging behaviour has been well documented, especially in terrestrial animals, because it is relatively easy to monitor and essential for survival. In natural habitats, resources are spatially and temporally distributed in a heterogeneous environment so that animals are therefore expected to make decisions that maximise their fitness. During breeding, many animals forage for provisioning at distance patches and transport loads to the central location where they nest or raise young (Orians and Pearson 1979; Wetterer 1989). Theoretical models predict that food load is determined by travel time, a prediction that has been tested in several systems (*e.g.* ants: Rissing 1983; Rudolph and Loudon 1986; bees: Kacelnik et al. 1986; starlings: Kacelnik and Cuthill 1987), and the load size could also be varied by prey load styles such as single or multi-prey loaders or internal loaders (Lessells and Stephens 1983).

Foraging theory was seldom assessed in ecological or behavioural contexts under natural conditions until the 21st century, and earlier work has only been carried out on study systems that were typically small and under controlled conditions. This apparent limitation was largely due to the logistic hurdles as it has until recently been quite impossible to observe or manipulate animals, especially those leaving in a marine environment. Recent technological advancements enable us to study movement patterns during foraging behaviour, in particular in those marine animals. While various on-board data-loggers or monitoring devices provide us with large amounts of data from our study animals, our knowledge about how those movement patterns are linked with life-history traits and the consequence of the decisions on fitness is still limited. The main goal of this thesis is therefore to examine how movement patterns, particularly those involved in foraging, vary amongst animals with different life-histories, focusing on wild birds in the context of both ecology and behaviour. I use data obtained from a range of bio-logging technologies to address questions related to foraging theory (Chapters 2 and 3), exclusion competitive principles (Chapters 4 and 5), dual-foraging strategy (Chapter 6) and carry-over effects (Chapter 7). This thesis extends our knowledge not only by adding more species to test predictions in wild animals, but also linking their behaviour with life-history traits.

1.1 Why study at-sea behaviour?

At-sea behaviour of pelagic seabirds has mainly been recorded by people who spent their lives at sea such as sailors and fishermen, and who were familiar with the diversity of seabirds (Gaston 2004) – that is, until the advent of "bio-logging science" (Naito 2004). With the development of bio-logging, we have acquired a set of tools to study at-sea behaviour remotely, allowing us to move far beyond direct observations made at the colony or at sea from a boat or an aircraft. By combining bio-logging science and direct observations, our knowledge of seabird behaviour has hugely progressed in the last few decades (Kooyman et al. 1971; Wilson 1995; Wilson et al. 2002; Naito 2004; Wilson et al. 2007; Wilson and Vandenabeele 2012). Spatial information related to the distribution, habitat use, movement patterns, and foraging behaviour of pelagic seabirds have been collected and our understanding of these different aspects of seabird ecology has thereby considerably improved.

Marine top predators such as seabirds are generally considered good indicators of marine ecosystem health (Cairns 1987); indeed, seabirds are effective environmental markers as variations in their diet, foraging range, foraging styles (*e.g.* surface feeders, divers, scavengers) can reflect environmental changes at a wide range of levels (Cherel and Weimerskirch 1995). While knowledge of their movement patterns, foraging behaviour or habitat use is essential to use them successfully as indicators, our understanding of at-sea behaviour is largely limited to a few species, usually large seabirds such as albatrosses (*e.g.* Lecomte et al. 2010) or penguins (*e.g.* Putz et al. 1998), because the size and weight of bio-loggers is often a limiting factor. Moreover, seabird species have a unique life-history with high adult survival, slow population growth and low fecundity (Ricklefs 1990). This suggests that once a population declines, the process of recovery is longer than in short-lived animals,; this makes them potentially particularly vulnerable to negative impacts induced by human activities (*e.g.* fisheries, offshore energy farms, etc) (Grémillet and Boulinier 2009). To develop effective conservation plans, a clear understanding of the natural behaviour of each species, what influences it, and how it may be affected, is essential. Knowledge at the species level is useful because species may respond differently. In this context, I focus throughout this thesis on improving our knowledge of the natural history of marine top predators, while addressing scientific questions related to both foraging and life-history theory.

1.2 Free-ranging colonial seabirds as a study system

Most birds are terrestrial, but about 5% of species live partly or wholly away from land, except while they breed (Gaston 2004). Considering the orders of study species (*Procellariiformes* and *Charadriiformes*) which diverged from their terrestrial ancestors (Schreiber and Burger 2002), we can wonder what prompted their return to the sea. Seabirds are indeed currently foraging in places in the ocean where no obvious landmarks are available, and where prey distributions may be unpredictable. In this regard, seabirds may behave differently from the predictions of theoretical models developed for domestic and/or terrestrial animals. Because of their unique life-history (Lack 1968) and physiological adaptations (Whittow and Rahn 1984; Ellis and Gabrielsen 2002), it is reasonable to assume that seabirds may show different responses from land animals and hence provide us with an opportunity to test various theoretical predictions related to their life-history under “at-sea” conditions.

One of the most pronounced advantages of using breeding seabirds as a study system is that it is relatively easy to collect information based on large sample sizes. The seabirds studied in this thesis are all colonial breeders and their nests are easy to find in the field. Another advantage of using nesting seabirds is that they must return to their nest regularly to care for their young. The habit of frequent visits to their nest during breeding and the fact that some seabirds nest in burrows allows us to capture and recapture birds for deployment and retrieval of telemetry devices, which is more difficult in terrestrial birds. This is critical because all the data loggers used in this thesis are unable to transmit data remotely, and so need to be retrieved as they store data on the logger itself. Moreover, our study species nest in burrows where it is possible to make a short-access tunnel to each nest, which allows us to minimise handling time and to reduce potential disturbance to birds (Shoji and Gaston 2010).

While movement patterns in large species such as penguins and albatrosses have been well documented (Weimerskirch et al. 1994; Phalan et al. 2007), at-sea behaviour is not well understood for small and medium-sized seabirds. Furthermore, seabird colonies on Skomer offer various possibilities for addressing interesting questions. For example, I used Razorbills to investigate why birds increase travel distance during, for this species, most energetically expensive breeding period. Razorbills have high flight costs which are expected to provoke strong selection for minimising transit costs. Thus, increasing travel distance seems counter-intuitive, therefore it is interesting to test why Razorbills do this. Similarly, Puffins and Razorbills feed on similar prey, but their life-histories differ as Puffin chicks are altricial while those of Razorbills are intermediate fledgers, making these two species ideal for a comparative study of diving behaviour in sympatric auks. Lastly, Manx Shearwaters are trans-equatorial migrants and so are good candidates to test whether carry-over effects during the non-breeding period exist.

Taken together, studies on colonial seabirds provide many advantages and provide us with the opportunity to gain invaluable information of a range of scientific interests, as well as insights into conservation and management.

1.3 Impacts of handling and deployments

In this thesis, I used three types of bird-borne data loggers: GPS loggers, time-depth-temperature recorders (TDR) and geolocators, to address a range of questions, which are explored in this introduction chapter. These devices provide us with valuable insight into animal behaviour, but there is always a potential impact on animals. For example, simply our presence on the colony may have an impact on behaviour and stress levels. We are responsible for minimising our impacts on animals for ethical reasons, therefore it is critical to assess the potential effect of bird handling in particular during device deployment. For example, some auks are known to be sensitive to human disturbance and they are likely to desert their egg if they are disturbed during the incubation period (Gaston and Jones 1998). Capture and handling of birds during deployment and removal of devices can cause an impact on the behaviour, mostly on a short-term scale (unless they desert the nest), but the behaviour of individuals carrying devices may have been altered by the deployment and therefore not reflect natural behaviour. Device effects are highly dependent on the mass (Elliott et al. 2007; Passos et al. 2010), size, shape and position of the device attached (Phillips et al. 2003; Burger and Shaffer 2008). In this study GPS loggers are likely to have the biggest impact on birds as both TDRs and geolocators are much smaller. In this thesis, the total mass of a GPS logger including attachment materials was between 3 and 5% of adult body mass for all study species, which is within the range given by the British Trust for Ornithology as a good practice guidance. Negative impacts such as nest desertion, extended trip duration and smaller meal size have been reported in several species of seabirds carrying loads comprising between 0.6 and 6.0 % of body mass (Saether et al. 1993; Phillips et al. 2003), though many of those reported deployments were of longer duration than in our study.

Our field procedures have been approved by the British Trust for Ornithology (BTO), the Skomer Island Advisory Committee and the Countryside Council for Wales; the mass of our deployments was always under the upper limit of the obtained approvals that has been based on a previous study (Phillips et al. 2003). Furthermore, through experience in the field by previous and current Oxford Navigation Group members, we have developed our own rules for GPS logger deployment as follow:

1. Use flat and streamlined packages to reduce impacts of the shape and buoyancy of the devices (see Figure 2);
2. Use failsafe tesa-tape that disintegrates 2-3 weeks after deployment;
3. Do not deploy the device for two consecutive-tracking periods where possible.

Additionally, where possible, we have monitored the impact of our deployments on the breeding success of the birds, compared to undisturbed birds within our study site or nearby sub-colony. The results of previous control tests suggest that our procedures did not have any detectable impact on hatching success, fledging success, provisioning rate, chick growth rate or foraging behaviour of Manx Shearwater parents carrying devices (Guilford et al. 2008; Dean 2012; Dean et al. 2012). Currently, we are unable to have a true control for at-sea behaviour as we cannot monitor at-sea behaviour without devices. However, the analysis of at-sea behaviour data requires common sense when interpreting the results, as it is always possible that logging devices affect the birds' behaviour.

TDR and geolocators are much smaller than GPS loggers (< 4 g). While the TDRs used in this thesis were for short-term deployment (< 14 days), geolocators were useful to study non-breeding spatial distribution and at-sea behaviour year-round. The advantage of geolocators is their small size (<2g), which reduces the influence of the device on behaviour (Wilson 2001; Phillips et al. 2003; Ropert-Coudert and Wilson 2005). Geolocators make long-term tracking possible for species which are too small to carry satellite transmitters (Hatch et al. 2000; Stutchbury et al. 2009; Gaston et al. 2011). However, the effect of the year-round deployment of geolocators has mainly been examined with respect to reproductive success (Carey 2011) which is relatively insensitive to small changes in nutritional conditions. In fact, several studies found that even light devices (as small as 0.7 % of body size) have caused a reduction in adult body mass, nest attendance, and provisioning rates (Wanless et al. 1988; Ackerman et al. 2004; Paredes et al. 2005). Elliott et al. (2012) found that Brünnich's Guillemots (*Uria lomvia*) equipped with a geolocator for one year increased baseline corticosterone, but survival rate, return body mass and chick feeding rate were not different from control birds without geolocators. This result suggests that even small devices like geolocators can cause chronic stress by being deployed for long-term periods, and survival or reproductive success is not adequate to determine the impact. In case of the Manx Shearwaters that carried a geolocator all year round, there was no significant difference in breeding success and/or feeding rates to their young after the deployment (Guilford et al. 2009), so we consider the impact to be insignificant. To what extent at-sea behaviour such as trip length or diving parameters can be affected by the impacts of device deployment remains to be determined.

Figure 2. A Manx Shearwater carrying a GPS logger on its back while flying at sea. - *Photo: I. Juarez-Martinez* -

1.4 Aims and structure of this thesis

The aims of this thesis are: (i) to examine at-sea behaviour of free-ranging animals with respect to their life-history, the consequence on their reproductive performance and how at-sea behaviour during winter affects subsequent breeding attempts, and (ii) to document the foraging behaviour of diving seabirds.

Although I always aim to build questions/hypotheses/predictions before collecting data, sometimes it was not possible to have such a scientific process, because there were no prior data. Thus, I approached this thesis with the aim of describing behaviour as "observed" through devices and to address questions whenever patterns emerged. In this regard, "bio-logging technology" can be used to address questions based on hypotheses, but also potentially to provide the hypotheses themselves. As some data can be used to address more than one question, especially long-term data (outside my data collection periods), some data are shared to address different questions in more than one chapter.

The following chapters are presented as self-contained manuscripts, and each is intended to be readable independently. As I used extended sampling periods, data were not collected only by me, but also by former and current OxNav students, researchers and collaborators. As a result, many people contributed to the work of one or more chapters in various ways: Tim Guilford, Chris Perrins, Stéphane Aris-Brosou, Kyle Elliott, Annette Fayet, Holly Kirk, Dave Boyle, Ben Dean, Oliver Padget, Ignacio Juarez-Martinez, Ellie Owen, Mark Bolton, Robin Freeman, Luke McClean, Julian Greenwood, Kerry Leonard, Toshiyuki Nakata and Antica Culina (see Author Contributions for details). The six data chapters are presented to address five questions. I briefly introduce each chapter below.

1. Why do central-place foragers increase their travel distance?

Chapter 2 examines the benefits to central-place foragers of undertaking longer foraging trips, using Razorbills which have extremely high flight costs. Theoretical models predict that central-place foragers should use nearby patches unless net energy gain per unit time is higher at distant patches (*i.e.* reward is high enough to travel further). Empirical data from a range of animals have supported this prediction, but it is not well established in marine animals (Elliott et al. 2009). A simple explanation for increase in travel distance is that animals could not find food nearby (in this case, prey at nearby patches may be depleted and therefore birds need to extend their travel distance). Alternatively, animals may extend travel distance because distant patches are better in prey abundance and quality (in this case, one would expect foraging success to increase with distance). I tested these contrasting hypotheses by using simultaneously co-deployed GPS loggers and time-depth-temperature recorders (TDR) on breeding Razorbills.

2. How do birds search for food at-sea with flexibility?

Chapter 3 explores how variations in proximate environmental conditions influence search patterns in Razorbills, depending on breeding stage when they have different constraints. Environmental conditions have previously been shown to affect movement patterns in seabirds, but our understanding of how breeding stage affects search pattern is poor. I determine the effect of breeding stage on search patterns and how birds respond to proximate environmental conditions in relation to their search patterns.

3. How do sympatric seabird species coexist at the most energetically demanding phase?

Chapter 4 investigates how diving behaviour in Atlantic Puffins differs from sympatric Razorbills breeding at Skomer Island at the same time of year. It has previously been shown for a range of seabirds that sympatric species feeding in a similar dietary niche coexist, but differ in resource use (*e.g.* auks: Thaxter et al. 2010, penguins: Mori and Boyd 2004; Wilson 2010, petrels: Navarro et al. 2013, albatrosses: Weimerskirch et al. 1988). The aims of this chapter are two-fold: to document diving behaviour in Atlantic Puffins, which has never been reported in the primary literature; and to compare puffin diving behaviour to that of Razorbills. We considered dive profiles based on TDRs by simultaneously tracking breeding populations of those species at their Skomer colony. Furthermore, as predicted from the hypothesis that a trade-off between oxygen stores and oxygen utilization drives variation in dive duration, we test how dive duration would scale with mass across auks using new data from Atlantic Puffins and Razorbills in Chapter 4 and Black Guillemots in Chapter 5, as well as previously collected data within the literatures.

4. Why do seabird parents switch between short and long foraging trips?

Chapter 6 assesses the resource allocation between offspring and parents Manx Shearwaters during the energetically demanding chick-rearing period. A dual foraging strategy has been reported in many seabird species to benefit parents by alternating foraging trip durations. While they mainly forage for offspring during short trips, they perform a long trip for self-feeding on occasion (Ropert-Coudert et al. 2004). However, these studies normally consider trip duration as a function of adult body mass before and/or after each trip, or reproductive success, but how at-sea behaviour and food load size to offspring differ during these trips is poorly understood. I examine foraging effort (measured by number of dives) and food load size (measured by food load size transferred from parent to young) for each trip in relation to trip duration, distance and foraging locations.

5. How do individual differences in phenology and behaviour result in reproductive performance at the population level?

All the data chapters I presented so far aimed to examine at-sea behaviour of central-place foragers during the breeding season. In Chapter 7, I extended this approach to explore how at-sea behaviour during the non-breeding period influences subsequent breeding success. In iteroparous animals, there is a trade-off between current reproductive success of an individual and its future survivals (Williams 1966). Thus, it is not befeficial for those animals to maximise (extend) parental care when the future success may be sacrificed. For example, migratory birds are expected to recover their body conditions during wintering period and breeding phenology is often linked with the body conditions of the adults in some animals (Newton 2010). Unlike some animals, Manx Shearwaters (*Puffinus puffinus*) appeared to have fixed breeding phenology within individuals (Kirk, H. Unpublished). Manx Shearwaters have a long breeding phase and are long-distance migrants (Brooke 1990) and thus, this species is a good candidate to study seasonal interactions on breeding success. At-sea behaviour of marine predators has largely been studied using breeding individuals and studies of non-breeding phases of those are largely restricted to investigations of spatial distribution, habitat use, phenology, return weight and steroid hormones. To the best of my knowledge, there is only one study that examined how non-breeding behaviour affects breeding success in a following year using a short-distance migrant, Black-tailed Gulls (*Larus fuscus*: Kazama et al. 2013). As migratory phenology is generally a good indicator of breeding success within a population of migratory animals, I examined whether phenology and the non-breeding at-sea behaviour were linked to subsequent breeding success in Manx Shearwaters by using salt-water immersion data collected from geolocators over five migratory seasons.

A General Discussion (Chapter 8) synthesises the key findings of this thesis and assesses the extent to which its aims were achieved.

References to Electronic Supplementary Materials are made and attached at the end of each chapter.

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Chapter 2

Flexible foraging strategies in a diving seabird with high flight cost

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Marine Biology (2014): 161:2121–2129

ABSTRACT

How central-place foragers change search strategy in response to environmental conditions is poorly known. Foragers may vary the total distance travelled and how far they range from the central place in response to variation in the distribution of their prey. One potential reason as to why they would extend the length of their foraging trip and its distance from the colony would be to increase prey quality or quantity, despite incurring higher transit costs. To test this trade-off hypothesis in a species with high flight costs, we recorded the foraging behaviour of Razorbills (*Alca torda*) using state-of-the-art techniques that log both individual horizontal (flight activity) and vertical (dive activity) movements. We show that the distance that Razorbills travelled to foraging locations increased with sea-surface temperature, which may relate to higher prey quality or quantity. This relation is supported by an indirect index of patch quality, based on dive profiles, which also increased with travel distance from the colony. Furthermore, we show that this index was highest during the daily peak in diving activity, around midday. Taken together, these results suggest that Razorbills are capable of adjusting their search strategies sensitively in response to proximate environmental cues.

Key words: Razorbill, optimal foraging, GPS, TDR, wildlife telemetry, navigation

1. INTRODUCTION

Foraging is a critical activity in an animal's life, and energy costs relative to energy intake determine many aspects of animal ecology. In particular, the ability to adjust foraging strategy in response to variable food availability can be critical to survival and reproductive success. Making appropriate movements to locate sufficient prey efficiently is important for successful foraging, and is especially challenging for marine predators whose prey distribution is patchy and scarce (Ricklefs 1990; Weimerskirch 2002; Sala et al. 2012). Central-place foragers, which travel back and forth between a breeding colony and foraging grounds, are expected to minimise time spent away from their offspring and maximise total energy gain by selecting the nearest exploitable resources (minimising movement costs) and/or foraging on abundant or high-quality prey (maximising energy intake; Baird 1991; Ydenberg et al. 1994; Saunders and Ydenberg 1995; Ropert-Coudert et al. 2004). Thus, the Central-Place Foraging Theory predicts that animals are expected to extend foraging trip distance only if their net energy gain (via quality and availability of prey) increases with respect to what they would gain foraging at patches near the colony (Houston and McNamara 1985; Cuthill and Kacelnik 1990; Waite and Ydenberg 1996). This effect has been demonstrated in some seabirds (Birt et al. 1987; Gaston et al. 2007; Balance et al. 2009), but this is not always observed in a number of central-place foragers (Jenkins 1980; Alonso et al. 1994; Frey-roos et al. 1995; Grémillet 1997).

Since the availability of food resources to marine predators can be highly variable in time and space, the costs and benefits of foraging at more distant locations are expected to depend on proximate environmental conditions. The availability of marine prey resources may be linked to local environmental variables such as sea surface temperature (Pajaro et al. 2005), wind conditions (Haney and Schauer 1994) and tide (Burger and Powell 1990). Thus, when foraging conditions near the colony are poor, central-place predators may increase their foraging success by expanding their search to include more distant locations. Indeed, central-place foragers sometimes deplete the area around the colony of prey, a phenomenon known as "Ashmole's Halo" (Ashmole 1963; Gaston 2004); as a result, it can be expected that extending foraging distance results in greater return per unit of time. In this context, foraging success (prey capture per unit time away from the colony) would be expected to increase with distance from the colony. Because of the difficulty of measuring foraging success in wild marine animals at sea, the prediction that foraging efficiency will increase with travel distance has seldom been tested in any experimental system.

The aim of this study was then to test whether breeding Razorbills (*Alca torda*), central-place foraging seabirds with high flight costs, adjust their foraging effort to changing environmental conditions and prey distribution. Razorbills are coastal foragers that mainly feed on sandeels, during the breeding season (Hipfner and Chapdelaine 2002). Unlike many other seabird taxa, members of the auk family including the Razorbill have exceptionally high flight costs because of their relatively high wing-load (Pennycuick 1987). As a result, energy expenditure in foraging auks is expected to increase substantially with foraging distance from the colony (Gaston 1985) and foraging movements are likely to be highly constrained by energy expenditure. In addition, the foraging behaviour of diving animals including auks is constrained by vertical transit costs underwater. Most of the energetic costs of diving are associated with overcoming drag and buoyancy during the descent phase (Hansen and Ricklefs 2004; Lovvorn et al. 2004). By contrast with flight, auk wing morphology is well adapted for efficient diving (Elliott et al. 2013), but still energetic costs may be higher for longer dives and for deeper dives with extended descent phases. As with flight costs, foraging seabirds are expected to increase their diving costs only if there is a greater expected payoff in net energy gain, thus diving profiles have previously been used as a proxy for prey patch richness (Mori et al. 2005). We combine such a proxy with information on foraging location and environmental conditions to show that Razorbills can adjust their foraging effort to changing environmental conditions and prey distributions.

2. MATERIALS AND METHODS

Study site and field methods

Our observations were made at a Razorbill colony on Skomer Island (54°44′N, 5°17′W), Wales, UK, during the breeding seasons of 2011 and 2012. We successfully obtained GPS tracks from eight birds during the chick-rearing period in 2011 and four different birds during the incubation period in 2012. Data on each bird were collected only once. In both years, an adult from each nest (only one member of any pair to reduce possible impacts) was captured at the nesting crevice with a leg hook and fitted with two data-logging devices: a global positioning system (GPS) logger (unpackaged i-gotU GT-120: Mobile Action; mass=12 g; length= 43 mm; width= 24 mm; height = 9 mm; sampling interval = 5 min) and a time-depth-temperature recorder (TDR: Cefas Technology Ltd, Lowestoft, UK). TDR loggers were secured with either TESA marine cloth tape attached to the central four tail feathers or duct-tape to the plastic leg ring cylindrically (mass=2.7 g; diameter=1 cm; length=3.3 cm; sampling interval for pressure = 1 s, temperature = 15 s). GPS loggers were sealed in heat shrink plastic (model number = CLR-20/50, Finish Adapt Ltd, Swindon). Simultaneously, we secured GPS loggers with thin strips of TESA marine cloth tape to a small number of contour feathers on the bird's back. The total mass of devices with attachment materials in each deployment was approximately 19 g (always < 4.0 % of adult body mass); device attachments (tesa® tape with water soluble adhesive) naturally fall off within 3 weeks as a failsafe. Handling time was always less than 15 min, and usually less than 10 min. Because of the small size of the accessible colony at this site, and to minimise total disturbance, it was not possible to monitor nests intensively throughout the season or to compare potential impacts directly with controls. However, observationally birds appeared to behave normally at the colony, and to complete foraging trips of typical duration (Hipfner and Chapdelaine 2002). Similar techniques employed on another (but smaller) seabird, the Manx Shearwater *Puffinus puffinus,* did not lead to measurable impacts relative to controls on reproductive success, chick growth rates, or foraging trip lengths (Dean 2012) .

Data processing

GPS and TDR data were used to study horizontal and vertical movement patterns, respectively. Combining GPS tracks with TDR data, we derived time spent in flight, diving and on the water. All position fixes were converted to metres using the Universal Transverse Mercator coordinate system for further processing. Horizontal ground speed was calculated from interpolated positions by using cubic splines of GPS position fixes. Combined with pressure data from TDRs, lower speeds were considered to indicate drifting on the surface while higher values were interpreted as flight (Guilford et al. 2008). As the definition of non-flight / flight based on speed may be subjective, we assessed the robustness of our results against two flight speed thresholds, set at 5 and 10 km/h. These pressure/speed profiles were then used to calculate the individual number of flights, stops and dives per foraging trip. Duration of foraging trips was calculated from the time of the first flight activity as the birds left a 1 km radius boundary around their colony to the time of the last flight activity within the boundary on return.

Behavioural analysis of dive data recorded by the TDRs was conducted using diveMove (Luque and Fried 2011), which corrected for device drift and subdivided dives into bouts using a bout-ending criterion (Mori et al. 2001). We obtained dive depth, duration and surface pause duration for all dives and determined bouts based on sequential differences (Mori et al. 2001). Only dives deeper than 1 m were analysed, as shallower dives often occur during bathing or other activities that are not associated with foraging. We calculated the index of patch quality (IPQ) as described by Mori et al. (2002) and Elliott et al. (2008b), except that dive-specific parameters were estimated for each bird individually based on our data, rather than averaged over all the birds. We identified behaviour bouts (dives) as *per* Mori et al. (2001). Daily variation in IPQ was extracted on an hourly basis from 1 AM to 12 midnight (hour 24). This variation in hourly mean IPQ values, y, was modelled by fitting a sinusoidal model to the data as:

$$y = A + B\sin(\tfrac{2\pi}{\theta}t) + C\cos(\tfrac{2\pi}{\theta}t) \tag{1}$$

where the dominant frequency θ was first determined by a Fast Fourier Transform over the time series for $t \in [1,24]$ and parameters A, B and C were estimated by least-square. As this phenomenological model aimed at describing the overall daily variation of IPQ, individual bird identities were not factored in.

Environmental data

To examine how environmental conditions affect foraging effort in Razorbills, hourly oceanographic data including wind speed, SST (Sea Surface Temperature: MODIS in 1.1 km cell resolution) and bathymetry data (GEBCO bathymetry in a 30" grid, approximately 1 km cell resolution) for the period of the study were provided by the NERC Earth Observation Data Acquisition and Analysis Service (www.neodaas.ac.uk). In the case of wind data, while direction, speed and impacts of gust were considered, only a model with wind speed improved the model. Therefore, only the results including wind speed are presented in this study. Tide height at Milford Haven and tidal streams at Skomer Island were obtained from various sources (www.tidetimes.org.uk for tide height; www.llantrisantdivers.com for tidal streams: accessed on 11 December, 2012).

Statistical analyses

To assess the validity of our data, we first tested whether mean IPQ during a bout (= a foraging patch) is correlated with frequency of dives and dive/pause duration ratios. To investigate whether distant foraging is linked to better foraging conditions (higher prey patch quality), we used (i) number of dives per dive bout, (ii) surface-pause duration and (iii) IPQ as proxies for patch richness. Then, we used linear mixed models (LMMs) to test for associations between these proxies and distance from the colony at each dive location. LMMs were also employed to identify effects of oceanographic conditions on foraging strategy, in particular with respect to sea-surface temperature, hourly estimated tide height and wind speed. To examine effects of local foraging conditions on foraging strategies, we considered four models that included a null model (intercept only), SST, hourly estimated tide height and hourly wind speed for describing either IPQ or distance from the colony. To examine whether surface-pausing in Razorbills is anticipatory or reactive for diving, surface-pause duration was compared with (i) preceding dive duration and (ii) succeeding dive duration. As multi-trip data were collected for each individual, we needed to account for pseudoreplication, and thus we included individual identity as a random effect in the models (*e.g.*, Crawley 2007; R Development Core Team 2011). As data were collected from chick-rearing birds in 2011, and incubating birds in 2012 (sampled from different individuals between years), we performed separate analyses for each stage/year.

We tested for normality and homoscedasticity, and variables were log-transformed where necessary. Model selection was based on Akaike's information criterion (AIC) and ΔAIC from the null model (intercept-only). Means are presented as ±1 standard deviation unless otherwise stated. All analyses were conducted in R version 2.15.1 (R Development Core Team 2011).

3. RESULTS

Eleven Razorbills breeding on Skomer Island were tracked while commuting between their colony and foraging areas at sea, totalling 67 trips (Table 1; Fig S1a,b,c,d, S2). Of these trips, 49 were logged in 2011 during the chick-rearing period and 18 in 2012 during incubation. We found a bimodal distribution of speeds consistent with previous work (Weimerskirch et al. 2002; Guilford et al. 2008). We used a threshold of 5 km/h to distinguish between flight and non-flight based on the distribution of flight speeds (Fig S3) in this study. To assess the effect of our choice of threshold we used both 5 and 10 km/h cut-offs, which did not affect the results (*e.g.*, two-sided Kolmogorov-Smirnov test on cumulative speed distributions between both thresholds: $D = 0.0451$, *P* = 0.4554). Thus, we conservatively used the lower threshold of 5 km/h to remove potential non-foraging activity. Body mass at deployment had no effect on either IPQ (LMM, estimate = -0.003 ± 0.00, ΔAIC = 10) or distance travelled (LMM, estimate = -0.001 ± 0.00, ΔAIC = 11) so we did not consider body mass effects in subsequent analyses. During the study period, the average foraging trip duration was 8.17 ± 7.23 h (range = 0.66-34.22 h; Fig S4) and birds covered an average distance of 75.95 ± 66.65 km (range = 14.48-494.42 km) per trip. For presentation purposes, we report some results separately here between incubation and chick-rearing birds. Compared to chick-rearing birds, incubating birds had longer trip durations (CHICK: 6.9 ± 5.3 h, INC: 16.1 ± 7.9 h; LMM, estimate = 1.02 ± 0.27, ΔAIC = -4.6; Fig S4) and travelled farther away from the colony (CHICK: 50.0 ± 24.9 km, INC: 139.4 ± 115.8 km; LMM, estimate = 0.45 ± 0.11, ΔAIC = -6.0: Fig 1). Although year and stage effects are confounded, our focus here is on the importance of environmental factors on search patterns.

Table 1. Deployment and recovery information.

Ring #	Year	State	Deployment	Recovery	Days	Number of trips obtained	Mass at deployment (g)	Mass at recovery (g)
M27931	2011	Chick rearing	21-Jun	25-Jun	4	4	645	625
M27788	2011	Chick rearing	13-Jun	18-Jun	5	9	662	605
M93995	2011	Chick rearing	13-Jun	18-Jun	5	11	627	600
M93925	2011	Chick rearing	8-Jun	11-Jun	3	3	600	550
M93992	2011	Chick rearing	15-Jun	21-Jun	6	12	607	590
M93994	2011	Chick rearing	1-Jun	3-Jun	2	5	590	605
K24793	2011	Chick rearing	8-Jun	11-Jun	3	5	610	625
K24827	2012	Incubation	29-May	6-Jun	8	1*	585	570
K24828	2012	Incubation	29-May	7-Jun	9	6	695	635
K24830	2012	Incubation	30-May	6-Jun	7	7	632	568
K24835	2012	Incubation	1-Jun	4-Jun	3	4	620	610

* GPS data were recorded only until June 1st.

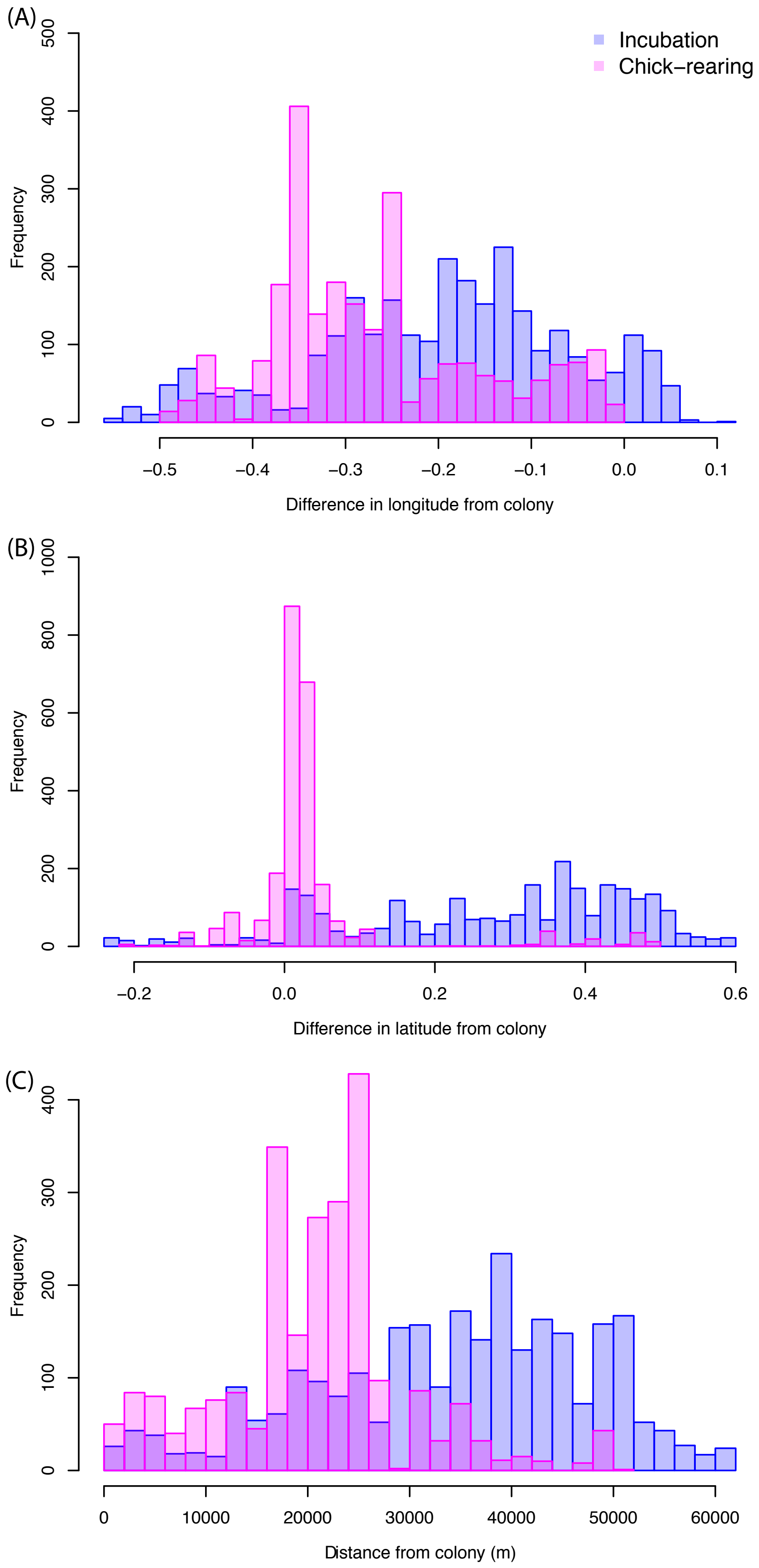

(A)
Incubation
Chick–rearing
Frequency
0
100
200
300
400
500
−0.5
−0.4
−0.3
−0.2
−0.1
0.0
0.1
Difference in longitude from colony
(B)
Frequency
0
200
400
600
800
1000
−0.2
0.0
0.2
0.4
0.6
Difference in latitude from colony
(C)
Frequency
0
100
200
300
400
0
10000
20000
30000
40000
50000
60000
Distance from colony (m)

Figure 1. Distribution of differences of GPS fixes between individual positions during foraging and the colony during the two reproductive stages: (A) in terms of longitude, (B) in terms of latitude, (C) distance from the colony.

The number of flight bouts and dives per trip both increased with total time per trip and total distance per trip (Fig 2A,B). AIC model selection against the null model demonstrated that, although chick-rearing (2011) birds performed fewer flights (3.75 ± 1.72) than incubating (2012) birds (5.62 ± 2.96, LMM, estimate = 0.40 ± 0.15, ΔAIC = -3.8), strong positive correlations existed between total time per trip and (i) number of flights (LMM, estimate = 452.1 ± 21.4, ΔAIC = -109) and (ii) number of dives (LMM, estimate = 5816 ± 1255, ΔAIC = -30.6). Similarly, we also found strong positive correlations between distance from the colony and (i) number of flights (LMM, estimate = 177.7 ± 25.6, ΔAIC = -30.3) and (ii) number of dives (LMM, estimate = 3597.1 ± 550.7, ΔAIC = -42.7).

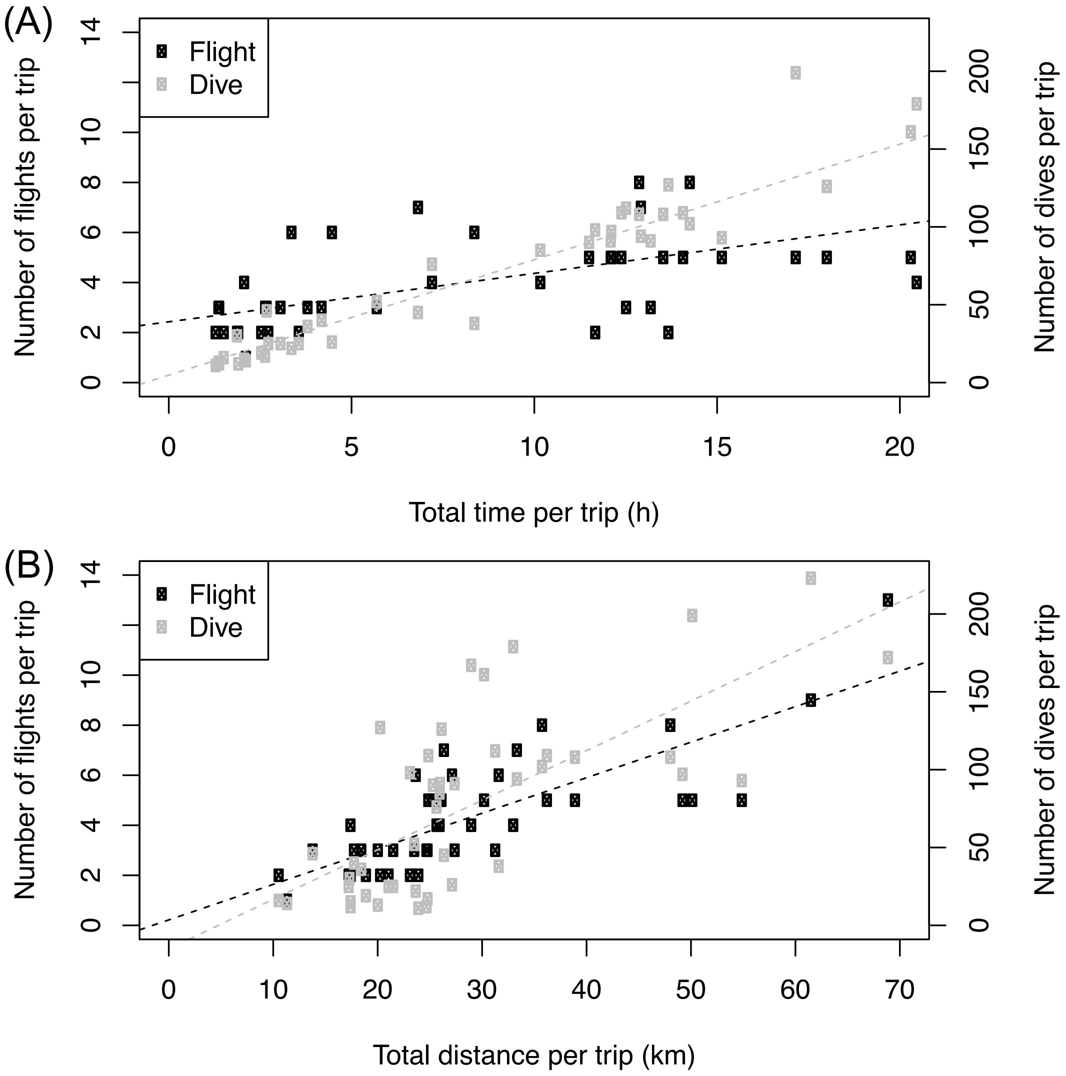
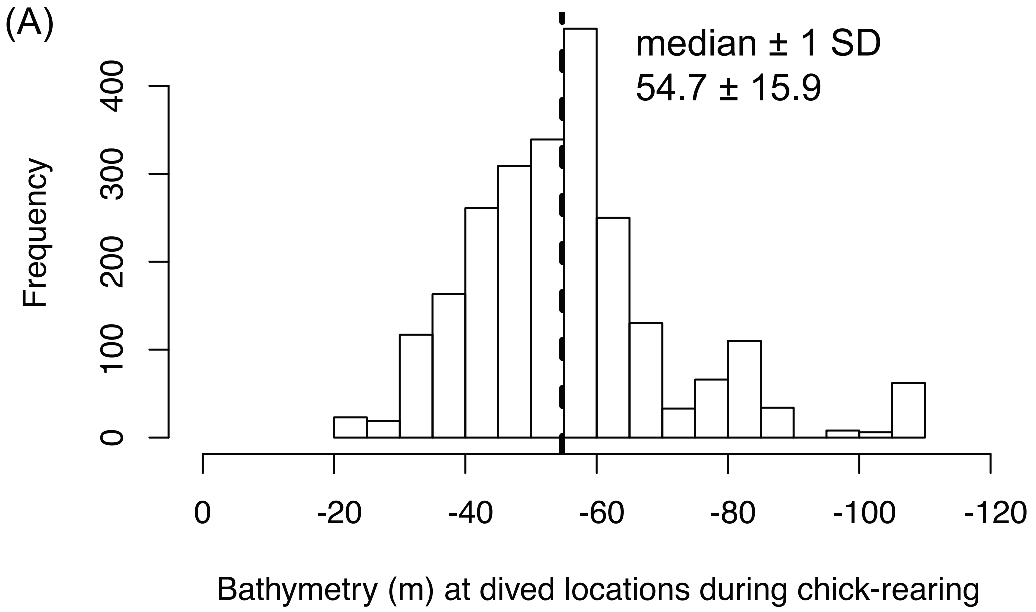


Figure 2. Number of flight bouts and dives per trip as a function of (A) total trip duration and (B) total trip length. In both panels, the number of flights is in black and number of dives is in grey.

Vertical searching

Razorbills generally foraged in areas of shallow water (Fig S1B). However, chick-rearing birds restricted the foraging area to water depths averaging 55.6 ± 15.9 m (Fig 3A), whereas incubating birds foraged in deeper water (74.9 ± 21.7 m; Fig 3B). This is consistent with our result that incubating birds foraged further away from the colony (Fig S4), as dived depth increased with distance from the colony. There was no difference in dive depth between chick-rearing birds (7.6 ± 4.1 m) and incubating birds (7.5 ± 3.8 m; LMM, estimate = 0.3 ± 0.5, ΔAIC = -1.2). Birds dived up to 26 m below the sea surface but 76% of dives were to depths <10 m. Overall, dives lasted on average 20.47 ± 13.54 s and we did not find any difference in dive duration between chick rearing (20.58 ± 13.42) and incubation periods (20.24 ± 13.44; LMM, estimate = 0.06 ± 0.11, ΔAIC = +2). Overall, surface-pause duration had a median value of 30 ± 38 s. We found a strong non-linear relationship between the time spent on the surface and the minimum dive duration in a given dive (dive duration = 52.8 × (1- exp (-0.13 × surface-pause duration)), $R^2 = 0.75$). The time birds spent on the surface was positively correlated with the duration of the subsequent dive, but not with the duration of its preceding dive (ΔAIC = -20). Overall, dive bout duration lasted on average 4.2 ± 5.6 s and while frequency of dives during dive bouts was independent of IPQ (LMM, estimate 0.01 ± 0.002, ΔAIC = 10; Fig S5A), dive-pause ratio of dive bouts decreased with IPQ (LMM, estimate -0.04 ± 0.01, ΔAIC = -10; Fig S5B). We found that IPQ per trip during incubation (-1.94 ± 0.79) was higher than that during chick rearing (-2.09 ± 0.90; estimate = 0.20 ± 0.18, ΔAIC = -6).



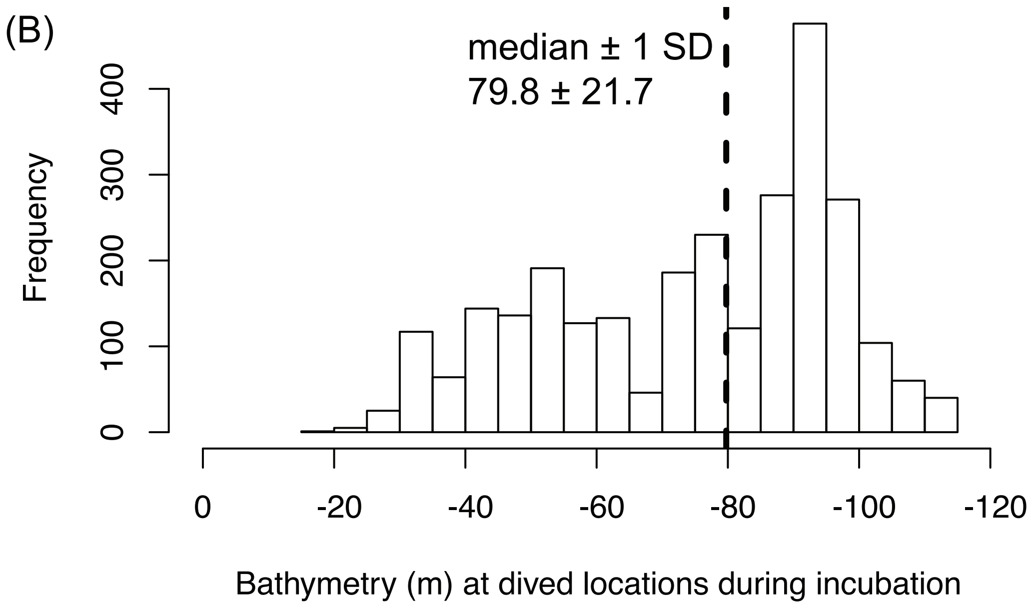


Figure 3. Distribution of bathymetry (m) at dive locations: (A) for chick-rearing birds; (B) for incubating birds. Broken vertical lines indicate median values.

Energy gains

IPQ is essentially a measure of dive profiles. On average over all pooled data, after accounting for bird identity, IPQ was significantly positively correlated with distance from the colony (LMM, estimate 24.76 ± 23.74, ΔAIC = -12; Fig 4), thereby supporting the hypothesis that patch richness increases as birds travel farther. In the travel distance model in this study, SST was selected in the best model based on AIC, but both tide height and wind speed failed to receive any support (Table 2). On the other hand, in the IPQ model, none of the oceanographic parameters were selected in the best model, while the null model had the smallest AIC, suggesting that there is no environmental effect on IPQ (Table 2). On average across all birds, IPQ was affected by time of day, being lowest at the very first dive and late evening and peaking around midday ($F_{17} = 15.84$, $R^2 = 0.69$, $P = 0.00013$; Fig 5). Note that no dives were observed between 10 PM and 2 AM.

Table 2. Model selection for explaining IPQ and distance travelled from the colony (DTC) as a function of oceanographic conditions. 'Stage/year' identity was included as a fixed effect and 'Individual' identity was considered as a random effect in this analysis. The most parsimonious model (minimum AIC) is in boldface.

	IPQ		DTC	
	ΔAIC	AIC weight	ΔAIC	AIC weight
Null	**0**	**0.91**	644	0.00
SST	6	0.04	**0**	**0.99**
Tide height	9	0.01	416	0.00
Wind speed	6	0.04	571	0.00

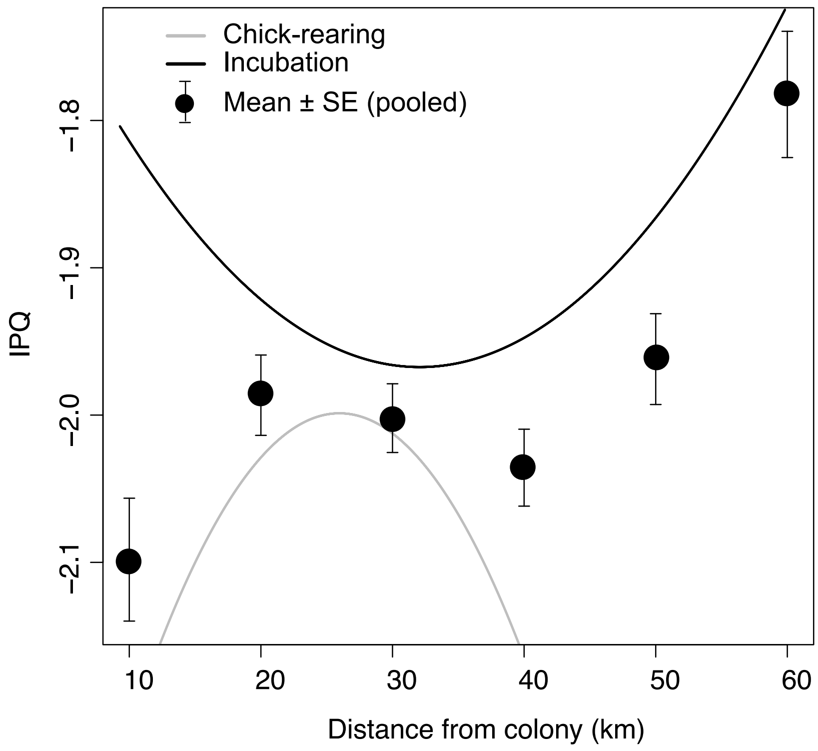


Figure 4. The relationship between IPQ and distance travelled from the colony. Means ± SE are shown. Quadratic fit in black indicates chick-rearing birds and in grey indicates incubating birds.

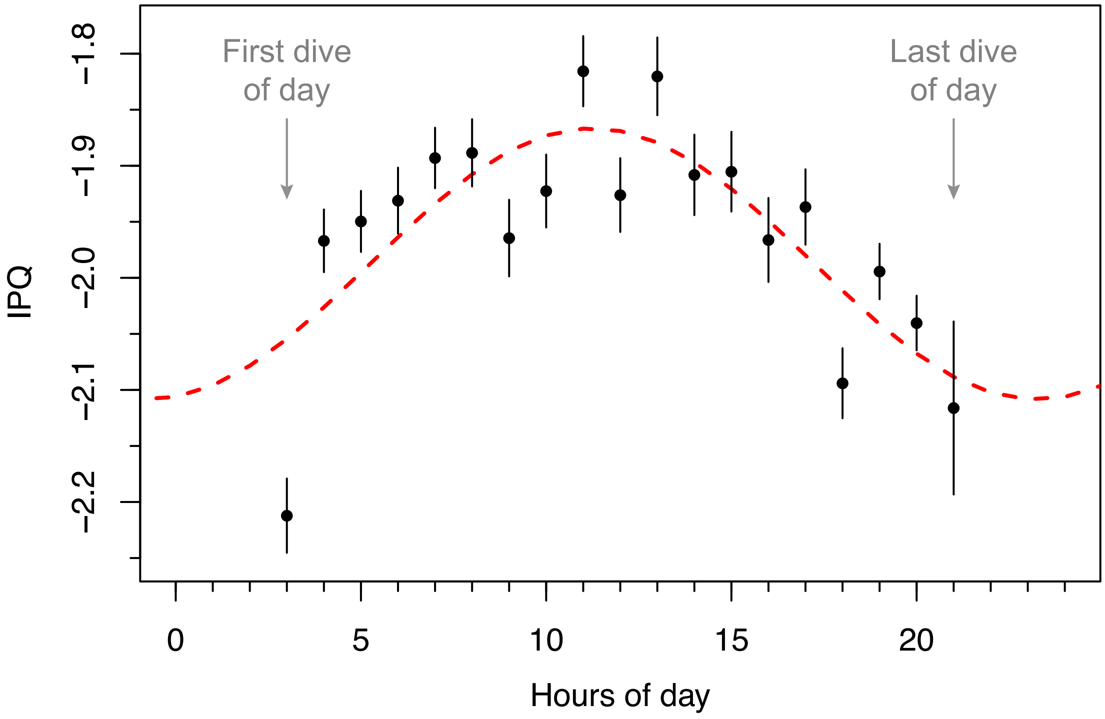


Figure 5. Mean hourly fluctuations in IPQ for breeding Razorbills. Solar time is shown as observed time at the study site. Bars represent one SD. The curve represents the model fitted by a sinusoidal model (parameter estimates as in Eq. (3): $\hat{A} = -1.99$, $\hat{B} = 0.02$, $\hat{C} = -0.12$, R^2 = 0.69; $P = 0.0013$).

4. DISCUSSION

Central-place foragers are expected to increase their foraging range only if net energy gain (*e.g.* larger size, more prey, higher energy contents) is higher further out than just around the colony (Houston and McNamara 1985; Cuthill and Kacelnik 1990; Waite and Ydenberg 1996). Supporting this expectation, our multifaceted data acquisition on foraging effort, IPQ and surface-pause duration all corroborate the hypothesis that patch richness (*i.e.* food abundance, prey quality, ease of prey capture) increases with travel distance (Schoener 1971; Houston and McNamara 1985; Cuthill and Kacelnik 1990; Waite and Ydenberg 1996). We found that Razorbills increase their distance from colony with trip duration (or *vice versa*). As a result, Razorbills increased their foraging effort as they travelled longer and further (Fig 1). Indeed, when data were pooled, both the number of dives and IPQ increased with distance from the colony, and surface-pause duration decreased with no change in dive duration. High quality prey patches for Razorbills, such as schooling fish (Hipfner and Chapdelaine 2002), are ephemeral, so that their likelihood to persist decreases with time, and hence, over dive bouts. Thus, it may be more beneficial for Razorbills to return to patches as quickly as possible after each successful dive to maximise their foraging efficiency before the prey patch disappears. Flight costs in large auks such as Razorbills are exceptionally high; as a result, Razorbills are expected to alter their time budget to reduce flight time and hereby balance their overall daily energy expenditure (Elliott et al. 2013). Thus, Razorbills might be particularly under strong pressure to minimise their travel distance and use distant patches only when the foraging area directly around the colony is depleted, as can occur for large colonies (Elliott et al. 2009). However, a higher investment in foraging effort does not necessarily translate into larger energetic rewards. IPQ, which indirectly reflects foraging effort, was previously shown to correlate with patch richness in another species of auk, the Brünnich's Guillemot (Elliott et al. 2008a; Elliott et al. 2008b), as well as in another diver, the Weddell seal *Leptonychotes weddellii* (Mori et al. 2005). Therefore, IPQ may well establish the link between foraging effort and energetic reward. Here, we showed that pause/dive ratio of dive bouts decreased with IPQ (Fig S5), supporting the idea that IPQ indicates foraging effort within dive bouts as a consequence of the presence of prey. The independence of IPQ with respect to the number of dives suggests that birds were generally able to catch a prey so that they did not need to dive many times. If IPQ did not indicate prey richness and that Razorbills were just exploring underwater to search prey, pause/dive ratios of dive bouts should not decrease with IPQ (Kooyman and Ponganis 1998; Elliott et al. 2008a). Studies of other experimental systems are needed to confirm our results that central-place foragers increase their foraging effort in order to increase foraging efficiency rather than in response to generally poorer conditions.

In this study, birds did not extend vertical distance (dive depth) with IPQ or travel distance. We showed that surface pause duration appeared to be anticipatory in Razorbills, correlating better with subsequent dive duration than with preceding dive duration. Thus, surface pause duration may be dictated by the time required to hyperventilate in anticipation of the air stores needed for the next dive (Jodice and Collopy 1999; Mori et al. 2002; Wilson 2003), perhaps indicating that birds anticipate the target depth of foraging before each dive. We observed shallower dives than those reported for guillemots (Elliott et al. 2008b), most likely because transit efficiency for propulsion underwater in Razorbills is lower than guillemots because of their relatively longer wings (Thaxter et al. 2010). As a result, extending dive depth may be more costly for Razorbills.

While we showed that travel distance increased with SST, IPQ on the other hand was independent of the oceanographic conditions considered here (SST, tide height and wind speed). Although the importance of physical oceanography in marine predators is well known in determining prey abundance (Hunt and Schneider 1987; Burger and Powell 1990; Hofmann and Murphy 2004), it is possible that seabirds use several cues to maximise their foraging efficiency. For instance, a previous study reported that gannets and shearwaters follow flocks of anchovy while terns and gulls follow aggregations of zooplankton (Duffy 1983). Previous studies reported a link between oceanographic conditions and foraging in seabirds: for instance, (Irons 1998) reported that foraging patterns in kittiwakes are linked with tidal current; (Schneider and Piatt 1986) suggested that Brünnich's Guillemots use environmental cues such as tidal current or fronts to detect high profit prey aggregations; and SST and tide currents are known to be linked to marine productivity and/or to prey aggregations (Schneider 1990; Decker and Hunt 1996; Menge et al. 1997). Here we further show that SST increased significantly with distance from the colony. This correlation could be due to physical characteristics of the study site, but could result from habitat selection, where Razorbills would use SST as an environmental cue (Hunt et al. 1992), or obtain food source information by following other predators (Weimerskirch et al. 2010). The lack of a relationship between SST and IPQ on the other hand could imply that, while birds use SST as a cue, high SSTs do not necessarily lead to good prey patches.

We also found that IPQ followed a clear daily pattern, being lowest at the first dives of the day, peaking around midday, and decreasing thereafter. However, other studies have found that Razorbills' chick feeding rate is higher in the morning than in the afternoon (Harris and Wanless 1986; Chapdelaine and Brousseau 1996). One solution to this apparent paradox is that the very earliest dives are less successful than later in the day and therefore require a substantial foraging effort (many dives) that decreases IPQ. This might be so because birds that dive early do not know yet where good patches are located; further during the day, good patches have been identified, hereby requiring less foraging effort and leading up to higher IPQ, which then decreases still later in the day as birds are completing their foraging excursions. In support of this explanation, Wright and Bailey (1991) reported that sandeel shoals in Northern Atlantic peaked near sea surface during mid-morning. Alternatively, the large number of Common Guillemots that also breed on Skomer (as a sympatric species) may lead to foraging segregation, as reported in petrels (Navarro et al. 2013) and in guillemots (Elliott et al 2010, Regular et al. 2011). Furthermore, our IPQ pattern follows a daylight pattern, so that foraging efficiency may also be linked to visibility and the observed midday IPQ peak would hence be related to the ability of Razorbills to locate their prey visually (Wanless et al. 1999; Regular et al. 2011). Perhaps the increase in the morning and decline in the evening is related to commuting because it takes time for Razorbills to get to distant foraging patches where high values of IPQ were observed in this study. Altogether, the midday IPQ peak documented here could result from a combination of information flow among predators of prey location, prey movement patterns and/or foraging segregation among populations of ecologically similar sympatric predators. Further studies should directly investigate the potential role of interspecific communication or other social cues in prey location and foraging success, which cannot be assessed by the logging techniques employed here.

To conclude, we show that Razorbills adjust search strategy in response to changing environmental cues, where the term *environment* is here taken in a broad sense, both in terms of physical parameters such as SST (which is expected to affect prey distribution) and in the sense of other foragers (who can provide good foraging cues). Likewise, the linear increase in number of dives and flights with travel distance, trip duration and SST all suggest that search strategy in this species is responsive. Environmental variability can therefore play a key role in determining search patterns of foraging seabirds such as Razorbills.

5. ACKNOWLEDGEMENTS

We thank P. Collins who dedicated time for our projects during the 2012 field season. We also thank A. Flack, M. Mac, L. Yates, S. Harris, and C. Taylor for assistance in the field, the Wildlife Trust of South and West Wales, the Countryside Council for Wales and C. Taylor, Skomer Warden, for logistic support. T. Gaston, K. Elliott and E.E. van Loon provided comments on an earlier version of the paper. We also thank Paul Regular and two anonymous reviewers, whose comments improved the manuscript significantly. Financial support came from Japan Student Services Organization (AS), the American Animal Behavior Society (AS), the Department of Zoology and Merton College (AS), the Natural Sciences and

Engineering Research Council of Canada (SAB), Environment Wales through the 'Seabirds Cymru' project which is co-ordinated by RSPB. All work was conducted after ethical approval by the Countryside Council for Wales, the Skomer Island Advisory Committee, and the British Trust for Ornithology's Unconventional Methods Committee (BTO permits: Guilford, 5311; Perrins, 660; Shoji, 5939).

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7. SUPPLEMENTARY MATERIALS

Table S1. Examples of studies examining whether the size of prey captured increases with the distance to the patch in central-place foragers.

Life-style	Animals	Locomotion mode	CPFT *	Reference
Aquatic mammals	Canadian beaver (*Castor canadensis*)	swimming	Y	Fryxell and Doucet 1991; Gallant et al. 2004; Jenkins 1980
Colonial seabirds	Adelie penguin (*Pygoscelis adeliae*)	swimming	Y	Ainley et al. 1998
Colonial seabirds	European shag (*Phalacrocorax aristotelis*)	flying	Y	Wanless, Harris and Russell 1993
Colonial seabirds	thick-billed murre (*Uria lomvia*)	flying	Y	Elliott et al. 2009
Nesting song birds	red-backed shrike (*Lanius collurio*)	flying	Y	Carlson 1983
Nesting song birds	white-fronted bee-eater (*Merops bullockoides*)	flying	Y	Hegner 1982
Nesting song birds	European bee-eater (*Merops apiaster*)	flying	Y	Krebs and Avery 1985
Nesting birds	hummingbirds	flying	Y	Tamm 1989
Nesting birds	European starling (*Sturnus vulgaris*)	flying	Y	Cuthill and Kacelnik 1990; Kacelnik 1984; Kacelnik and Cuthill 1990; Kramer and Nowell 1980
Nesting birds	grey jay (*Perisoreus canadensis*)	flying	Y	Waite and Ydenberg 1996
Nesting birds	white stork (*Ciconia ciconia*)	flying	N	Alonso et al. 1994
Nesting song birds	water pipit (*Anthus spinoletta*)	flying	N	Frey-roos, Brodmann and Reyer 1995

Raptors	merlin (*Falco columbarius*)	flying	N	Sodhi 1992
Rodents with central caches	pine squirrel (*Tamiasciurus hudsonicus*)	Walking	Y	Elliott 1988
Rodents with central caches	Brandts' whistling rat (*Parotomys brantsii*)	Walking	Y	Sodhi 1992
Rodents with central caches	Eastern chipmunk (*Tamias striatus*)	Walking	Y	Barrette and Giraldeau 2008; Bowers and Ellis 1993; Giraldeau et al. 1994
Social insects	ants (*Solenopsis invicta*)	Walking	Y	Martin and Vinson 2008

*CPFT: whether the result agreed with prediction of Central-Place Foraging Theory (Y) or not (N).

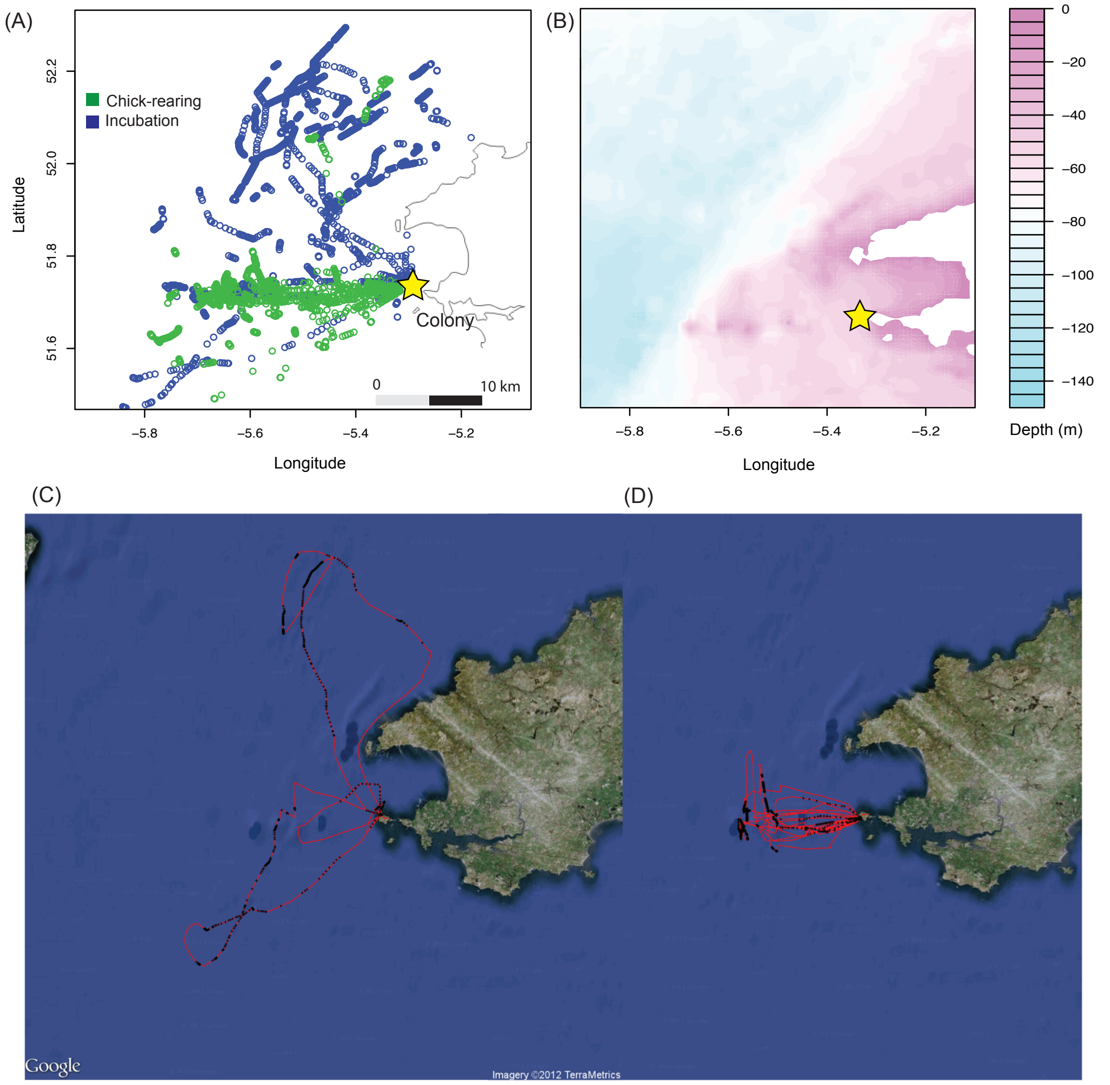

Figure S1. (A) Razorbill dive locations. Star indicates the position of colony at Skomer Island, Wales. Symbols in green indicate data from birds tracked during chick-rearing (2011) and those in blue indicate data from the incubation period (2012). (B) Bathymetry (GEBCO bathymetry in a 30 arc second grid with a 0.25 m resolution) covering the whole foraging range of Razorbills recorded in this study. Examples of recorded trajectories by GSP (in red lines) and dived locations recorded by TDR (black dots): (C) one track during incubation and (D) another track during chick rearing.

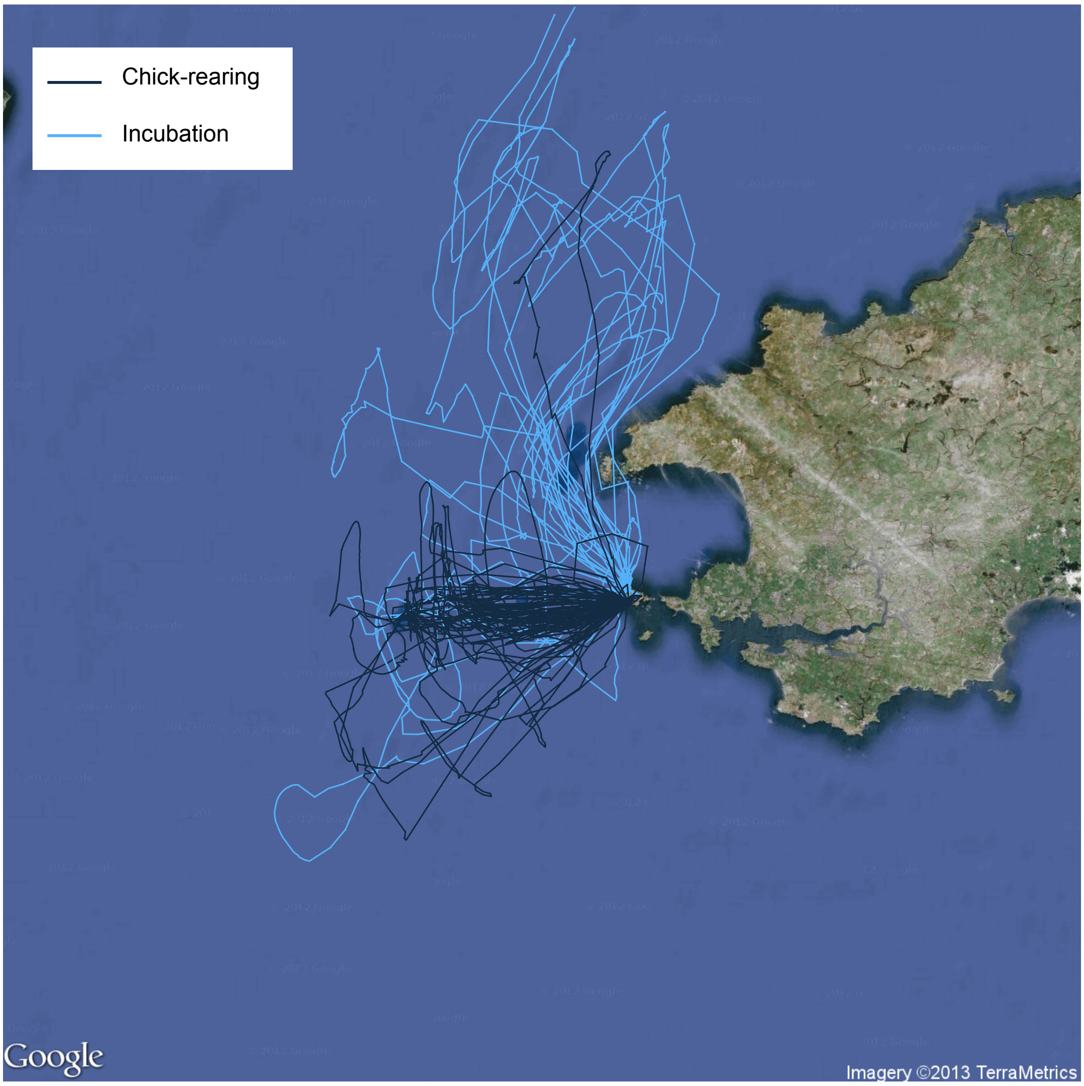

Figure S2. Flight routes followed by chick-rearing (2011) birds (dark blue) and incubating (2012) birds (light blue).

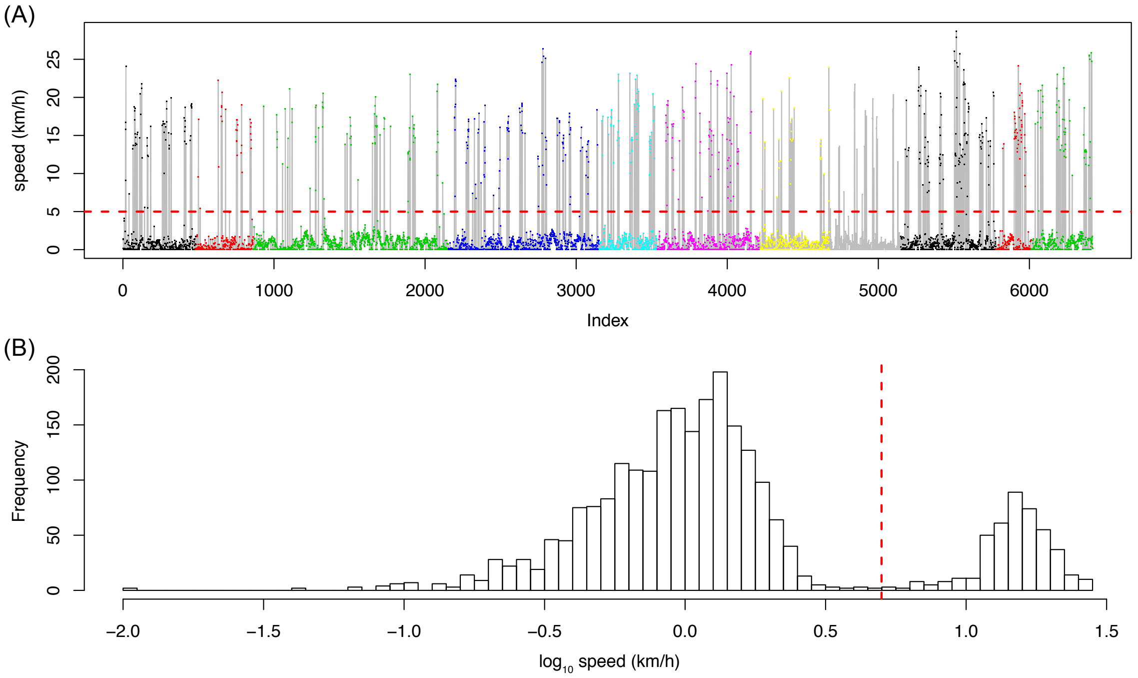

Figure S3. Razorbill movement speeds. (A) Trace of speeds recorded by the GPS loggers. Individual birds are identified by alternating colours. (B) Distribution of horizontal surface speed during foraging trips of Razorbills on a $\log_{10}$ scale ($N = 11$ birds, $n = 67$ trips; only speeds exceeding 2.5 km/h are considered – see broken horizontal line in panel A). The red broken lines in (A) and (B) indicate the cut-off value of 5 km/h used as a flight threshold in this study.

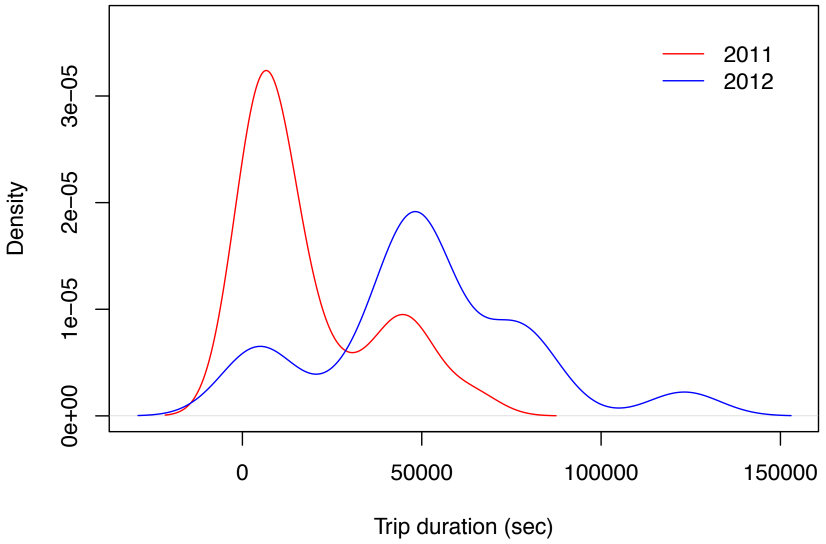

Figure S4. Mean trip duration for chick-rearing birds (in blue) and incubating birds (in red).

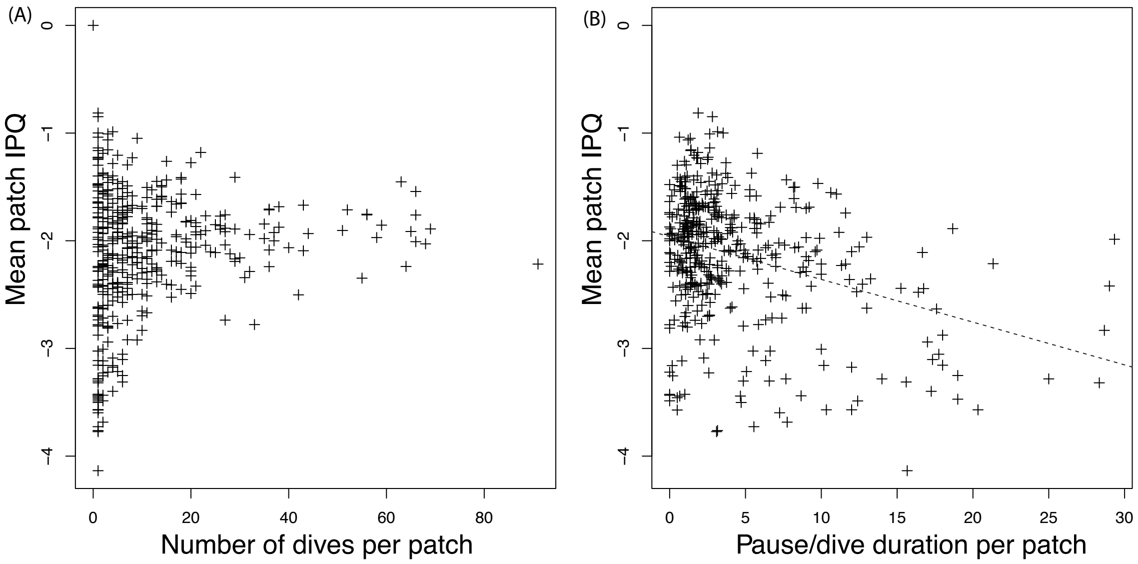

Figure S5. Relationship between mean patch IPQ and: (A) number of dives per patch; (B) pause/dive duration per patch.

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Chapter 3

Adaptive foraging strategies during breeding in a free-ranging seabird

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Currently under review.

ABSTRACT

In order to maximise foraging efficiency in a varying environment, predators are expected to resort to search strategies when resources may become patchy and/or unpredictable. While environmental conditions have been shown to explain the movement patterns in some animals, individual characteristics such as breeding stages are often overlooked so that a demonstration of the mechanisms responsible for such behavioural shifts is missing. To assess how different breeding stages affect search strategies, we deployed data loggers recording both position and dive activity on a colonial breeding seabird, the Razorbill *Alca torda*. We first show that Razorbills are able to adjust their feeding location to resource availability. The potential mechanism underpinning this adaptive behaviour is independent of breeding stage, but the magnitude of flight reorientations was found to be scale-dependent: small reorientations followed heavy-tail patterns associated with searching, while large reorientations followed exponential patterns associated with foraging bouts. Altogether, our results demonstrate that Razorbills are capable of adjusting their foraging behaviour in response to proximate environmental conditions. This suggests that these seabirds are capable of reading cues from their environment, including congeners, to optimise their foraging adaptively.

Key words: GPS, Razorbill, TDR, movement patterns, navigation, wildlife telemetry

1. INTRODUCTION

How animals adjust their foraging behaviour in response to environmental changes is a fundamental question in the context of optimal foraging theory (Stephens and Krebs 1986). In particular, under the assumption that animals maximise net energy gain, and where animals forage in a patchy environment, the marginal-value theorem (MVT) describes quantitatively how long an animal should keep searching before giving up and moving on to the next patch or returning to the nest (Charnov 1976; Orians and Pearson 1979). However, MVT has been developed and tested only in limited model systems characterised by small scale and low travel costs (Stephens and Krebs 1986). In actuality, foragers such as seabirds cover a large foraging range where prey distribution may be scarce and unpredictable. Furthermore, many central-place foragers not only commute between the colony and prey patches, but also load food for their young. Classical foraging theory predicts that prey load size should increase with the distance an animal has to travel, but carrying prey to their young for longer distance increases energetic expenditure for travel, which is therefore costly (Cuthill and Kacelnik 1990). The cost of transporting prey also depends on the loading modes, as the transport cost of carrying prey in the beak is energetically more expensive than carrying it internally. Thus, foraging behaviour is determined by balancing trade-offs between energy expenditures and gains. Although central-place foraging models provide useful predictions concerning when animals should increase foraging distances, or how prey patch quality should influence this decision (Schoener 1979), the models do not account for environmental uncertainty of search behaviour in many animals, as they were developed based on limited systems.

The adoption of efficient search is critical for successful foraging, especially when animals need to invest both in their own survival and in reproduction. This may be especially challenging in time and space for avian marine predators whose prey distribution is often patchy and sparse (Ricklefs 1990; Sala et al. 2012; Weimerskirch 2002), and who face the dual complexity of the energetics of maintaining self-condition and, during breeding, of the need to return to the nest located at a terrestrial colony. Constraints are likely to be stage-dependent because parents must commute frequently to feed young during rearing while during incubation the pressure is instead on buffered self-maintenance (Gaston and Jones 1998). This is particularly the case for Razorbills, members of the auk family *Alcidae*, which are colonially breeding diving predators that feed mainly on fish during summer (Wanless, Harris and Morris 1990). Compared to many other seabirds, auks have high flight costs because of their relatively high wing loading (Elliott et al. 2013; Pennycuick 1987). As a result, their energy expenditure is expected to increase substantially with foraging distance, as has been shown in the closely related Common Guillemots *Uria aalge* (Gaston 1985). Due to the high energetic costs associated with commuting during the breeding season, Razorbills may be under strong pressure to minimise transit costs (Elliott et al. 2013; Thaxter et al. 2010) despite their wide-ranging life-style. Moreover, field observations have shown that some auks use local enhancement, where the presence of foragers at a patch makes the patch more obvious to other conspecifics (Buckley 1997), so that Razorbills are good candidates for studying effective search strategies under a complex natural regimen.

However, it is still unclear which strategy marine predators should use to maximise the profit of foraging. Here we used an empirical approach based on data from three field seasons to test how Razorbills optimise their search strategy at two different breeding stages in an environment where resource availability changes during the season. More specifically, I hypothesised that Razorbills change search strategy depending on their breeding stage and/or environmental conditions, because travel time is expected to be different between incubation (less frequent visits) and chick-rearing (more frequent visits) as well as under different environmental conditions (more *vs*. less resource availability). By combining data from horizontal (global positioning system; GPS) and vertical (time-depth-temperature recorders; TDR) search patterns, we show that Razorbills adopt search patterns that are dependent on the scale of their movement (in terms of horizontal redirections), but that are surprisingly time-independent in a changing environment.

2. MATERIALS AND METHODS

Study site and field methods

Our observations were made at a Razorbill colony on Skomer Island (54°44'N, 5°17'W), Wales, UK, during the three breeding seasons between 2011 and 2013. We successfully obtained data during the chick-rearing period in 2011 ($N = 8$ birds), incubation period in 2012 ($N = 4$ birds), and both incubation ($N = 6$ birds) and chick-rearing periods in 2013 ($N = 6$ birds). In all years, an adult from each nest was captured at the nesting crevice with a leg hook and fitted with two data logging devices: a global positioning system (GPS) logger (unpackaged i-gotU GT-120: Mobile Action; mass of device = 12 g [< 15 g including heat-shrink]; length = 43 mm; width = 24 mm; height = 9 mm; sampling interval = 5 min) and a time-depth-temperature recorder (TDR: Cefas Technology Ltd, Lowestoft, UK). We attached TDR loggers with either TESA marine cloth tape attached to the central four tail feathers (2011) or duct-tape to a darvic leg ring cylindrically (2012, 2013; mass = 2.7 g; diameter = 1 cm; length = 3.3 cm; sampling interval for pressure = 1 s, temperature = 15 s). We also simultaneously secured GPS loggers with thin strips of tape that were attached to the back underlying a small number of contour feathers. Heat shrink plastic (model number = CLR-20/50, Finish Adapt Ltd, Swindon) was used to seal GPS loggers. The total mass of devices with attachment materials was less than 19 g (always < 4% of adult body mass) and feather attachments were designed to fall off naturally within 3 weeks if not retrieved. Handling time was usually <10 min and always <15 min.

Data processing

GPS and TDR data were used to study horizontal and vertical movement patterns respectively. Combining GPS tracks with TDR data, we derived time spent in flight, diving and on the water. Data processing and analysis were conducted in R ver. 2.15.2 (R Development Core Team 2011). All positional fixes were mapped using the Universal Transverse Mercator coordinate system. GPS-logged horizontal ground speed and TDR-logged temperatures were interpolated using cubic splines at a frequency of 1 Hz. Analysis of TDR-based dive data was conducted using the R package diveMove (Luque and Fried 2011), which corrected for device drift and extracted dives based on the bout-ending criterion (Mori, Yoda and Sato 2001). Only dives deeper than 1 m were considered, as shallower dives often occur during bathing or other activities that are not associated directly with foraging. Combined with pressure data from TDRs, lower speeds were considered to relate to drifting or foraging on the surface while higher values were interpreted as flight (Guilford et al. 2008). An appropriate speed threshold was selected based on the distribution of speeds (Fig. S1). Foraging trips were defined as trips made beyond a 1 km radius area surrounding the colony. Primary productivity (chlorophyll *a*) data for the 2011-13 breeding seasons were supplied by the NERC Earth Observation Data Acquisition and Analysis Service (www.neodaas.ac.uk). This environmental covariate is assumed to be a proxy for prey abundance and has previously been shown to be an important predictor of foraging behaviour (Votier et al. 2010). Primary productivity data consisted of satellite images at a 500×500 m^2 resolution taken three to five times a day and formatted to the Unidata's netCDF. An R script supplied by NEODAAS was used to read these files and was modified to extract productivity data for each dive given its date and coordinates. Bathymetry was obtained from the US National Oceanic and Atmospheric Administration with the R package marmap (Pante and

Simon-Bouhet 2013).

Data analyses

Foraging behaviour was analysed in terms of inter- and intra-individual similarities and in terms of search strategies. First, route similarity, which gauges the potential use of memory and learning both within and between individuals (Guilford and Biro, 2014), was analysed by comparing foraging trips based on a Nearest Neighbour Analysis (NNA; Freeman et al. 2011). NNA quantifies the spatial similarity between a focal trip t_f and a comparison trip t_c. As this results in an asymmetric distance d, the mean of the two distances $d(t_f ; t_c)$ and $d(t_c; t_f)$ is calculated. Because we were interested in foraging movement patterns, rather than homing patterns, only outbound trips (defined as the period of the trip up to the point when distance from colony stops increasing, excluding resting periods) were considered. Trip similarity was quantified by performing a hierarchical clustering analysis (complete linkage method, Euclidean distances) on the resulting symmetric distance matrix. Tracks containing fewer than ten position fixes were excluded from this analysis. Significance was assessed by 1000 bootstrap replicates (BP; Efron & Tibshirani 1993) and by the Approximately Unbiased (AU; Shimodaira 2002) test using the pvclust package in R (Suzuki and Shimodaira 2011). Two-dimensional density plots were based on the smoothScatter function in R that computes a binned 2D bivariate Gaussian kernel approximation based on Fast Fourier Transform convolutions.

Our results identify a Region Of Interest (ROI) to which birds are attracted. To assess the significance of this ROI, a bootstrap procedure was implemented to select an area of the exact same size and perform the comparisons between (i) ROI *vs*. not ROI during incubation, (ii) ROI *vs*. not ROI during chick rearing and (iii) incubation *vs*. chick rearing within ROI, as in the main text. Briefly, a position was selected at random from a bivariate uniform distribution to represent the lower left corner of the resampled ROI, which was then reconstructed by using the same dimensions as the original ROI. The test statistics of the three tests (*t*-tests) were then computed 10^5 times. In each case, the null hypothesis tested is about the absence of a difference between "treatments": if the original ROI is indeed truly special, then bootstrapped ROIs should show no significant differences.

Second, reorientation (measured as the angle based on the three consecutive position fixes; see Fig S3) patterns were analysed for flying behaviours. Two types of data were extracted from the GPS recordings. As our GPS sampling rate was 5 min, all steps with a time interval > 8 min were ignored (because these are likely to be due to GPS errors). Bearings θ, *i.e.* the angle between the colony and where birds either dived or flew, were first calculated to gauge the general direction taken by birds for each kind of activity during each breeding stage (Fig. S2). Reorientations were then used to define steps and their associated length using Turchin's method based on the change of angle α between three consecutive GPS logs (before interpolation; Turchin 1998; de Jager et al. 2011; de Jager et al. 2014). Two thresholds were examined to test the impact of mild ($\alpha = \pi/4$, or 45°) and radical ($\alpha = 7\pi/8$, or 157.5°) reorientations.

Exponential and power-law models were fitted to the complementary cumulative distribution of normalised step lengths by least square using the general model outlined by (Edwards et al. 2007) where the probability distribution of step lengths l is given by $\left(1-\mu\right)l_{\min}^{1-\mu}\, l^{-\mu}$, where $l_{\min}$ is the minimum step length and μ is the scaling exponent. Minimum step lengths were set empirically to the minimum observed length as in (de Jager et al. 2014). Scaling exponents between 1 and 3 correspond to heavy-tail movement while $\mu > 3$ is the signature of exponential motion (de Jager et al. 2014). Only reorientations were considered.

3. RESULTS

Foraging behaviour clusters by breeding stage

GPS recorders logged a total of 56 foraging trips from 18 breeding Razorbills (average of 3.1 ± 1.8 trips/individual, range 1-7). Visual inspection of individual routes suggested the existence of two foraging patterns: one with a dispersed foraging range, during incubation, and one with narrow and repeated routes, during chick rearing (Fig. S4).

The NNA confirmed that while there is no evidence for intra-individual route fidelity, the difference between the two types of foraging range was largely explained by breeding stage identity (incubation *vs*. chick rearing; Fig. 1, S5). Indeed, after excluding tracks with < 10 position fixes (Methods), 49 outbound tracks were analysed. Of these, 97% (36 out of 37) of chick-rearing tracks were grouped together (node A in Fig. 1: AU support = 86%) with only one chick-rearing track being misclassified (Bird 3 Track 7). As a result, foraging tracks during chick-rearing are highly similar (any AU support value > 70% is considered significant at the 5% level; (Suzuki & Shimodaira 2006)). However, during incubation, only 42% of tracks (5/12) were grouped together and more incubation tracks were misclassified than were chick-rearing tracks. Incubating birds therefore showed less track fidelity than chick-rearing birds. Could this pattern be due to birds having longer trips both in terms of time and distance during incubation than during chick rearing?

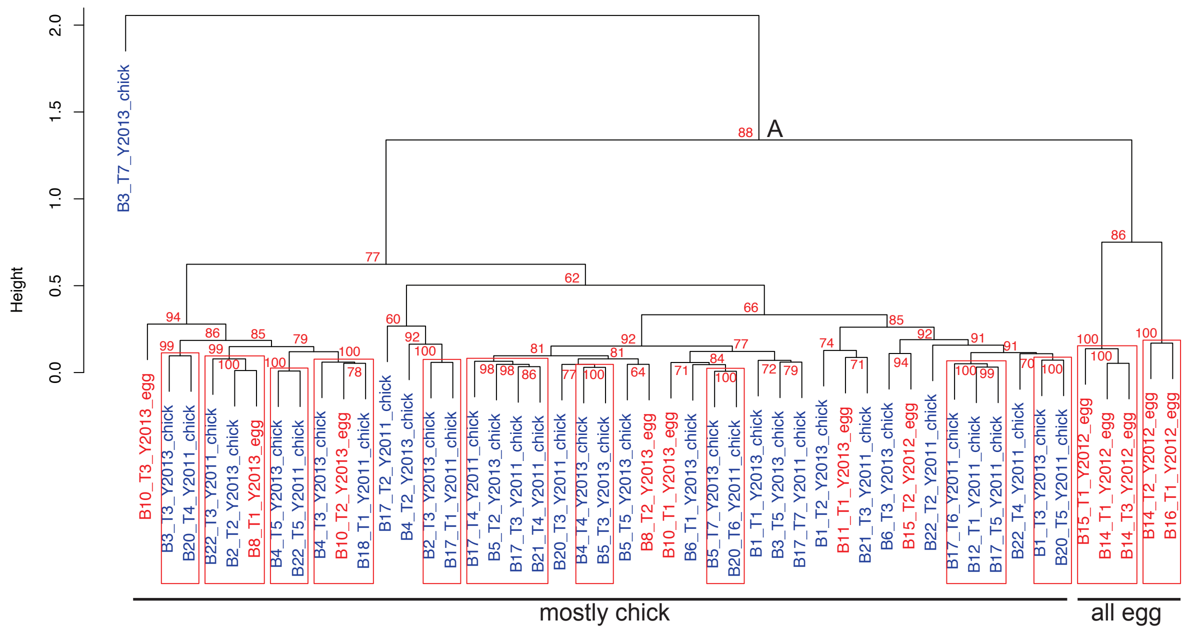

Figure 1. Hierarchical clustering of nearest neighbour analysis distances among individual outbound paths. Node support in the tree was assessed with the Approximately Unbiased test; clades with at least 95% support are indicated by rectangles. Node labels show bird identity (B), track identity (T) and collection year (Y), and are color-coded by breeding stage (incubation in red, chick rearing in blue). The vertical axis shows the Euclidian distance between NN distances.

To address this question, we first examined average trip durations and lengths. The global mean (± SD) foraging trip duration was 16.6 ± 13.5 h (range = 1.4-56.7 h) and covered a mean (± SD) distance of 75.95 ± 66.65 km (range = 14.48-494.42 km) per trip. However, incubating birds had longer mean trip durations (INC: 23.7 ± 12.9 h and CHICK: 14.6 ± 13.4 h; GLMM, estimate = 1.02 ± 0.27, ΔAIC = -4.6) and travelled further from the colony (GLMM, estimate = 0.45 ± 0.11, ΔAIC = -6.0) than chick-rearing birds.

To confirm this pattern, we conducted an analysis of the distribution of bearings θ between the colony and where birds were either diving or flying. Figure 2 shows that while all birds dived and flew to/from the colony at an absolute angle $|\theta|$ of about 180°, incubating birds left the colony at angles varying between +90° and +160° (KS test; dives: $D = 0.3531$, $P < 2.2\times10^{-16}$; flights: $D = 0.2896$, $P < 2.2\times10^{-16}$). A density plot of the different activities shows that incubating birds travelled and dived over a larger and more dispersed area than chick-rearing birds (Fig. 3). This more focused area during chick-rearing was visually defined as our Region of Interest (ROI), extending between approximately -5.73 and -5.3 degrees latitude and 51.65 and 51.82 degrees longitude (Fig. S4). These coordinates were chosen to fit the area of highest density in dive density, which is therefore not a completely arbitrary choice.

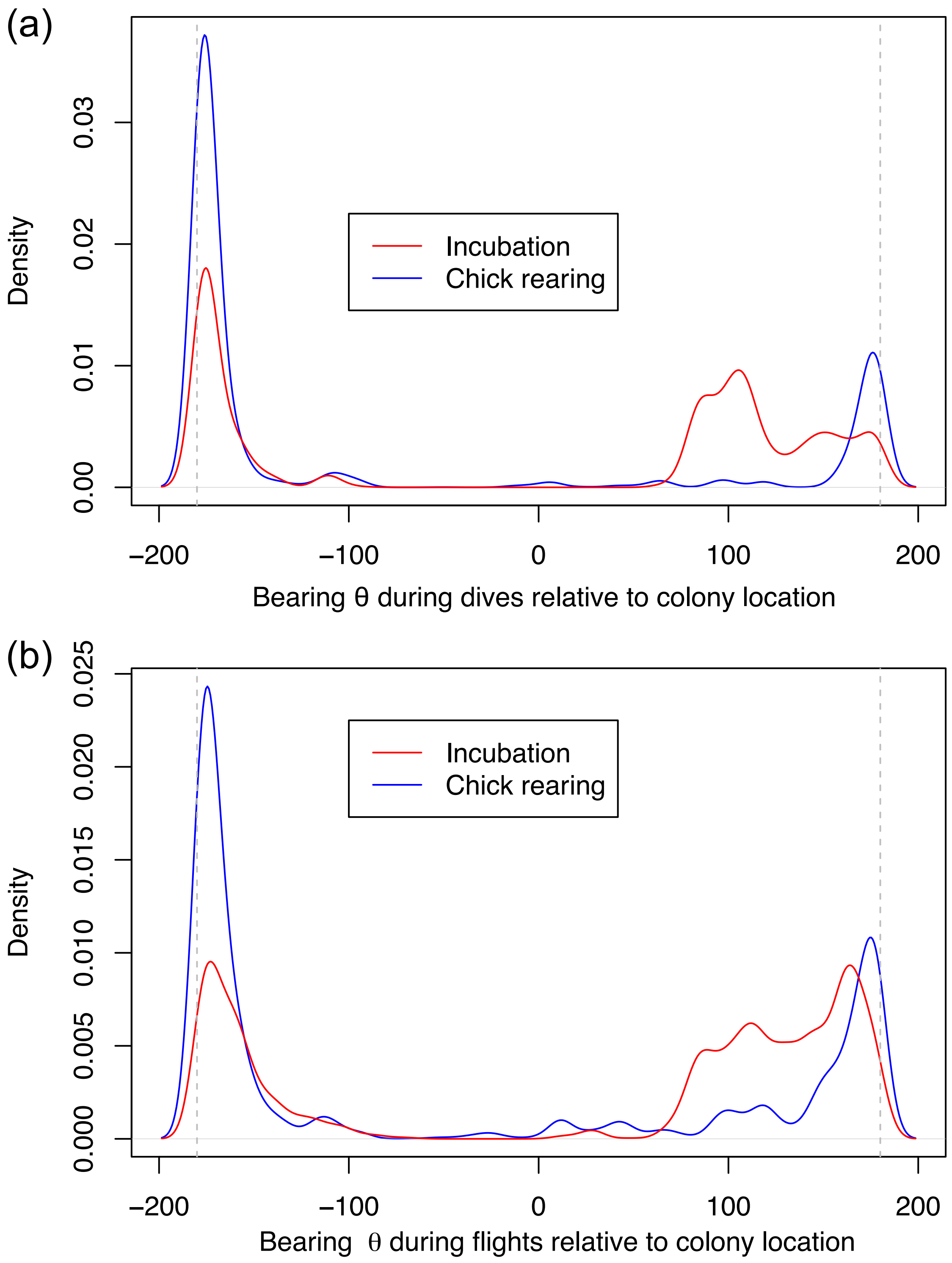

Figure 2. The distribution of bearing θ between the colony and GPS fixes. (a) For diving locations; (b) for fixed recorded during flight. Kernel density estimates during incubation are shown in and during chick rearing period in blue. Gray broken lines indicate θ of 180/-180.

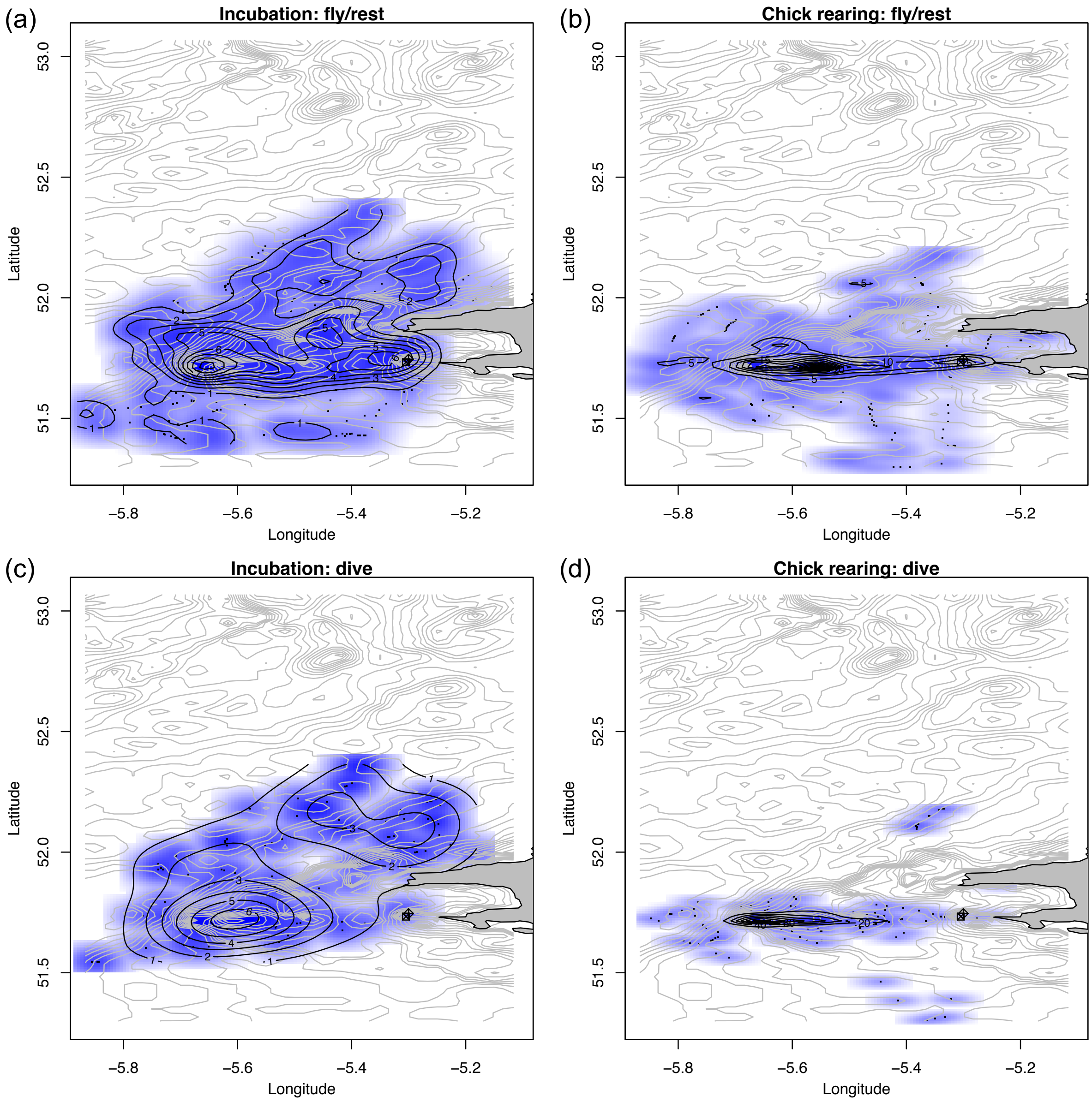

Figure 3. Contour plots of the kernel density distribution of diving and non-diving and activity during the two breeding stages. Non-dive (flying/resting) densities are shown for (a) incubating and (b) chick-rearing birds, while corresponding diving densities are shown in (c) and (d), respectively (black lines). Bathymetry lines are shown in light grey. The tip of Wales, UK, is shown in solid dark grey. Colony locations are shown by crossed squares and diamond.

Primary productivity as a potential driver of foraging strategy shift

The distribution of available of prey is one potential reason explaining the change in flight and dive locations between breeding stages, with a shift at the start of chick rearing to feed essentially within the ROI. During the study period, Razorbills exclusively brought sand eels (*Ammodytes*) to their young (Boyle, per. obs). However, no data exist to quantify prey availability exactly when and where the birds foraged. As a proxy for resource availability (Eliasen et al. 2011), we extracted data on primary productivity (PP) for each bird at each dive location (12,761 dives in total). Our results show that there was no difference in PP during incubation between foraging within and outside the ROI ($t = -0.63$, df = 1591.58, $P = 0.5258$), suggesting that foraging during this stage is not linked to PP, which is homogeneous in space. However, PP is very significantly higher within the ROI than outside during chick rearing ($t = -10.48$, df = 889.258, $P < 2.2\times10^{-16}$, two-tailed *t*-test: Fig. S6). Further testing suggests that the foraging shift to the ROI between the two breeding stages may be due to an increase in PP in the ROI ($t = -3.84$, df = 910.182, $P = 6.7\times10^{-5}$). These last two results remain significant even after applying the conservative Bonferroni correction for multiple tests. Furthermore, a bootstrapping strategy confirms that PP within the ROI is significantly higher than in the surrounding area (Fig. S7).

Horizontal search patterns are scale-dependent but not stage-dependent

While birds change their foraging behaviour in response to a shift in prey availability, we still do not know by which mechanism this adaptive behavioural response takes place. To test the hypothesis that this behavioural change reflects a change in search pattern, from a random exploration of their environment (exponential patterns) to a power-law distribution (heavy-tail patterns), reorientation patterns during flight were analysed separately for each breeding stage. Reorientation was found to be scale-dependent, with exponents at large angles ($\mu > 3$

in both cases, all SDs < 0.01, Fig. 4b) and exponents at small angles ($\mu < 3$ in both cases, all SDs < 0.01, Fig. 4a).

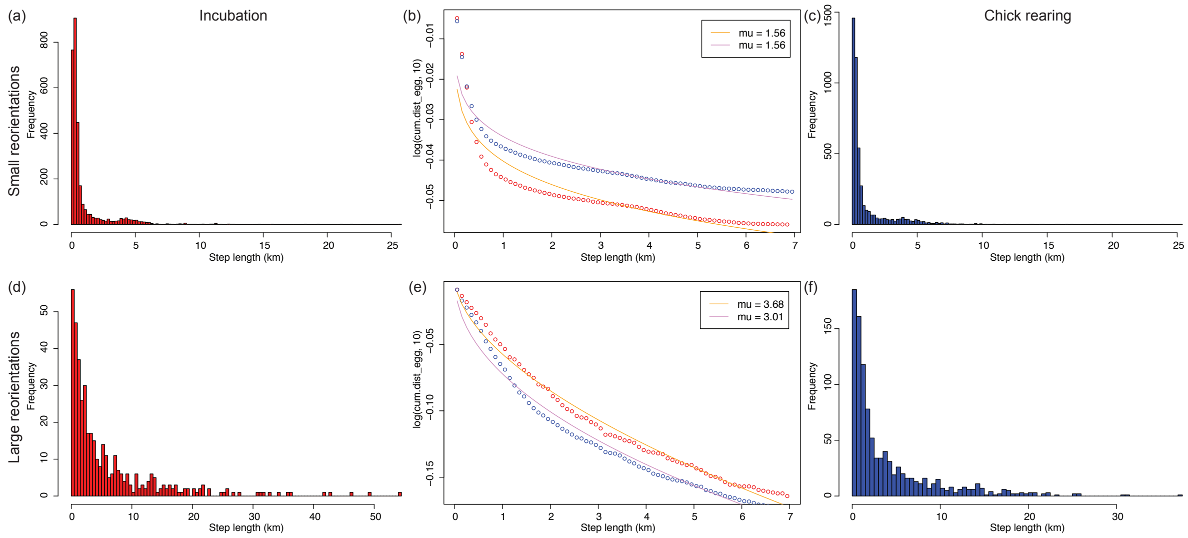

Figure 4. Reorientation patterns during flight during incubation (red line) and chick-rearing periods (blue line). (a) Histogram of small-scale reorientation step lengths in incubating birds, (b) distributions of small-scale reorientation step lengths during flight, (c) histogram of small-scale reorientation step lengths in chick-rearing birds. (d) Histogram of large-scale reorientation step lengths in incubating birds, (e) distributions of large-scale reorientation step lengths during flight, (f) histogram of large-scale reorientation step lengths in chick-rearing birds. Estimates of μ are shown ±1 SD.

4. DISCUSSION

Our data show that when foraging in areas of high productivity, Razorbills make repeated trips to the same location. However, these areas of high productivity are ephemeral, so that birds need to adjust their search strategy depending on resource availability. Behavioural shift can occur when foragers use small steps if prey are found and large steps if prey are not found (Pinaud & Weimerskirch 2005). Although effects (year and/or stage) are potentially confounded, my focus in this chapter is on how and when behavioural shifts occur in relation to resource availability. Here, we show that the principal driver shaping foraging patterns is resource availability based on primary productivity.

If resource availability can shape foraging patterns, in addition to the constraints on Razorbill parents to change their frequency of commute depending on breeding stage, then Razorbills should be able to adjust their search strategies to explore their environment efficiently. Such behavioural shifts are usually described by a shift from exponential to heavy-tail search patterns, in particular when resource availability becomes unpredictable (Bell 1991; de Jager et al. 2014; Humphries et al. 2010; Humphries et al. 2012; Raposo et al. 2011) or in situations where memory could play a role (Gautestad and Mysterud 2013). Here we report a further mechanism: change in reorientation patterns according to spatial scale. Although never identified before, this result is not completely unexpected: once a bird identifies an area rich in prey (*prey patch*), which are typically of a small size, random (exponential) foraging ($\mu > 3$) is the most efficient strategy if prey are distributed uniformly within the patch (Bartumeus & Catalan 2009; Humphries et al. 2010; Sims et al. 2012; Viswanathan et al. 1999; Viswanathan et al. 2011). On the other hand, heavy-tail foraging ($1 < \mu < 3$) is more efficient when prey are patchily distributed at larger scales in an unpredictable environment. This effect is in line with the "win-stay / lose-shift" strategy

(Bicca-Marques 2005; Weimerskirch 2007). This may reflect either the uncertainty of the exact location of the prey (Reynolds 2008) and / or prey / congener encounters (de Jager et al. 2014), while radical changes of direction such as U-turns are consistent with exponential patterns of movements.

Such a scale dependency may appear at odds with a stage-independent foraging strategy in the context of higher foraging site fidelity during chick rearing compared with incubation (temporal change). Indeed, the Lévy flight foraging hypothesis was developed based on the assumption that birds forage with no prior knowledge of prey distribution (Sims et al. 2012). Our results did not detect any connection between movement patterns and memory use, because route similarity was found within the breeding stage (chick-rearing period in this case), but not within individuals. Consequently, instead of using memory as a primary cue for foraging, birds consistently use the same search patterns over breeding stages and read cues from their environment, including from conspecifics (Buckley 1997; Weimerskirch 2007). Because of the high correlation between the inbound and outbound flight directions during chick rearing (Fig. 2a, b), it is possible that birds departing from the colony on a foraging trip recognise returning birds that had a successful foraging trip and fly out towards this direction. Indeed, one demonstrated advantage of colonial breeding is that birds can detect a prey patch through either transmission of information (Weimerskirch et al. 2010) or a spatial concentration effect (Buckley 1997). This raises the question as to why only chick-rearing birds appeared to use this recognition and orientation process. It might be tempting to argue that birds learn during the breeding season to recognise foraging success in congeners, but our result suggest a simpler explanation: that high primary productivity is only available at a certain time of year in a restricted area. Our results therefore support the model that Razorbills increase their foraging site fidelity adaptively only as a function of resource availability.

Our analyses reveal both scale-dependent and stage-independent patterns with stage-dependent foraging destinations. The stage-independent pattern is the unexpected finding. Although probabilistic search patterns are well documented (Edwards et al. 2007; Humphries et al. 2012; Sims et al. 2008), stage-independent foraging in a scale-dependent pattern has never been documented before. Two potential reasons are that step lengths have mostly been analysed within a single breeding stage (Elliott et al. 2009), or that data from multiple stages were pooled (Humphries et al. 2012). Our results demonstrate that some animals such as breeding Razorbills can adjust their foraging and search patterns according to different life-history stages and do so adaptively in a seasonally changing environment.

5. ACKNOWLEDGMENTS

We thank J. Roberts and P. Collins who dedicated time to the project during the 2012 and 2013 field seasons. We also thank A. Flack, M. Mac, J. Roden, N. Stevens, W. Whittington, L. Yates, S. Harris, and C. Taylor for assistance in the field, the Wildlife Trust of South and West Wales, the Countryside Council for Wales and C. Taylor, B. Büche and E. Stubbings for logistic support. D. Knappett, K. Paxman and B. Taylor from NEODAAS for providing us with scripts to read the netCDF files for chlorophyll. E. van Loon, A. Flack, O. Padget and I. Juarez Martinez provided comments on an earlier version of the paper. Financial support came from Japan Student Services Organization (AS), the American Animal Behaviour Society (AS), the University of Oxford Department of Zoology and Merton College (AS), the Natural Sciences and Engineering Research Council of Canada (SAB), Environment Wales through the 'Seabirds Cymru' project which is coordinated by RSPB, Microsoft Research Cambridge and the University of Oxford. All work was conducted after ethical approval by the Countryside Council for Wales, the Skomer Island Advisory Committee, and the British Trust for Ornithology (BTO permits: Guilford, 5311; Perrins, 660; Shoji, 5939).

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7. SUPPLEMENTARY MATERIALS

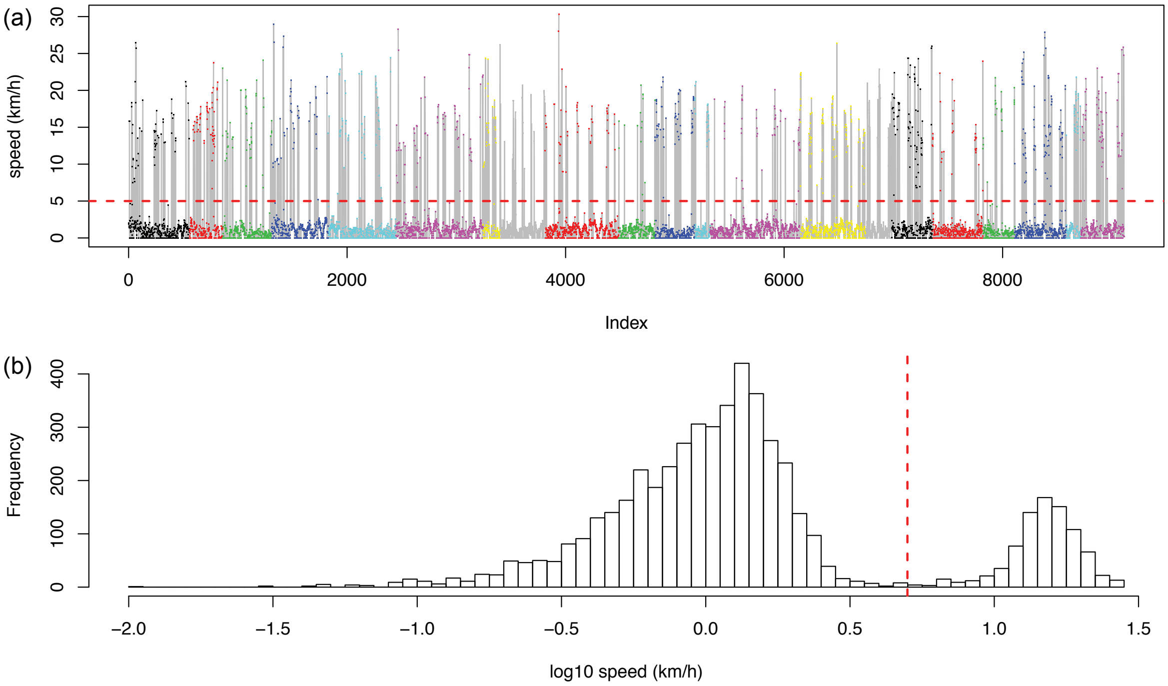

Figure S1. Distribution of Razorbill's speed for the 21 birds tracked. (a) Speed is represented for each of the GPS logs. Alternating birds are represented in alternating colours (note that colours are recycled). Speed unit is in kilometer per hour (km/h). The red horizontal broken line is the 5 km/h threshold. (b) This speed threshold was determined according to he speed distribution, here represented on a $\log_{10}$ scale; the threshold is represented with a red vertical broken line, which separates the two modes of the speed distribution.

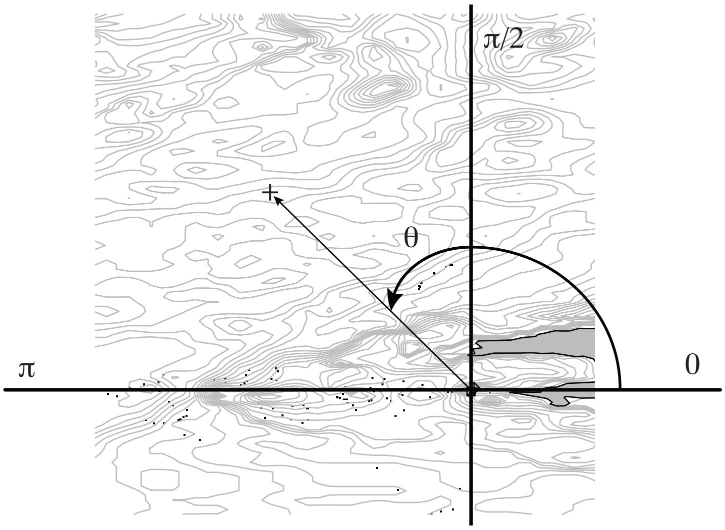

Figure S2. Computation of bearings θ. An orthonormal referential was centred on each colony location. The angle between the origin of the trigonometric circle and each position fix was calculated as described in the main text with the arctan2 function as θ = arctan(lat, lon), where lat and lon are the differences in coordinates between the focal point and colony location for latitudes and longitudes, respectively. The arctan2 function is such that angles θ > π are converted into negative angles and therefore each bearing θ in Fig. 2 is such that – π ≤ θ ≤ π.

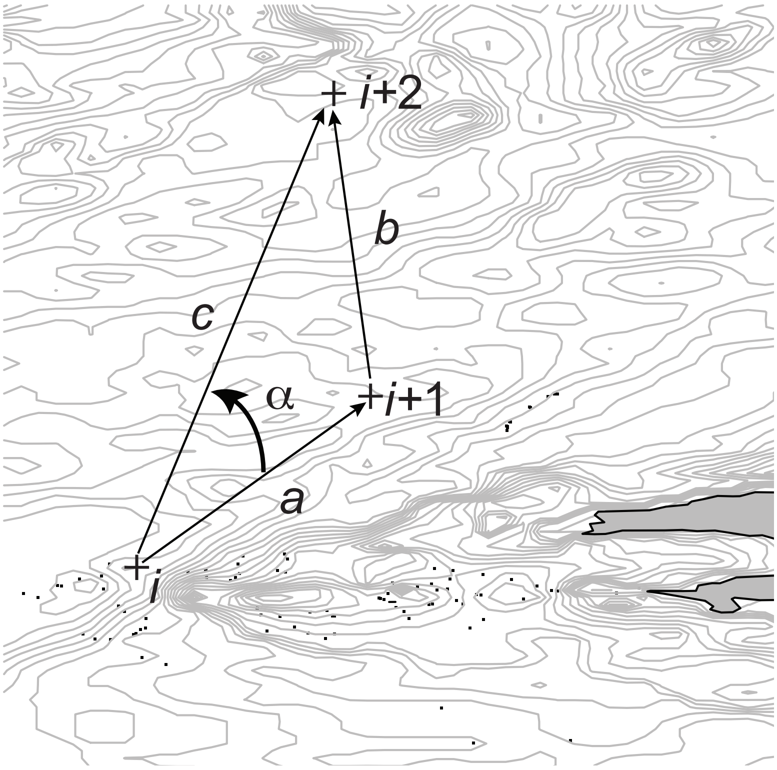

Figure S3: Computation of reorientation angle α. Three consecutive position fixes are required, here indexed as I, I + 1 and I + 2. Reorientation α is computed as described in the main text, based on segment lengths a, b and c: $\alpha = \arccos(b^2 + c^2 - a^2)/2ab$. Note that α is always ≥ 0.

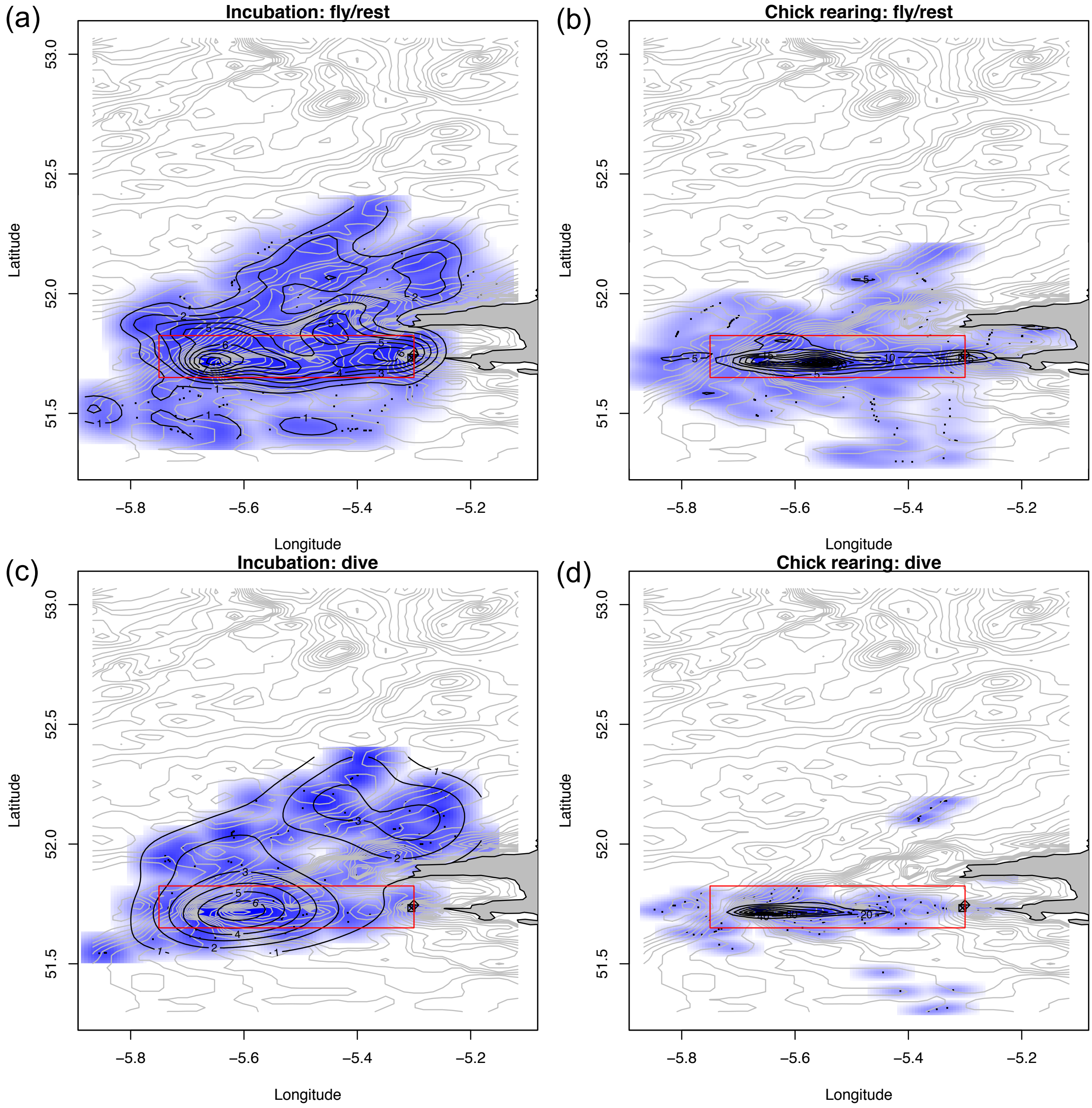

Figure S4: Activity maps across the two breeding stages and flying/nonflying birds. Nonflying activity maps are shown in panels (a) and (b) for incubating and chick-rearing birds, respectively. Flying maps are shown in panels (c) and (d) for incubating and chick-rearing birds, respectively. The shaded areas (in blue) show the density of each activity, where individual black dots show individual GPS (fly) or GPS/TDR (nonfly) logs. The Western tip of Wales is represented in dark grey, bathymetry is in light grey. Both colonies are shown. The position of the ROI is shown as a red rectangle.

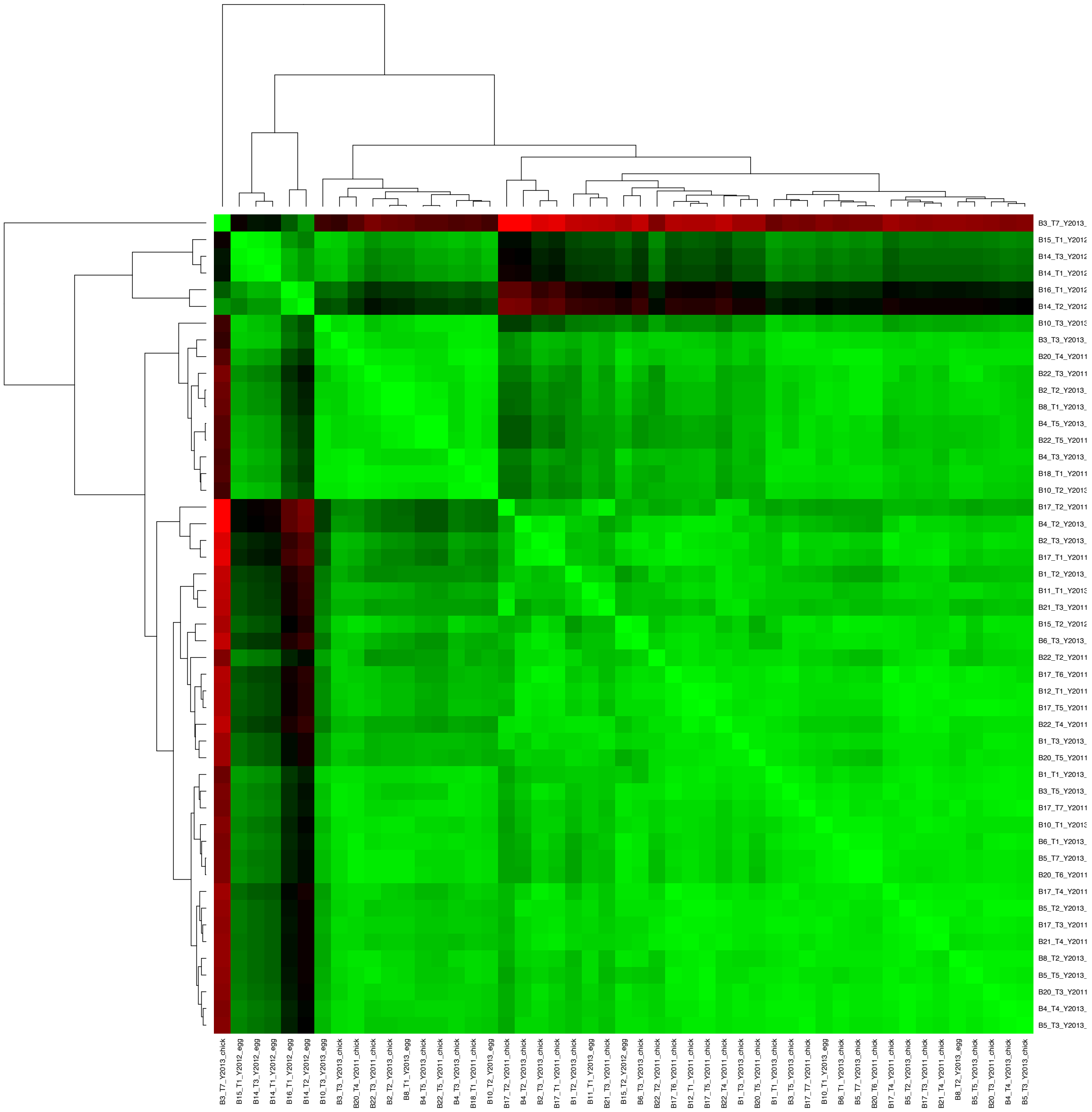

Figure S5. Heatmap of the Nearest Neighbour Analysis (NNA). The NNA was performed on the sum of the longitude and latitude of the outbound trips and the Euclidian distance was used to obtain a distance matrix of pairwise distances among the trips. This symmetric distance matrix is here represented as a heatmap, with green and red indicating small and large distances, respectively (black is intermediate). Each row / column of this matrix is labelled with an arbitrary bird ID “B” that uniquely identifies each bird, followed by a trip ID “T”, collection year “Y” and stage, either incubation (“egg”) or chick rearing (“chick”). The dendrograms on the top and left of the heatmap (both are identical) depict the hierarchical clustering as described in the main text (see also Fig. 1).

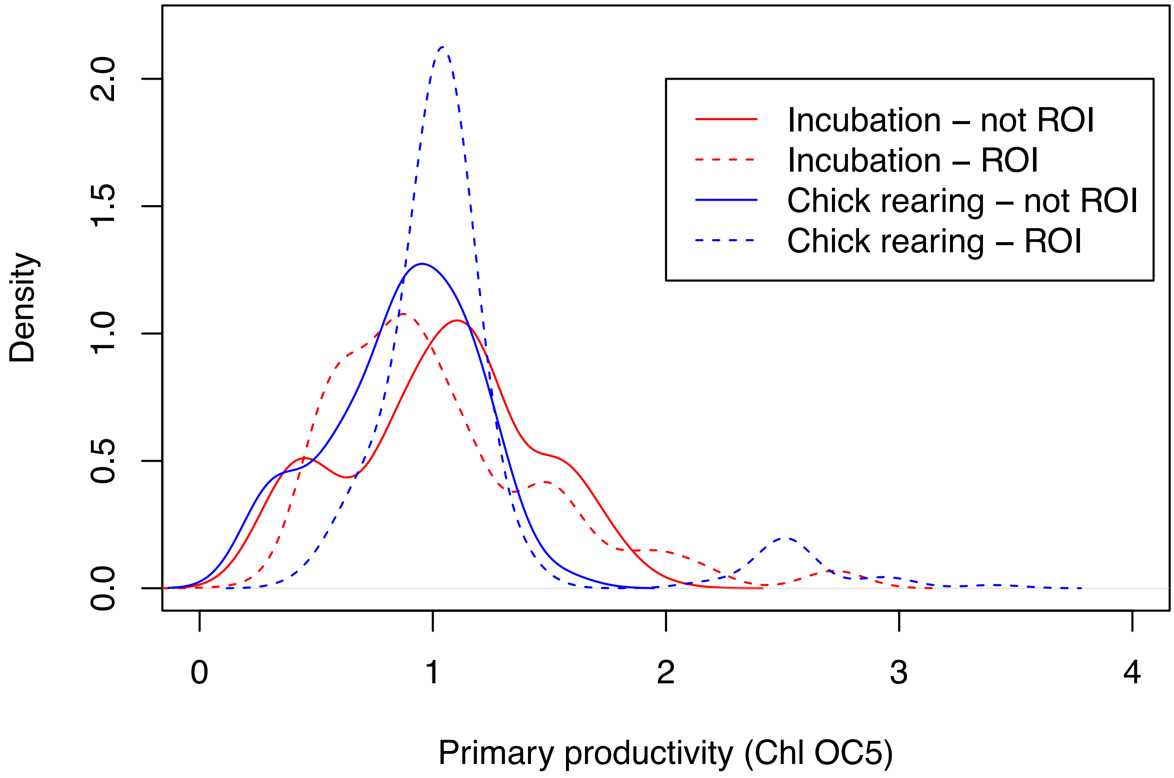

Figure S6: Densities of primary productivity across the four conditions. Densities of chlorophyll Chl OC5 are shown in red for incubating birds (solid lines: outside of ROI; broken lines: inside of ROI) and in blue for chick-rearing birds (solid lines: outside of ROI; broken lines: inside of ROI).

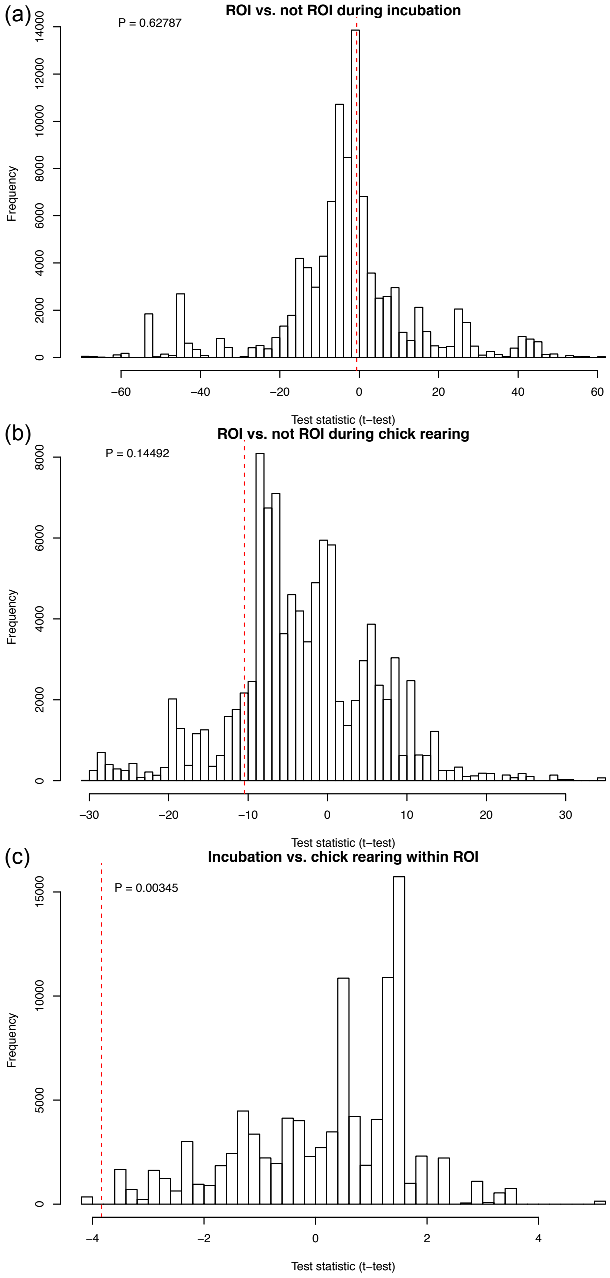

Figure S7: Bootstrap analysis of significance of ROI for the three tests performed in the main text. The three tests performed are for (a) ROI vs. not ROI during incubation, (b) ROI vs. not ROI during chick-rearing and (c) incubation vs. chick-rearing within ROI. The observed values of the test statistic are shown in red (broken line) and the corresponding P-value is indicated (based on 10^5 replicates).

Chapter 4

Foraging behaviour of sympatric Razorbills and puffins

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Marine Ecology-Progress Series (2015): 520: 257-267

ABSTRACT

Many marine predators coexist at colonies, creating a zone where there could be significant inter- and intraspecific competition. To minimise the potential for direct competition, under the principle of competitive exclusion, sympatric predators may differ in their foraging behaviour at the colony. At Skomer, Wales, Razorbills (*Alca torda*) and puffins (*Fratercula arctica*) both breed at the same time of year, and forage on sand eels (*Ammodytes*) and their populations are stable (puffins) or declining (Razorbills), meaning that they may be close to carrying capacity and experiencing competition. To examine how they differ in their foraging behaviour, time-depth-temperature recorders were attached to the legs of chick-rearing individuals of both species. Puffins have lower wing-loading and lower total oxygen stores than Razorbills, and are therefore expected to invest more time in flying and less in diving than Razorbills. Mean dive depth was 11.8 ± 0.45 m (mean ± SE) for puffins and 8.2 ± 0.21 m (mean ± SE) for Razorbills while mean dive duration was 40 ± 0.45 s (mean ± SE) for puffins and 24 ± 0.21 s (mean ± SE) for Razorbills. Both species spent most of their dive time making shallow, V-shaped dives during daylight hours. In contrast to our prediction, foraging behaviour was very similar between the two species, although puffins tended to spend more time both diving and flying. The higher diving and flying rates of puffins may be associated with multiple prey loading, as puffins tend to bring back many, smaller prey items than Razorbills.

Key words: diving behaviour, auks, bio-logging, alcids

1. INTRODUCTION

The principle of competitive exclusion, a basic tenet of ecology, states that complete competitors cannot coexist (Gauze 1934, Hutchinson 1959, Schoener 1974). That is, the n-dimensional niche hyper-volume between any two sympatric (and therefore competing) species must differ (Macarthur 1958, Hutchinson 1959, Pianka 1969, Wilson 2010). Nonetheless, many seabird and marine mammal colonies are characterized by several co-existing species with apparently similar dietary niches (Diamond 1978, Croxall and Prince 1980, Gaston 2004). Competition is likely strongest during the reproductive period because all individuals are constrained to feed within a limited radius of the central place and cannot wander entire oceans searching for an optimal foraging patch (Ashmole 1963, Gaston et al. 2007). Many cliff- or burrow-nesting seabirds are apparently not limited by nest-sites and competition must occur at sea (Elliott et al. 2009b, Masello et al. 2010, Wakefield et al. 2013), presumably leading to differences in their foraging niches over evolutionary time. In support of this theory, sympatric seabird species often have different foraging strategies (Ishtiaq et al. 2010, Barger and Kitaysky 2012; Table 1).

In northern oceans, several auk species coexist at many colonies and apparently utilize different foraging strategies (Gaston 2004, Elliott et al. 2010b, Thaxter et al. 2010). For instance, Common Guillemots (*Uria aalge*) have higher total oxygen stores and proportionately smaller wings, and are more efficient at diving than Razorbills (*Alca torda*); guillemots dive deeper with longer bottom times (Paredes et al. 2008, Thaxter et al. 2010). Thus, although both species feed predominately on sand eels (*Ammodytes* sp.) in the North Sea, guillemots exploit sand eels at deeper depths than Razorbills (Thaxter et al. 2010). Atlantic Puffins (*Fratercula arctica*) are a third species of auk that is often sympatric with both Razorbills and guillemots and also predominately feeds their chick with sand eels and sprats (*Sprattus* sp.) (Harris and Wanless 2012). Both puffins and Razorbills have similar mass-specific oxygen stores (Table 2), but puffins (~420 g) are lighter than Razorbills (~600 g) so their dive capabilities are likely to be lower due to higher mass-specific oxygen consumption rate (Watanuki & Burger 1999). Likewise, because Razorbills have a 55% greater wing-loading than puffins (Table 2), Razorbills may spend more time diving and less time flying than puffins (Thaxter et al. 2010). Whereas guillemots can carry only a single, large sprat back to their young, Razorbills provision their young with 2-10 smaller sand eels and puffins carry up to 50 small sand eels back to their young (Harris and Wanless 2012).

The dive behaviour of puffins has been reported with non-electronic recording devices such as capillary tubes, which only provide a single maximum depth value, and only two recent studies have reported puffin dive behaviour with a electronic recording (*e.g.* Harris and Wanless 2012). The purpose of this study was two-fold: (1) to document the diving behavior of chick-rearing puffins; (2) to determine how puffins' foraging behaviour might differ from that of sympatric Razorbills. We studied birds during the mutual chick-rearing period, because this is when birds are likely to be particularly constrained by sympatric competition due to the higher energy costs of chick-provisioning (Hansen 2003, Elliott et al. 2013a).

Table 1. Summary of studies that have directly investigated differences in the foraging behaviour of seabirds feeding on similar prey.

Species	Foraging	Reference
Macaroni Penguin *Eudyptes chrysolophus* Gentoo Penguin *Pygoscelis papua*	Macaroni penguins dived more and were more efficient at shallow depths	Mori and Boyd 2004
Humboldt Penguin *Spheniscus humboldti* Magellanic Penguin *S. magellanicus*	Variation between species in foraging range and dive depth was greater than between sexes, with Magellanics diving deeper	Raya Rey et al. 2013
Adélie Penguin *P. adeliae* Chinstrap Penguin *P. antarctica* Gentoo Penguin	Gentoos are inshore, deep divers; the other two are offshore, shallow divers. Furthermore, Adélies finish chick-rearing as chinstraps begin to crèche	Trivelpiece et al. 1987
Adélie Penguin Chinstrap Penguin Gentoo Penguin	<10% overall (horizontal and vertical) overlap between species. Adélies were most efficient at shallow depths, chinstraps at intermediate depths and gentoos at deep depths, and each species foraged primarily where they were most efficient	Wilson 2010
Rockhopper Penguin *E. chrysocome* Gentoo Penguin Magellanic Penguin	<20% overall horizontal overlap between species, with additional segregation in dive depth and time of day. Strong horizontal segregation between colonies from the same species	Masello et al. 2010

Scopoli’s Shearwater *Calonectris diomedea* Cory’s Shearwater *C. borealis*	During incubation, but not chick-rearing, foraging ranges largely do overlap	Afan et al. 2014
Common diving Petrel *Pelecanoides urinatrix* South Georgia diving Petrel *P. georgicus* Blue Petrel *Halobaena caerulea* Antarctic Prion *Pachyptila desolata*	Blue petrels forage primarily at night while Antarctic prions forage during the day; no difference in diving behaviour. Both diving petrels dive deeper, with commons diving more often but for shorter duration	Navarro et al. 2013
Wandering Abatross *Diomedea exulans* Black-browed Albatross *D. melanophris* Grey-headed Albatross *D. chrysostoma*	Strong spatial segregation in the foraging area of the three species, except in an area where high trawler traffic increases food abundance	Weimerskirch et al. 1988
Red-legged Cormorant *Phalacrocorax gaimardi* Rock Shag *P. magellanicus*	Almost complete segregation with red-leggeds feeding closer to the colony than rocks; in isolation, rocks foraged closer to the colony than in sympatry	Frere et al. 2008
Ancient Murrelet *Synthliboramphus antiquus* Cassin’s Auklet *Ptychoramphus aleuticus*	Although smaller, auklets have higher oxygen stores and therefore dive deeper, more often and with a longer bottom time	Elliott et al. 2010b

Common Guillemot *Uria aalge* Razorbill *Alca torda*	Murres had higher wing-loadings and oxygen stores, flew less, dived longer and spent more time at the bottom of their dives	Paredes et al. 2008; Thaxter et al. 2010
Common Guillemot Brünnich's Guillemot *U. lomvia* Razorbill	Overlap in foraging area during the breeding season, but Razorbills winter farther south. Overlap in dive depth during the breeding season between guillemots, but Razorbills dive shallower	Linnebjerg et al. 2013
Atlantic Puffin Razorbill	Puffins dived slightly longer than Razorbills, and tended to spend more time diving and flying	Our study

Table 2. Differences in the three species of auks feeding on sand eels.

	Guillemot	Razorbill	Puffin	Source
Body mass (g)	1000	600	420	Harris and Wanless 2012, Elliott et al. 2013b
Oxygen stores (ml O_2 kg^{-1})	51	57.2	57.8	Hansen 2003, Elliott et al. 2013b
Wing-loading (Nm^{-2})	205	167	108	Elliott et al. 2013b
Number of fish delivered	1	2-10	Up to 50	Harris and Wanless 2012
Fish size	Large	Medium	Small	Harris & Wanless 2012

2. MATERIALS AND METHODS

Study populations

Our study was carried out at a Razorbill colony (The Basin) and a puffin colony (North Haven) on Skomer Island (51.73’61°N, 5.29’63°W), Wales, UK. On Skomer Island, the population size of Razorbills is about 6,500 individuals and that of puffins is about 19,000 individuals (Büche et al. 2013). Individuals were selected from certain locations for both species to avoid potential effects of the nesting locations on diving behaviour. The fledging strategy differs between the two species with puffins being fully altricial (young go to sea near adult size after ~44 d in the nest) and Razorbills being intermediate (young go to sea at ~30% of adult size after ~20 d in the nest). We attached time-depth-temperature recorders (TDRs) to eight Razorbills on 21 June-3 July 2013 and to twelve Atlantic Puffins on 22-28 June 2013. Data were recorded for up to three days (puffins) or seven days (Razorbills) and the devices were recovered after three days (puffins) and seven days (Razorbills).

Device attachment

Devices were attached to the leg bands of parental birds with young chicks. For the Razorbills, we attached CEFAS loggers (Cefas G5, Cefas Technology Ltd, Lowestoft, UK) that recorded pressure every second and temperature every 15 seconds for up to seven days (mass = 2.7 g; diamerter = 1 cm; length = 3.3 cm), alongside a 12-g GPS logger (unpackaged i-gotU GT-120: Mobile Action, Taiwan, mass = 12 g; length = 43 mm; width = 24 mm; height = 9 mm). GPS were sealed in heat-shrink plastic and attached dorsally using tesa marine cloth tape underlying a small number of contour feathers (Shoji et al. 2014). The total mass of devices with attachment materials in each deployment was approximately 19 g (always < 4.0 % of adult body mass: see (Phillips et al. 2003, Vandenabeele et al. 2012); device attachments naturally fall off within 3 weeks as a failsafe; Shoji et al. 2014). Because previous studies had shown that puffins were particularly susceptible to nest desertion

(Wanless et al. 1990, Gaston 2004, Whidden et al. 2007, Harris & Wanless 2012), we (i) worked exclusively with puffins with young chicks and (ii) attached smaller Lotek 1900 time-depth-temperature recorders (LAT 1900, Lotek Wireless Inc, St. John's, Canada) that recorded pressure every 4 s and temperature every 15 s for roughly one day (mass = 2.0 g; length = 17 mm; width = 9 mm; height = 16 mm). We extracted dive depth, dive duration and surface interval duration for each dive after accounting for device drift (Elliott & Gaston 2009). We used the sequential differences method to subdivide dives into bouts using surface intervals (difference criterion: 51 s for puffins; 60 s for Razorbills; Mori et al. 2001). We considered surface interval as a function of dive depth because surface intervals correlated slightly better with dive depth than dive duration (Razorbills: $R^2 = 0.116$ vs. 0.132; puffins: $R^2 = 0.343$ vs. 0.405), as is the case for closely-related guillemots (Elliott et al. 2008), as substantial energy during the dive is used overcoming buoyancy to descend to depth (Watanuki et al. 2003, Lovvorn et al. 2004). We classified dive shape as V-, U- or W-shaped (Elliott et al. 2008).

We used the temperature log to determine when the bird was flying (Elliott et al. 2009b; Linnebjerg et al. 2014). Leg tucks, which occurred primarily at night, were distinguished by the rapid rise to high temperature (Robertson et al. 2012). As recommended by Linnebjerg et al. (2014), we simultaneously attached GPS loggers (i-gotU) to Razorbills that recorded location every 15 minutes to validate our estimates of flight time. As our interpretation of the temperature log agreed with the GPS log >98% of the time, we were confident in our ability to record flight times for both Razorbills and puffins using temperature logs alone.

Statistical analysis

We used general linear mixed models with individual as a random factor to compare foraging behaviour between Razorbills and puffins. We considered species and dive depth, duration and frequency of dives as a function of time of day (circularly-transformed by cos (2π*hours since solar midnight) to provide a cycle that is in phase with light level). We included circularly-transformed time of day as a covariate because light levels are known to strongly impact the dive behavior of many animals (*e.g.* McMahon & Holanov 1995, White et al. 2007, Zimmer et al. 2008), including auks (Croll et al. 1992, Paredes et al. 2008, Regular et al. 2011). Prior to the analyses, we assessed the effect of time of day and individual identity on dive duration and dive depth by species judged by AIC (Burnham & Anderson 2002). Both time of day (dive duration: ΔAIC = 1,058, dive depth: ΔAIC = 899) and individual identity (dive duration: ΔAIC = 2,539, dive depth: ΔAIC = 2,400) increased the parsimony of models for dive depth and duration. Thus, we included time of day as a fixed effect and individual identity as a random effect in these models. We also considered surface interval duration and dive duration as a function of dive depth. Finally, we completed a principal component analysis to examine how puffins and Razorbills differed in their use of different foraging behaviours. We only included axes with eigenvalues >1.0. We used R 3.0.3 (R Development Core Team 2011) for all analyses.

3. RESULTS

We retrieved TDRs from seven puffins and seven Razorbills. All un-retrieved birds were spotted in the colony after deployment, but we failed to recapture them. No difference was found in breeding success between our study birds and control birds that are part of the long-term study run by the Edward Grey Institute at the University of Oxford. In total, we recorded 15,383 dives from Razorbills (*n* = 7 birds) and 3,414 dives from puffins (*n* = 7 birds). Dive duration was longer (t_{12} = -3.17, *P* = 0.008, GLMM with individual as random effect and cos (2π · local solar time in h) as a fixed effect) and dive depth tended to be deeper (t_{12} = -1.90, *P* = 0.08) for puffins than Razorbills (Table 3, Fig. 1). Dive duration was longer (t_{12} = -4.32, *P* = 0.001, GLMM with individual as random effect and depth as a fixed effect) and surface interval tended to be shorter for puffins than for Razorbills for a given dive depth (t_{12} = 2.14, *P* = 0.05, Fig. 1). More than 95% of dives were V-shaped for both species. Puffins spent 5.7 ± 3.3 % of the day flying with average flight duration of 7.47 ± 2.91 min while Razorbills spent 4.9 ± 1.4 % of the day flying with average flight duration of 6.45 ± 1.20 min. Including species (Razorbill/puffin) did not increase the parsimony for models explaining flight duration (ΔAIC = 1.0). The first three principal components explained >77% of the overall variance and no other axis explained more than 10% of the variance (Table 4). Dive depth and number of flights per day loaded heavily and negatively on the first axis while percent of time diving loaded heavily and positively on the second axis (Table 5). Razorbills tended to be associated with a positive first PC axis score while puffins tended to be associated with a positive second PC axis score.

Table 3. Dive parameters for Atlantic Puffins and Razorbills breeding on Skomer, including all dives >2.5 m in depth.

Individual	Mean ± SD depth (m)	Mean ± SD duration (s)	Max depth (m)	Max duration (s)	Mean dives per day	No. dives per bout	Avg bout length (s)
Atlantic Puffins							
515	15.7 ± 12.6	52.2 ± 29.9	47.6	123.1	310	19.6 ± 21.2	1320 ± 1368
200	9.8 ± 7.4	33.2 ± 19.8	33.7	90.5	460	25.0 ± 18.1	1023 ± 717
152	5.9 ± 3.4	28.0 ± 16.4	23.5	93.7	600	26.6 ± 18.6	1105 ± 817
1	7.5 ± 5.9	27.9 ± 19.7	23.9	82.7	416	43.6 ± 28.7	1587 ± 1524
523	13.8 ± 11.2	42.6 ± 25.6	37.6	95.5	510	23.6 ± 16.8	1320 ± 771
518	12.8 ± 13.5	36.6 ± 27.9	46.4	116.6	283	25.6 ± 26.1	1321 ± 871
148	9.7 ± 7.6	57.4 ± 25.4	39.4	105.8	283	11.6 ± 12.8	818 ± 904
Mean	11.8 ± 4.2	39.7 ± 11.6	36.0 ± 9.7	101.1 ± 14.6	409 ± 123	25.1 ± 20.3	1213± 996
Razorbills							
k24763	8.9 ± 6.4	26.1 ± 16.2	56	93	417	17.0 ± 22.1	651 ± 749
k24909	5.8 ± 3.7	22.4 ± 10.9	25.1	69.8	448	27.0 ± 33.2	776 ± 946
k93793	10.3 ± 5.0	31.1 ± 13.6	25.2	71.4	234	17.1 ± 25.4	839 ± 1172
m27931	8.6 ± 4.9	24.1 ± 12.8	26.5	68.2	295	20.0 ± 19.5	724 ± 703
m93896	8.2 ± 5.8	22.4 ± 16.0	29.3	64.8	362	14.3 ± 4.5	660 ± 208
m93998	6.6 ± 3.2	17.8 ± 10.3	21.6	52.3	511	19.2 ± 26.4	638 ± 759
m93924	8.8 ± 5.4	23.5 ± 16.1	31.3	73.4	511	26.3 ± 39.4	1052 ± 1288
Mean	8.2 ± 1.5	24.0 ± 4.1	30.7 ± 11.6	70.4 ± 12.1	397 ± 105	20.1 ± 24.4	763 ± 832

Table 4. Loadings for principal components analysis of dive behaviour based on average values for each individual. Loadings < 0.1 are not shown. The component with the highest loading is shown in bold.

Variable	PC1	PC2	PC3
Percent of variance explained	32%	25%	20%
Average dive depth	**-0.490**	0.211	-0.300
Maximum depth	**-0.393**	0.302	-0.257
Average surface interval duration	**-0.282**	-0.278	-0.127
Residual of dive duration on dive depth	0.375	0.429	**-0.464**
Number of dives per day		0.349	**0.370**
Percent time spent diving	0.131	**0.656**	
Number of flights per day	**-0.480**		0.441
Percent of time spent flying	-0.367	0.222	**0.526**

Figure 1. Average (a) depth, (b) duration and (c) number of dives per hour relative to time of day, (d) dive duration relative to dive depth, (e) frequency of dives to different depths and (f) average surface interval duration relative to dive depth for Atlantic Puffins (black) and Razorbills (white/grey).

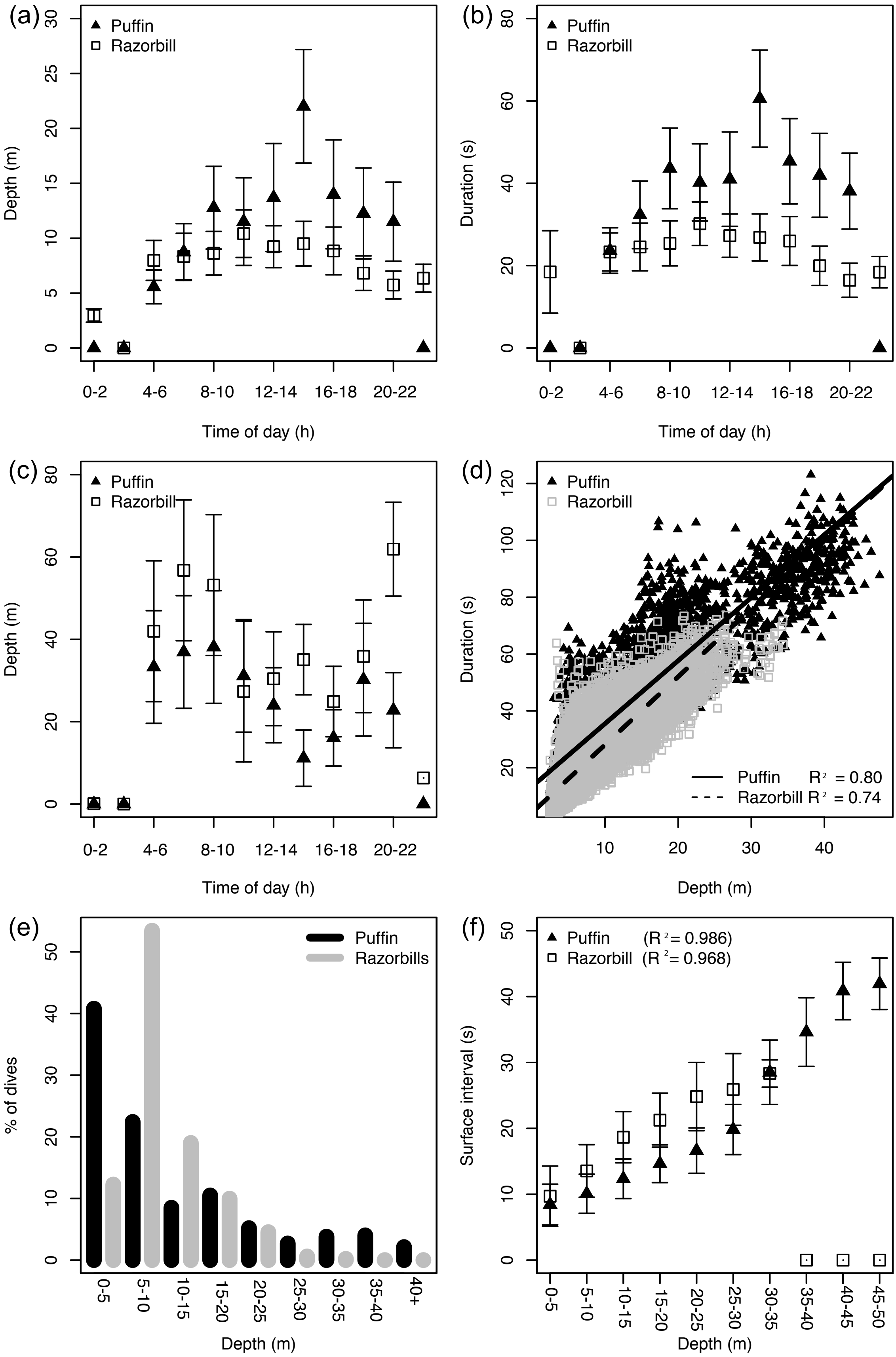
(a)
Puffin
Razorbill
Depth (m)
0
5
10
15
20
25
30
0-2
4-6
8-10
12-14
16-18
20-22
Time of day (h)
(b)
Puffin
Razorbill
Duration (s)
0
20
40
60
80
0-2
4-6
8-10
12-14
16-18
20-22
Time of day (h)
(c)
Puffin
Razorbill
Depth (m)
0
20
40
60
80
0-2
4-6
8-10
12-14
16-18
20-22
Time of day (h)
(d)
Puffin
Razorbill
Duration (s)
20
40
60
80
100
120
Puffin R² = 0.80
Razorbill R² = 0.74
10
20
30
40
Depth (m)
(e)
Puffin
Razorbills
% of dives
0
10
20
30
40
50
0-5
5-10
10-15
15-20
20-25
25-30
30-35
35-40
40+
Depth (m)
(f)
Puffin (R²= 0.986)
Razorbill (R²= 0.968)
Surface interval (s)
0
10
20
30
40
50
0-5
5-10
10-15
15-20
20-25
25-30
30-35
35-40
40-45
45-50
Depth (m)

Table 5. Dive behaviour of puffins as recorded at different locations and by different instruments. Average values of dive behaviour (maximum values in parentheses) were presented.

Location	Depth	Duration	Instruments	Source
Isle of May, Britain	4 (20)		Time-depth recorder	Harris and Wanless 2012
Isle of May, Britain		30 (114)	Radio telemetry	Wanless et al. 1988
Isle of May, Britain	(33)		Capillary tube	Wanless et al. 1990
Petit Manaan, Maine		9.7 (40.7)	Time-depth recorder	Spencer 2012
Newfoundland	(60)		Fishing nets	Piatt and Nettleship 1985
Newfoundland	(68)		Capillary tube	Burger and Simpson 1986
Norway	(45)		Capillary tube	Barrett and Furness 1990
Labrador	(41)		Capillary tube	Baillie 2001
Skomer, Britain	(27)		Capillary tube	Davidson 1994
Skomer, Britain	11.8 (47.6)	39.7 (123)	Time-depth recorder	Our study

4. DISCUSSION

Puffin diving behaviour

Puffin dive behaviour was quite similar to other non-*Uria* auk species, consisting primarily of many shallow (~5-20 m) V-shaped dives during daylight hours. Not surprisingly, dive depth was apparently limited by visibility as it was deeper during the middle of the day and no diving occurred at night (Croll et al. 1992, Regular et al. 2011). The number of dives per hour peaked in the morning and evening (Fig. 1), which coincides with the peak in feeding rates of offspring by parental puffins at Skomer (Büche et al. 2013). Similar peaks in dive rates after dawn and before dusk were observed with puffins at the Isle of May (Wanless et al. 1990, Harris and Wanless 2012). We speculate that such a relationship reflects a need to provide food for the offspring before and after the nighttime fasting period and perhaps it requires more energy/investment to feed.

Puffin dive behaviour at Skomer was quite similar to the dive behaviour elsewhere (Table 1), although they were shallower than recorded in some cases by capillary tubes (capillary tubing, closed at one end and dusted with icing sugar, can be used to determine a single maximum depth over the course of deployment based on the maximum distance sea water extended into the tube and dissolved the icing sugar; Kooyman et al. 1971). Capillary tubes can be inaccurate even over short deployments, leading to erroneously deep maximum depths for a species (Elliott & Gaston 2009). Nonetheless, our maximum depth (48 m) was deeper than that recorded at our study site using capillary tubes (27 m; Davidson 1994). Both maximum and average depth of puffins at Skomer was deeper than Isle of May, perhaps because the bathymetry within the foraging range of the puffin is generally shallower at Isle of May than at Skomer (Fig S1). Average dive duration was slightly shorter and maximum duration was slightly longer than predicted based on allometric relationships across all auks (predicted average duration: 47 s; predicted maximum duration: 114 s; Watanuki and Burger 1999).

Puffins dived on average 409 times per day compared with 1,148 times per day at the Isle of May (Harris and Wanless 2012). Although average dive duration at Skomer was longer, the average hours per day submerged at the Isle of May (7.8 h) was higher than at Skomer (4.6 h). The discrepancy is partially explained by the timing of deployments, as the puffins observed at Isle of May included puffins with older offspring, which likely had higher energy demands necessitating more food and higher dive rates (Harris and Wanless 2012). If we assume that puffins need to capture 447 sand eels per day to feed their young and maintain their own body weight (details in Harris and Wanless 2012), then, based on our data, puffins at Skomer likely catch just over one fish per dive, compared with less than a fish every other dive at the Isle of May.

At Skomer, most puffins apparently forage relatively close to the colony. Puffins averaged about 1.4 h per day flying. Assuming they flew at 19.2 km/h (based on the allometric equation $19.05M^{0.12}$ for auks in (Elliott et al. 2013b) and always flew directly away or directly towards the colony, this gives an average foraging range of 42 km. In reality, birds visit the colony multiple times per day to feed offspring and likely move in different directions. The foraging range of 7.7 km, based on average flight duration (7.5 min), might be more typical. This coincides with the observation that 85% of puffins carrying fish were within 15 km of the Skomer colony and 99% within 25 km (Stone et al. 1992). Instead, at the Isle of May, one puffin spent 64% of its time within 2 km of the colony (Wanless et al. 1990). Recent observations demonstrated that puffins sometimes forage much farther away, especially overnight, but the large GPS units used in that study may have disrupted foraging patterns (Harris and Wanless 2012).

In summary, puffin dive behavior in our study was similar to that reported elsewhere. Most dives were V-shaped, shallow and diurnal, likely representing individuals foraging on sand eel schools in mid-water near the surface, and relative near to the colony (usually < 10 km). As extreme multi-prey loaders, puffins were able to exploit abundant prey (small sand eels) that were easily captured (perhaps one prey per dive) and therefore did not need to dive deep or fly far to obtain sufficient food. Typically, puffin dives were likely not limited by their oxygen stores or by visibility. By focusing on schools near the surface, it is possible that puffins may use local enhancement (feeding flocks) to cue in on suitable prey, because of the low chance in encountering shooling fish (Thiebault et al. 2014).

Comparison between sympatric Razorbills and puffins

Reproductive success in 2013 for both species was typical. Razorbills averaged 0.38 chicks per occupied nest compared to the last 10 year average of 0.39 ± 0.14 and puffins averaged 0.78 chicks per occupied nest compared to the last 10 year average of 0.75 ± 0.08 (Büche et al. 2013). Breeding puffins and Razorbills fed on similar prey at our study site in 2013 to those reported in (Büche et al. 2013), as they both almost exclusively brought sand eels to their young during the chick-rearing period, although puffins tended to feed their young smaller sand eels and occasionally sprat (Boyle, Shoji, pers. obs.). There are multiple species of sand eels, differing primarily in size (Harris and Wanless 2012), and it is possible that multiple species of sand eels were involved in the diets of auks in 2013.

Like puffins, Razorbill dive data at Skomer was quite similar to dive behaviour recorded elsewhere: in Iceland, where 70% of dives were shallower than 15 m, with most dives between 5 and 10 m deep (Dall'Antonia et al. 2001), the Baltic Sea, where 50% of dives were shallower than 15 m, with most dives between 5 and 10 m deep (Benvenuti et al. 2001), the Gannet Islands, Canada, where average dive depth was ~10 m and duration was ~50 s (Paredes et al. 2008) and the Isle of May, Scotland, where average dive depth was 6.5 m and duration was 23.1 s (Thaxter et al. 2010). Interestingly, the dive depth of Razorbills was shallower than puffins although Razorbills are larger; in general, dive depth and duration increases with body mass in auks (Watanuki & Burger 1999). Furthermore, whereas surface intervals in puffins were an accelerating function of dive depth, suggesting progressive constraint associated with on-board oxygen stores, surface intervals in Razorbills increased linearly with dive depth, suggesting little constraint. Thus, we suggest that the shallow dive behaviour of Razorbills was largely unconstrained by oxygen stores. Indeed, the oxygen stores of puffins (24 mL; Hansen 2003) and Razorbills (35 mL; Hansen 2003) would be depleted after 92 s and 97 s, respectively, assuming that average dive costs in watts are predicted by the equation: $0.0275(\text{Mass in g})^{0.873}$ ('wing-propelled diver' regression in Elliott et al. 2013b). Thus, no Razorbill dives and <5% of puffin dives would exceed the "calculated aerobic dive limit" or "lactate threshold" (Butler 2006), which contrasts substantially with the situation in larger auks that regularly exceed those thresholds (Croll et al. 1992, Elliott et al. 2008). In reality, dive costs are higher for shallow-diving auks than for penguins, especially during buoyant shallow dives, so that the "calculated aerobic limit" may be somewhat overestimated by those simplistic calculations (Elliott et al. 2013b).

There are several advantages to the shallow-diving behaviour of Razorbills and puffins. Although buoyancy changes substantially in the top 10 m (Watanuki et al. 2003, Lovvorn et al. 2004), meaning that these species spend a substantial proportion of each dive overcoming their buoyancy to descend, they can also use buoyancy to power ascent and rapidly attack schooling fish from below (Burger et al. 1993). Capturing shallow prey also means that it is relatively easy to track the movement of fish schools from the surface, either because the school is visible from the surface or because large concentrations of surface-feeding predators indicate the school ("local enhancement"; Porter and Sealy 1982, Davoren et al. 2003, Elliott et al. 2009a). Finally, oxygen stores are unlikely to be substantially reduced during short dives, necessitating less time at the surface and therefore a higher proportion of bottom time throughout a dive bout (Croll et al. 1992, Elliott et al. 2008). Apparently, there are many advantages to shallow-diving in auks, as with the exception of guillemots (Croll et al. 1992, Mehlum et al. 2001, Falk et al. 2002, Paredes et al. 2008, Thaxter et al. 2010), few auks regularly dive beyond 15 m in depth despite having the capability to do so (Burger & Powell 1990, Burger et al. 1993, Kuroki et al. 2003, Paredes et al. 2008, Elliott et al. 2010b, Thaxter et al. 2010, Brown et al. 2012).

In many ways, the foraging behaviour of Razorbills and puffins was remarkably similar given their difference in size. Certainly, there was no evidence for the clear segregation in dive behaviour and/or flight time apparent in many other seabird assemblages (Table 1). There is a possibility that the segregation may occur in the niche where I did not measure in this study and therefore we were unable to conclude that there is no segregation between the two species at all. Nevertheless, the segregation in dive behaviour was not detectable, which have been identified to be a good measurement for the niche sepration between sympatric species in some animals (Table 1). Although puffins dived ~3.5 m deeper, both species used almost exclusively V-shaped dives implying that, unlike other seabirds (Watanuki et al. 2008), neither was obtaining sand eels from the ocean floor; V-shaped dives are primarily associated with capturing prey in mid-water, at least in guillemots (Elliott et al. 2008). In contrast, guillemots have many fewer V-shaped dives than Razorbills and puffins, and they forage substantially on benthic fish (Paredes et al. 2008). Both puffins and Razorbills bring back multiple, small items to their young, but puffins tended to bring more, smaller items than Razorbills and the longer dives by puffins may have resulted from capturing multiple prey per dive. Thus, it could be expected that puffins have a longer bottom time at a fixed depth as they capture multiple prey items within a school. However, the similarity in shape—as demonstrated by a high proportion of V-shaped dives for both species and the similar relationship between depth and duration—suggests that there is little bottom time at fixed depth for either species. However, our sample size is relatively small and our study was conducted only within one season. Segregation in behaviour amongst species could perhaps occur in years of low but not high prey availability. Thus, future studies could benefit from evaluating behaviour over a longer period. Also, as we were unable to sex individuals within our study, and sex is known to play a strong role in determining dive behavior in auks (Paredes et al. 2005, Paredes et al. 2008, Thaxter et al. 2009, Elliott et al. 2010a, Stauss et al. 2012), it is possible that some variation was missed due to unbalanced or missing data from one sex for either species. Similarly, the constraints of accessibility and disturbance to colonies can be severe and therefore, we were unable to pick individuals randomly. Instead, study birds were chosen at locations with a history of successful breeding and no obvious anomalies. As breeding locations are known to affect foraging behaviour (Soanes et al. 2014), the potential role of sub-colony variation may have been missed.

One potential explanation for the similarity in diving behaviour is that since the diet is similar between the two species, they may have used similar conspecific or inter-specific cues to locate food and may have foraged on the same fish shoals. Unlike deep diving seabirds, puffins feed at low densities on small, low density shoals of fish near the surface, sometimes associated with tidal rips (Piatt 1990, Wanless et al. 1990, Harris & Wanless 2012). We suggest that Razorbills and puffins may have used similar oceanographic cues to feed on similar shoals near Skomer. Another possibility, as shown in guillemots, is that foraging niche may be differentiated only during years of poor food availability (Barger and Kitaysky 2012). When considered together in a multivariate framework, it was clear that many of the parameters were intercorrelated such that the main difference appeared to be that puffins worked harder than Razorbills: they dived deeper and spent more time flying and diving (Fig. 2). Puffins' ability to work harder, possibly associated with a 25% lower wing-loading and therefore lower flight costs leaving more residual energy to be expended on diving or additional flying, may lead to higher feeding rates and explain how they can provision their offspring on land for almost twice as long as Razorbills.

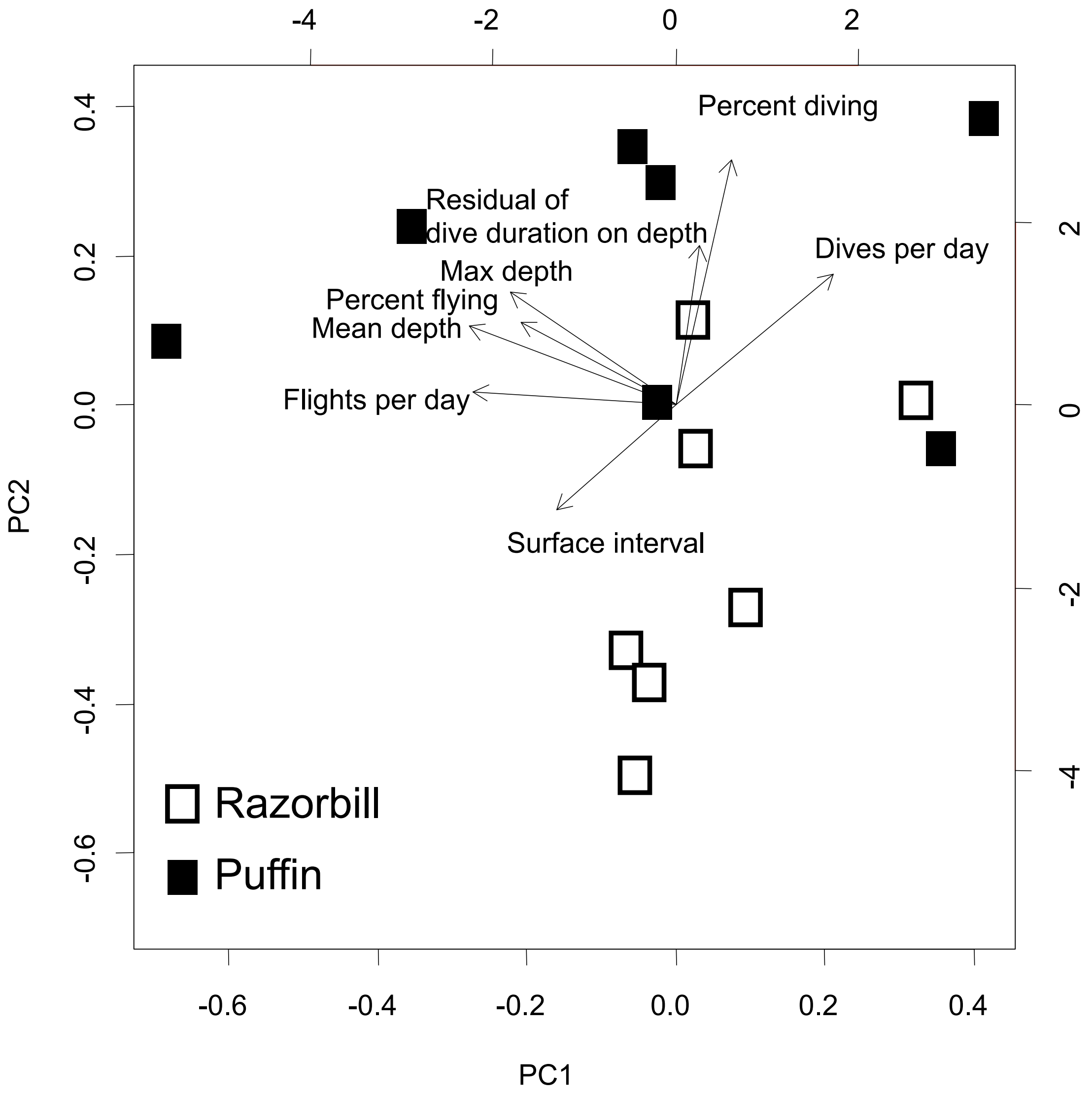

Figure 2. A principal component analysis of foraging behaviour averaged across each individual. Loadings of different parameters are shown as vectors within the principal component space. Parameters included were: average surface interval duration, average (mean) dive depth, maximum dive depth, average percent of day spent flying, average percent of day spent diving, average number of dives per day, average residual of dive duration on depth and average number of flights per day.

5. ACKNOWLEDGEMENTS

We thank the staff and volunteers of Skomer, particularly Jennifer Roberts, and Birgitta Büche and Ed Stubbings (Skomer wardens). We also thank the Skomer and Skokholm Islands Advisory Committee for permission to conduct the project on Skomer Island. AS received financial support through Japan Students Services Organization, Merton College, Department of Zoology at the University of Oxford and American Animal Behavior Society, and an NSERC Postdoctoral Fellowship for KHE. All work was conducted after ethical approval by the Countryside Council for Wales, the Skomer Island Advisory Committee, and the British Trust for Ornithology (BTO permits: Guilford, 5311; Perrins, 660; Shoji, 5939).

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7. SUPPLEMENTARY MATERIAL

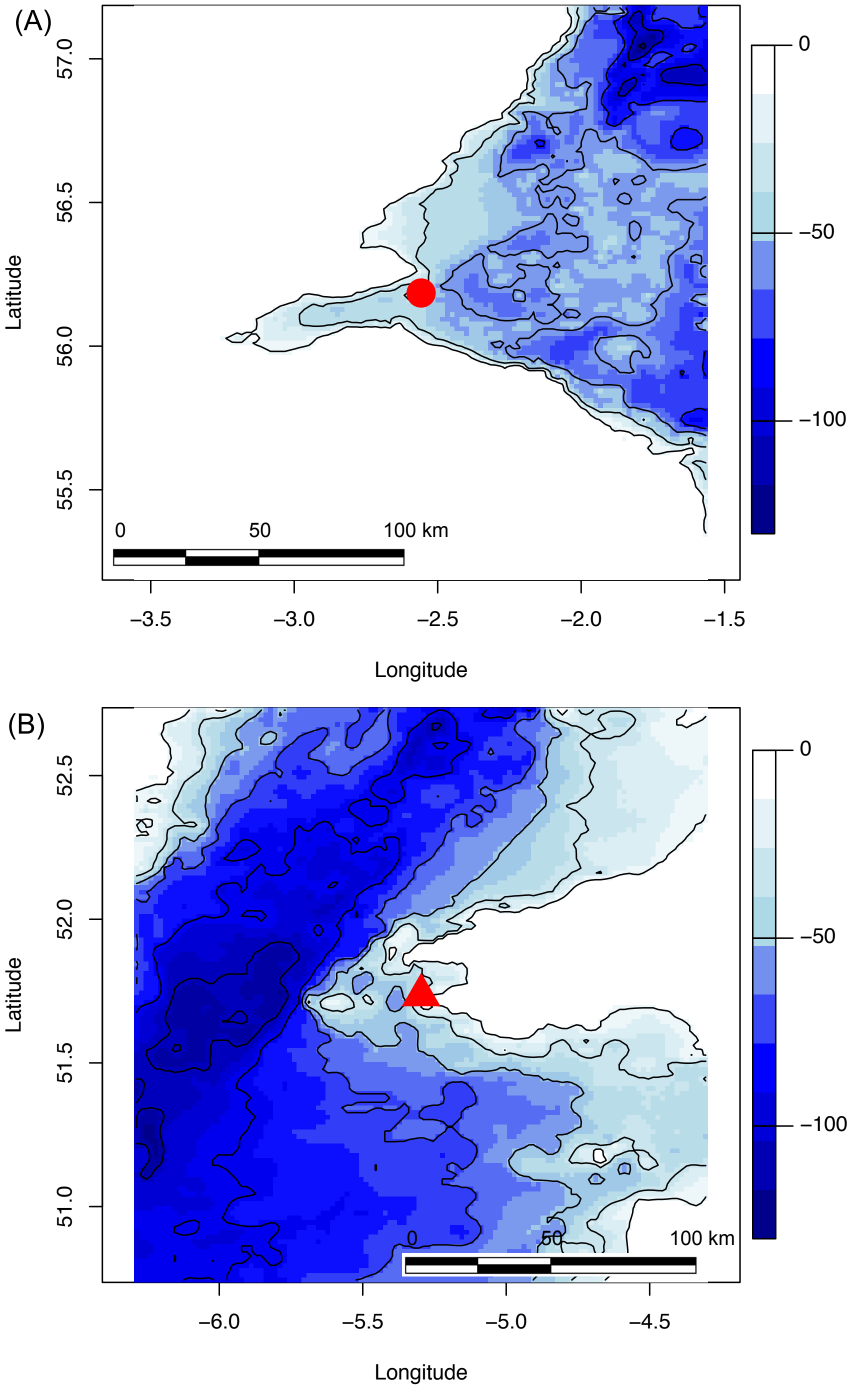

Figure S1. Bathymetry maps of puffin colony locations at (A) Isle of May and (B) Skomer Island. The red circle symbol indicates the Isle of May colony and the red triangle symbol indicates the Skomer Islan colony. The scale shown for bathymetry is in meters. Foraging radii that we suggest in the text and the typical maximum and mean depths at the two places are shown.

Chapter 5

Diving behaviour of benthic feeding Black Guillemots

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Bird Study, *In Press.*

ABSTRACT

Capsule. Auks are not exceptions to the hypothesis that a trade-off between oxygen stores and oxygen utilization drives variation in dive duration, but more data are required before we can be confident on this.

Aims. Muscle oxygen stores in small breath-hold divers are proportional to body mass$^{1.25}$ but diving oxygen consumption rates in wing-propelled divers are only proportional to body mass$^{0.87}$ implying that dive duration would scale with mass$^{0.38}$. We wished to test that idea across auks alongside new data on Black Guillemots, and document the diving behaviour of guillemots in Northern Ireland.

Methods. We compiled dive durations from auks alongside our own data from Black Guillemots breeding in Northern Ireland.

Results. Light availability apparently limited diving in Black Guillemots as dives only occurred during daylight. Dive shape implied most dives were benthic with a small number at the start of each bout associated with searching. Dive durations (max = 90 s; mean = 54 s) were shorter and dive depths (max = 15 m; mean = 9 m) were shallower than recorded for Black Guillemots elsewhere.

Conclusions. Across all species of auk, the equation for maximum dive duration (min) was $0.36M^{0.42}$, and the confidence interval included the predicted exponent of 0.38.

Key words: diving behaviour, *Cepphus*, bio-logging, alcids, allometry

1. INTRODUCTION

In diving animals, oxygen stores are generally believed to increase with body mass$^{1.0}$ while basal oxygen consumption rate scales to roughly body mass$^{0.7}$ (Lasiewski and Calder 1971, Hudson and Jones, 1986, Birt-Friesen et al. 1989, Halsey et al. 2006, Kooyman 1989). Therefore, body mass determines much of a species' capacity to make long breath-hold dives (Butler 1989, Kooyman and Kooyman 1995), and dive duration across species scales to body mass with an exponent of about 0.3 (mass ÷ mass$^{0.7}$; Halsey et al. 2006). Nonetheless, body mass alone does not always explain much of the variance in dive duration (Mirceta et al. 2013) and some animals dive deeper than expected for their body size based on the oxygen store/usage hypothesis and empirical data (Watanuki et al. 1996, Boyd and Croxall 1996, Elliott et al. 2008a). For instance, the mass exponent for dive duration in small auks—which are among the smallest marine breath-hold divers and would therefore be expected to be particularly limited by constraints on oxygen stores and use—is higher than the expected 0.3 (~0.7; Watanuki and Burger 1999). However, the auk data used in that study may have been inaccurate because they included estimates derived from direct observations of birds under unusual circumstances or radio tracking (which can overestimate dive duration if the signal is faint and therefore missed). There is therefore a need to obtain more information using more accurate electronic time-depth records from the various auk clades.

One possible explanation for the high allometric exponent observed in auks is that oxygen stores increase more rapidly with body mass than assumed by earlier writers (Watanuki and Burger 1999). Myoglobin concentration increases with mass$^{0.11}$ across animals or mass$^{0.25}$ across small animals (Supplement to Fig. 5 in Elliott et al. 2010, excluding the larger otariid seals and cetaceans) because the high mass-specific metabolic rate of small animals requires such high densities of mitochondria in muscle cells that there is insufficient space for high levels of myoglobin (Elliott et al. 2010, Mirceta et al. 2013). Assuming that similar trends are present in blood and respiratory air stores, we would expect that dive duration would scale with mass$^{0.55}$ in small animals (oxygen stores [body mass$^{1.25}$] ÷ oxygen utilization rate [body mass$^{0.70}$]), which is closer to the value of 0.735 recorded by Watanuki and Burger (1999). However, actual average diving metabolic rate for wing-propelled divers (penguins) scaled with mass$^{0.87}$ (Fig. 1b in Elliott et al. 2013), which would imply that dive duration should scale with mass$^{0.38}$ in wing-propelled seabirds.

The Black Guillemot (*Cepphus grylle*) is widely distributed in Arctic and northern Atlantic waters (Gaston and Jones 1998). This species is an inshore feeder during breeding and forages mainly on benthic prey, diving typically shallower than 30 m (Cairns 1992), making them potentially susceptible to tidal energy developments (Furness et al. 2012, Masden et al. 2013). Nevertheless, the dive behaviour of *Cepphus* guillemots has only been recorded in detail using electronic recorders by a single study reporting data from two individual birds (Masden et al. 2013). In this study, we deployed time-depth-temperature recorders (TDRs) to study the foraging behaviour of chick-rearing Black Guillemots breeding at Bangor Harbour and Lighthouse Island (Copeland Bird Observatory) in Northern Ireland. In this area, Black Guillemots mainly feed their young with butterfish *Pholis gunnellus* (Ewins 1986; Shoji pers. obs.). Knowledge of the feeding ecology of marine top predators is essential to understand their potential role in the marine ecosystems, and to conserve and manage those ecosystems (Ashmole 1971, Hunt and Schneider 1987), and there is a need for more data for these species since they have not been well-studied to date (Phalan et al. 2007). Our first goal was to describe the diving behaviour of Black

Guillemots at this site in detail. Our second goal was to revisit the allometric mass exponent of dive duration and dive depth for auks (Watanuki and Burger 1999) using new data that have become available in the 15 years since that seminal paper. We compare the relationship with our Black Guillemot results and discuss how Black Guillemots in this study fit in the model and the potential factors affecting those results.

2. MATERIALS AND METHODS

Study birds

Our observations were made at Black Guillemot colonies at Bangor Harbour and on Lighthouse Island, Northern Ireland (Bangor Harbour: 54.66° N, 5.67° W, Lighthouse Island: 54.67° N, 5.52° W) during the chick-rearing period in 2013. Population trends in other auks in northern Ireland are stable (Chivers et al. 2012). Bangor Harbour supported 38 pairs of nesting guillemots in 2013 (Greenwood 2014) and Lighthouse Island supported approximately 55-60 pairs of nesting guillemots. Our study birds were nesting in either concrete holes (Bangor Harbour) or artificial nest boxes that were installed in 2000 by Copeland Bird Observatory (Lighthouse Island).

Device attachment

Eight chick-rearing adult Black Guillemots (2 from Bangor Harbor, 6 from Lighthouse Island) were captured when they returned to the nest. TDRs (Lotek 1900 time-depth-temperature recorders, Lotek Wireless Inc, St. John's, Canada) were attached to a Darvic leg ring. TDRs recorded pressure every 3 s and temperature every 15 s for roughly one day (mass = 2.0g; dimension = 17 mm x 9mm x 16 mm). Seven of the birds also carried a GPS logger (unpackaged IgotU GT-120: Mobile

Action, Taiwan, mass = 13 g including attachment materials, dimensions = 43 mm x 24 mm x 9 mm). GPS units were sealed in heat-shrink plastic (Finishrink CLR-20/50) and attached dorsally using Tesa marine cloth tape (Tesa UK Ltd) underlying a small number of contour feathers (Shoji et al. 2014). The GPS units naturally fell off within 3 weeks as a failsafe (Shoji et al., 2014). Although our devices were near or just over the 3% limit (always <3.5% of guillemot body mass) recommended by Phillips et al. (2003), we did not observe any direct negative impact on reproductive success during the study period.

Allometric relationships between mass and dive profiles

We obtained body mass, dive depth (m) and dive duration (min) measured using electrical recorders (average and maximum) for auks from the literature and calculated the allometric mass exponent of maximum dive duration. The maximum dive duration may reflect the physiological limit of the species considered, but it is possible that variation in maximum values among species may simply reflect sampling bias and unbalanced sample sizes (Watanuki and Burger 1999). Thus, we considered both the maximum values and the mean values of dive duration. Dive depth may be a better index of oxygen consumption during the dive than dive duration because most of the cost of diving for seabirds is overcoming buoyancy to descend to depth, especially for benthic-foraging birds. In support, surface pause intervals correlate better with dive depth than duration in auks. To test if dive depth better represented the trade-off between oxygen stores and oxygen consumption in auks, we correlated dive depth with body mass.

Data analysis

We completed all calculations and statistics in R 1.5.2 (R Development Core Team 2011). We extracted dive depth, dive duration and surface interval duration for each dive, after accounting for device drift, using the diveMove package in R (Luque and Fried 2011). We used the sequential differences method to subdivide dives into bouts to identify patches using surface intervals (difference criterion: 66 s: Mori et al. 2001). We classified dive shapes into V-shape, U-shape and W-shape based on the criterion provided by Elliott et al. (2008b). As previous studies had examined patch quality (as assessed by index of patch quality, IPQ) on birds that primarily fed on schooling prey (Mori et al. 2002, Elliott et al. 2008a, Shoji et al. 2014), where patch quality is clear because it represents a school of high quality prey, we were interested in examining patch quality for birds that primarily fed on non-schooling, benthic prey. We tested whether birds remained at high quality patches when foraging on non-schooling prey. Specifically, we used general linear mixed models with individual as a random factor to examine how mean IPQ per patch is related to the number of dives per patch. Data were transformed when not normally distributed. Unless otherwise stated, mean ± 1 SD was presented.

3. RESULTS

Diving behaviour of Black Guillemots

We retrieved TDRs from one adult at Bangor Harbour and three adults at Lighthouse Island. All other birds returned to the colony and continued to breed normally, but we failed to recapture them. Only 1 of the 6 GPS loggers was successfully retrieved and the data were downloaded. The GPS logger had fallen off the remaining five birds, before recapture. All study birds raised young successfully with a mean departure mass of 386 ± 8 g. During the recording period, we observed 21 deliveries from TDR carrying birds at Lighthouse Island and all were butterfish (>20 cm). Total flight time was 1.66 h / day (assuming a speed threshold of 10 km/h) and the furthest distance from colony was 1.5 km, as measured by the GPS logger.

In total, we recorded 664 dives from chick-rearing Black Guillemots (N = 4 birds). Guillemot dives were constrained to daylight hours (Fig 1a). Mean number of dives per day was 186 ± 79 dives (Table 1; Fig 1a), mean dive depth was 9.3 ± 2.8 m (max = 14.7 m: Fig 1b) and mean dive duration was 53.6 ± 21.4 s (max = 89.5 s). Maximum and average dive duration (max = 90 s; mean = 54 s) were shorter and maximum and average dive depth (max = 15 m; mean = 9 m) were shallower than recorded for Black Guillemots elsewhere (Table 2). Dive depth and dive duration were highly correlated (r = 0.62; Fig 2). Mean total dive duration and mean total surface pause duration were also highly correlated (r = 0.99; Fig 3). Overall, W-shaped dives were most common (52 %), followed by U-shaped dives (32 %) and then V-shaped dives (16 %). However, there was also a clear variation among individuals (Fig 4). Thirty-one % of V-shaped dives were first dives of each dive bout and 22 % were second dives. Mean number of dives per patch was 2.62 ± 2.28 dives. In addition, most recorded V-shaped dives were shallower than the subsequent dives (Fig 5). Mean patch IPQ was independent of number of dives per patch (ΔAIC = 9.2, Estimate = 0.005 ± 0.003; GLMM with individual identity as random effect).

Table 1. Dive parameters for Black Guillemots in Northern Ireland, including all dives > 1m in depth. B = Bangor harbour; L = Lighthouse Island. GPS data from L97415 were also retrieved during the TDR recording period.

Individual	Mass (g)	Mean ± SD depth (m)	Mean ± SD duration (s)	Max depth (m)	Max duration (s)	Mean dives per day	Time underwater per day (h)
B60719	385	9.2 ± 1.3	68.6 ± 17.5	11.7	96	96	1.55
L97415	387	11.3 ± 2.7	60.0 ± 20.1	17.5	96	192	2.89
L97417	375	10.3 ± 2.9	50.7 ± 18.7	18.7	78	168	1.78
L97421	395	7.3 ± 1.8	45.1± 20.7	10.7	88	288	2.29
Mean	385.5 ± 8.2	9.3 ± 2.8	53.6 ± 21.4	14.7 ± 4.0	89.5 ± 8.5	186 ± 79	2.13 ± 0.60

Table 2. Summary of dive parameters for *Cepphus* species

Study site	Species	Mean dive duration (s)	Max. dive duration (s)	Mean depth (m)	Method	Source
Southern Vancouver Island, BC	*colomba*	87	144	10-45	Visual Obs.	Clowater and Burger 1994
Prince William Sound, Alaska, Benthic foraging	*columba*	86	-	-	Visual Obs.	Kuletz 1983
Prince William Sound, Alaska, Pelagic foraging	*columba*	47	-	-	Visual Obs.	Kuletz 1983
Rosario Head, Washington	*columba*	67	105	-	Visual Obs.	Thoresen 1989
Farallon Islands, California	*columba*	75	110	20	Visual Obs.	Ainley et al. 1990
Yaquina Head, Oregon	*columba*	36	69	-	Visual Obs.	Scott 1973
Olympic Peninsula, Washington	*columba*	41	-	-	Visual Obs.	Cody 1973
Lancaster Sound of the Canadian Archipelago	*grylle*	67	146	-	Visual Obs.	Bradstreet 1982
New Foundland, Canada	*grylle*	-	112	14*	Visual Obs.	Piatt and Nettleship 1985

Northeastern Hudson Bay	*grylle*	70.8	-	4-48	Visual Obs.	Cairns 1992
Holm of Papa Westray, Orkney	*grylle*	59	-	-	Radio	Walton et al. 1998
Stroma Island, Caithness	*grylle*	95	131	32	TDR	Masden et al. 2013
Lighthouse Island, Northern Ireland	*grylle*	54	90	9	TDR	This study

* Median values of provided depth ranges were used to calculate the mean depth (m.
Method: Visual Obs. = Visual observation; Radio = Radio tracking; TDR = time-depth-temperature recorders

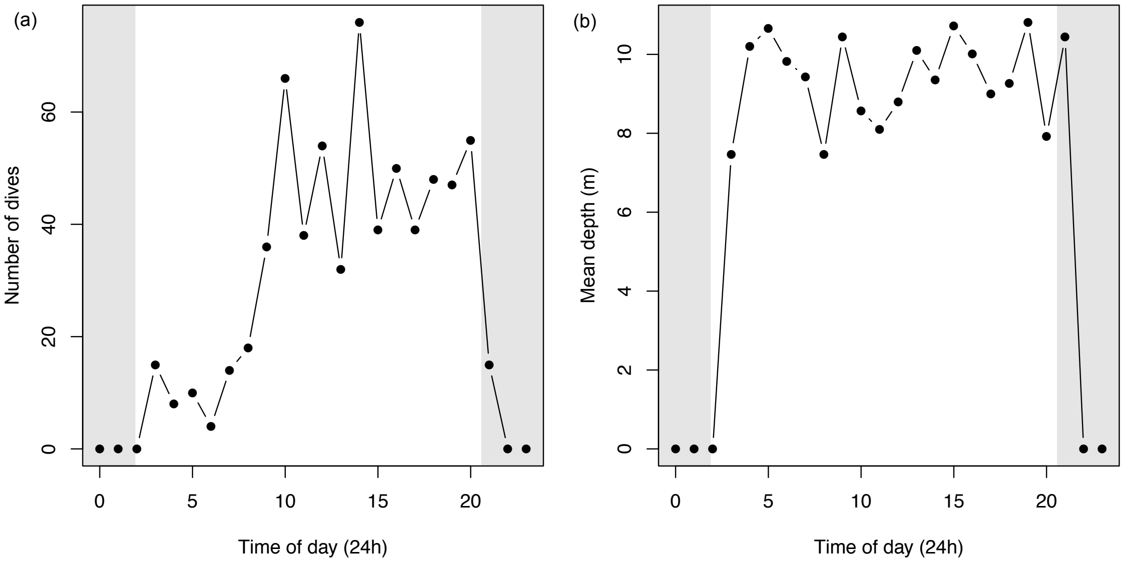


Figure 1. A: Number of dives per hour relative to time of day (*N* = 4 birds). B: Mean ± 1 SD of dive depth per hour relative to time of day (*N* = 4 birds). The grey box outlines the sunrise/set time.

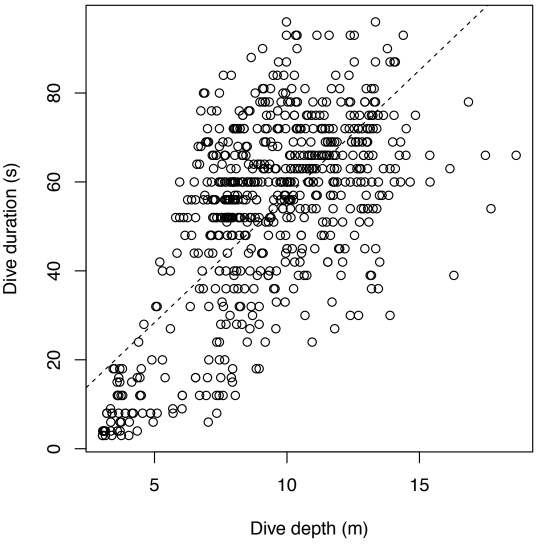


Figure 2. Relationship between dive duration (s) and dive depth (m);(*n* = 664 dives, *N* = 4 birds).

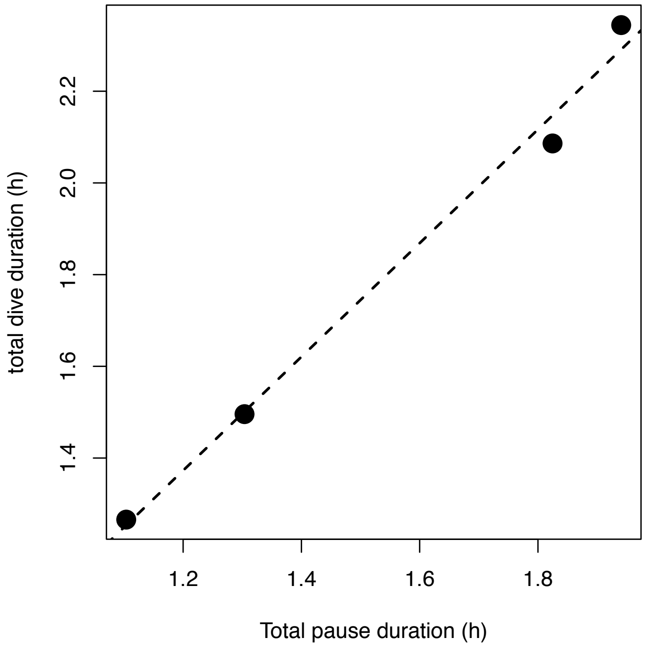


Figure 3.Relationship between total dive duration (h) and total pause duration (h); *n* = 664 dives, *N* = 4 birds).

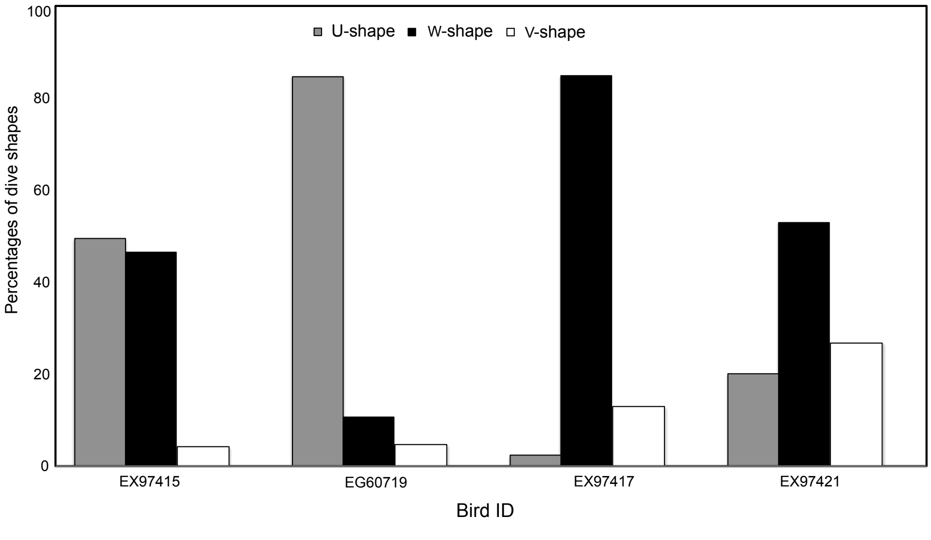
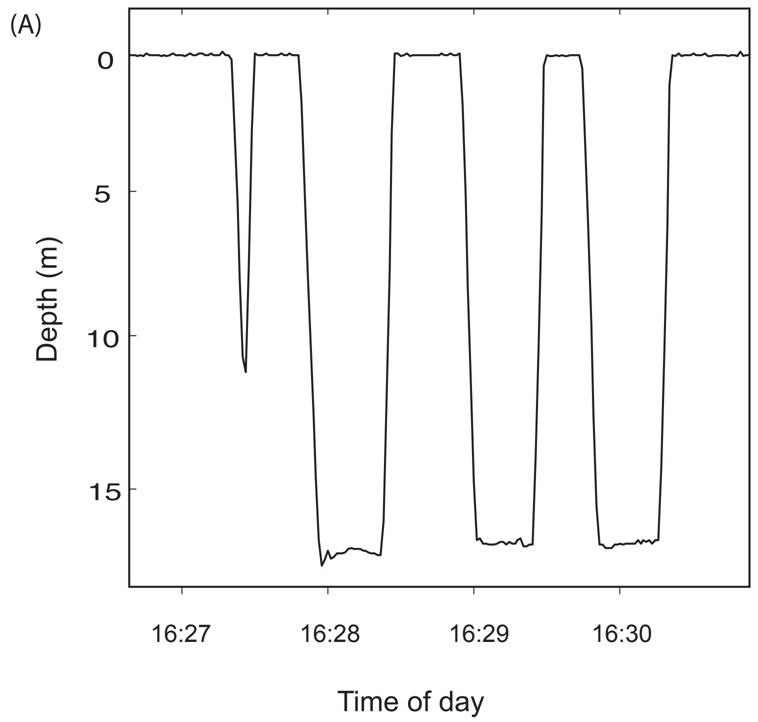


Figure 4. Percentage of dive shapes made by individual Black Guillemots. W-shaped dives were shown in white, V-shaped dives were shown in solid, U-shaped dives were shown in grey (*n* = 664 dives, *N* = 4 birds).



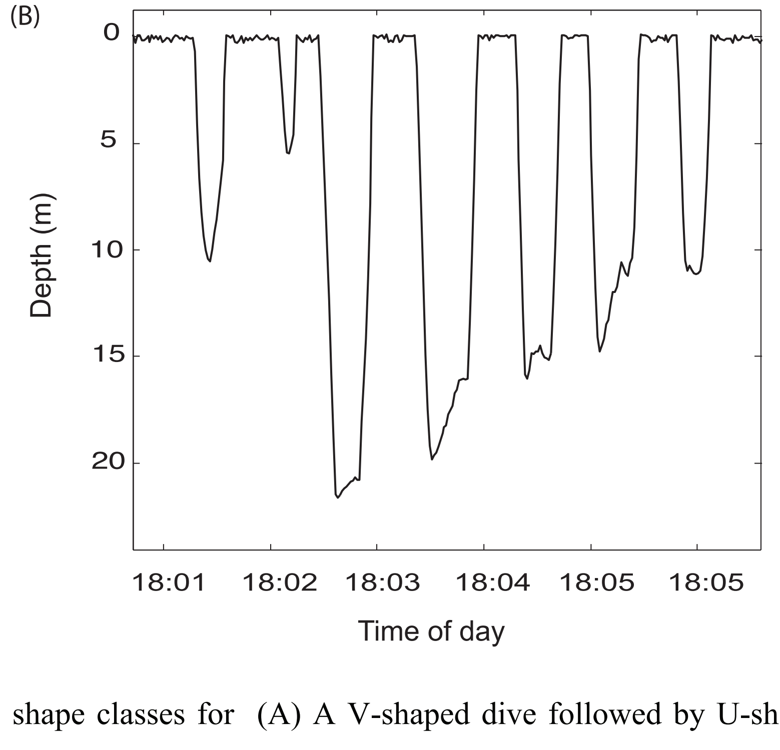


Figure 5. Dive shape classes for (A) A V-shaped dive followed by U-shaped dives and (B) V-shaped dives followed by W–shaped dives in Black Guillemots *Cepphus grylle*.

Allometric relationships

Maximum, but not average, dive duration increased with body mass in auks (Fig 6). For the dive duration:

$DU_{max} = 0.361\ M^{0.419}$ ($SE_{slope} = 0.10$, $r^2 = 0.67$, $t_8 = 3.75$, $p < 0.01$)

$DU_{mean} = 0.359\ M^{0.176}$ ($SE_{slope} = 0.08$, $r^2 = 0.37$, $t_8 = 2.05$, $p = 0.08$)

The 95% confidence interval of the mass exponent of maximum dive duration (0.22-0.62) included the exponent predicted by the oxygen store/usage hypothesis (0.38), as our estimate was smaller than the exponent for auks provided in a previous analysis (Watanuki and Burger 1999). The mass exponent of mean dive duration (0.18) was much smaller than 0.30 (predicted value) or the value 0.391 provided in (Watanuki and Burger 1999). The maximum diving duration made by Black Guillemots in this study was similar when scaled for body mass to the allometric relationship (Fig 6).

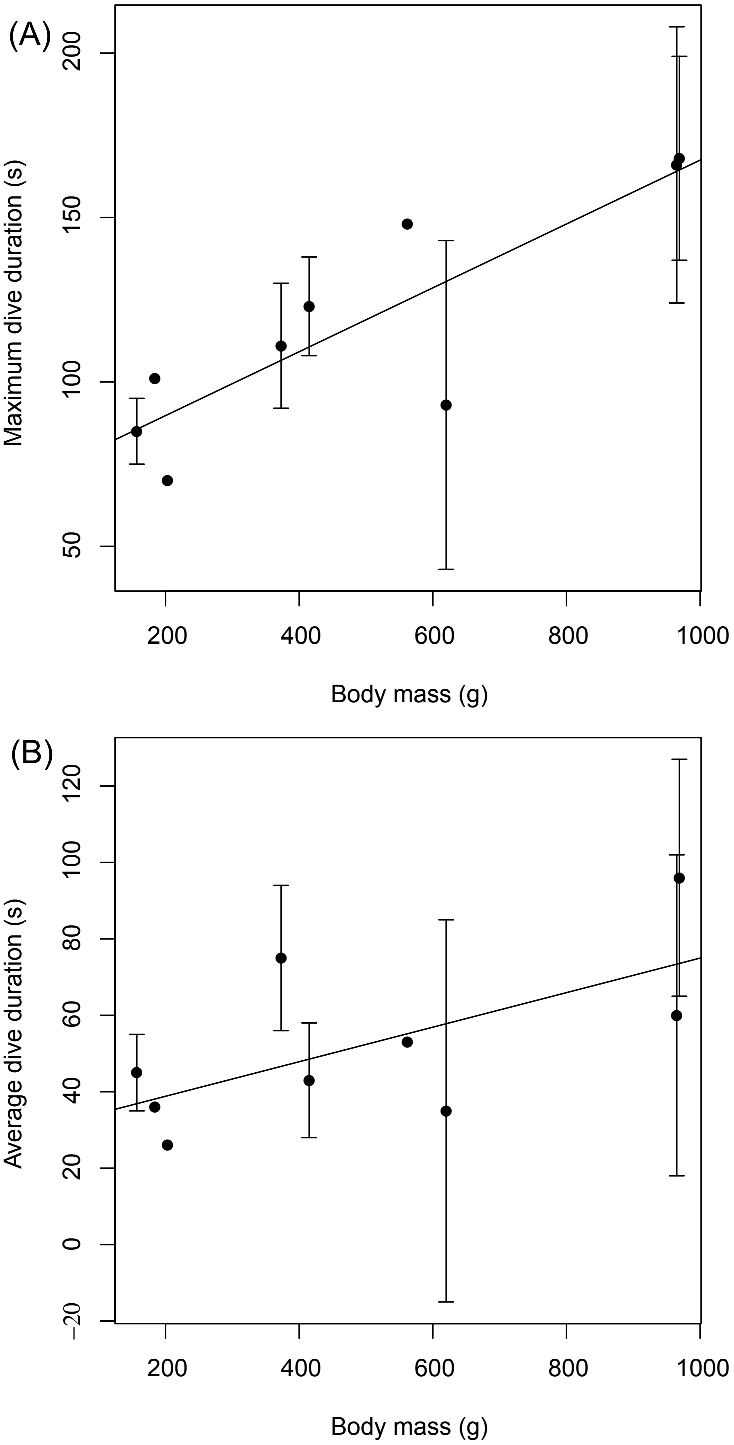


Figure 6. Allometric relationship ($\log_{10}$ scale) (a) between maximum dive duration (min) and body mass (g), and (b) between average dive duration (min) and body mass (g) for 9 species of alcids based on data given in Table 3. Means ± SD are presented.

Table 3. Body mass and dive duration and depth in alcids. Only dive behaviour obtained by electrical recorders was included. Maximum values represent the average of the maximum value recorded for each individual studied. Where multiple papers report values from the same species and the same colony, we included only the first value we encountered.

Species	Mass (g)	Max duratio (s)	Mean duratio (s)	Max depth (m)	Mean depth (m)	Reference
Common Guillemot *Uria aalge*	1000	212	64	152	30	Hedd et al. 2009
Common Guillemot *Uria aalge*	908	-	-	-	-	Thaxter et al. 2010
Common Guillemot *Uria aalge*	1000*	-	78	-	63	Evans et al. 2013
Common Guillemot *Uria aalge*	960	-	-	29	67	Watanuki et al. 2006
Common Guillemot *Uria aalge*	993	119	39	37	10	Tremblay et al. 2003
Brünnich's Guillemot *Uria lomvia*	1000*	196	97	136	45	Mehlum et al. 2001
Brünnich's Guillemot *Uria lomvia*	960*	-	105	-	-	Benvenuti et al. 2002
Brünnich's Guillemot *Uria lomvia*	960*	187	98	-	-	Jones et al. 2002
Brünnich's Guillemot *Uria lomvia*	970	-	-	120	48	Watanuki et al. 2006
Brünnich's Guillemot *Uria lomvia*	960*	175	105	114	48	Mori et al. 2002
Brünnich's Guillemot *Uria lomvia*	960	181	68	148	-	Elliott et al. 2008b
Brünnich's Guillemot *Uria lomvia*	941	-	104	110	27	Paredes et al. 2008
Brünnich's Guillemot *Uria lomvia*	1043	148	96	107	36	Takahashi et al. 2008
Brünnich's Guillemot *Uria lomvia*	960*	123	-	-	-	Falk et al. 2000
Razorbill *Alca torda*	600	93	31	56	8	Shoji et al. *In press*
Razorbill *Alca torda*	583	-	23	-	7	Thaxter et al. 2010
Razorbill *Alca torda*	591	-	-	41	-	Dall'Antonia et al. 2001
Razorbill *Alca torda*	706	-	50	36	10	Paredes et al. 2008
Razorbill *Alca torda*	620	-	-	8	31	Watanuki et al. 2006
Rhinoceros Auklet *Cerorhinca monocerata*	562	148	53	57	14	Kuroki et al. 2003
Atlantic Puffin *Fratercula arctica*	420	123	36	48	12	Shoji et al. *In press*

Atlantic Puffin *Fratercula arctica*	426	-	49	41	10	Spencer 2012
Atlantic Puffin *Fratercula arctica*	398	-	-	20	4	Harris and Wanless 2011
Black Guillemot *Cepphus grylle*	359	131	95	43	32	Masden et al. 2013
Black Guillemot *Cepphus grylle*	386	90	54	15	9	This study
Ancient Murrelet *Synthliboramphus antiquus*	203	70	26	37	9	Elliott et al. 2010
Cassin's Auklet *Ptychoramphus aleuticus*	184	101	36	28	9	Elliott et al. 2010
Dovekie *Alle alle*	164	90	52	27	10	Harding et al. 2009
Dovekie *Alle alle*	150	79	37	38	10	Karnovsky et al. 2011

* Body mass was not presented in the reference, and thus the typical value was entered.

4. DISCUSSION

Black Guillemot diving behaviour

The dive behaviour of Black Guillemots was similar to other small auks; all dives were shallower than 20 m and dive shape was highly variable among individuals (Fig 2; Fig 4). In general, V- and W-shaped dives are associated with capturing prey in mid-water in other auks, while U-shaped dives are associated with benthic feeding along the seafloor (Elliott et al. 2008b). The V-shaped dives occurred almost exclusively as the first or second dive of dive bouts, and tended to be substantially shallower than the remaining dives in each dive bout, suggesting that they were associated with probing the water column for prey availability and depth. For instance, birds regulate the degree of hyperventilation for the subsequent dive duration (anticipatory surface intervals) and to do that effectively they must know how deep to dive. Although guillemots fed their offspring almost exclusively on benthic butterfish, and guillemots are usually considered benthic foragers, the majority of dives were W-shaped, which is typical of mid-water feeding. Either guillemots fed themselves on alternative, mid-water prey, or the bottom topography or prey chases involved undulations in dive profiles. Dive depth was similar between individuals regardless of the proportion of dive shapes, suggesting that they foraged at the similar locations (or at least they foraged at locations with similar bathymetries, which is necessarily true given that guillemots forage close to the colony).

Diving behaviour was constrained by daylight (Fig 1) as no dive was recorded between 22:00 and 03:00 GMT. While number of dives per hour peaked at midday (Fig 1a), dive depth within the daylight hours was apparently constrained by bathymetry and the depth of prey availability rather than visibility, as dive depth was not affected by time of day (Fig 1b). At Lighthouse Island, fish delivery frequency is usually high in the morning and evening (Shoji pers. obs.). Likewise, fish delivery rate peaks at dawn for Black Guillemots in Shetland (Ewins 1986). In contrast, the number of dives was low in the morning and evening in this study and dive rate peaked at midday. Presumably, adults dived to feed themselves at midday and fed their chicks early or late in the day when dive rate would be lower due to the need to return to the offspring to deliver food. At Lighthouse Island, guillemots exclusively brought large butterfish (> 20 cm) as a single load to their offspring in this study. We were unable to observe what adults forage for themselves for this study, but Ewins (1986) reported a difference in diet between chicks and adults in Shetland, as is often the case in other auks (Davoren and Burger 1999, Wilson et al. 2004, Gaston et al. 1983). We speculate that the discrepancy between the daily dive pattern and the provisioning pattern reflect a foraging strategy by guillemots to target different prey items for offspring than for adults, which would also help explain the large number of W-shaped dives.

Patch quality was independent of number of dives per patch. Perhaps if guillemots are indeed capturing benthic prey items, these prey items are consistent over the scale of a dive bout, and there is no need to extend a single dive to capture as many prey as possible while they are present.

Black Guillemots usually forage close to the colony and the typical travel distance is within 1 km (Ewins 1986). Our retrieved GPS (*N* = 1) confirmed that this was also the case here. Dive depth and duration in our study was shallower (mean depth = 9 m) and shorter (mean duration = 57 s) than individuals at the Stroma islands in Scotland (median depth =32 m, median duration = 95 s; Masden et al. 2013). The guillemots in Scotland did not dive deeper because they were larger, as the Northern

Irish population was actually heavier than Scottish population (386 ± 8 g, 359 ± 19 g, respectively). Rather, local variation in bathymetry and prey selection may have caused the difference. Regardless, our values were more similar to that predicted by the allometric relationship across auks (Fig. 6) and therefore are likely more representative of the performance of most guillemots.

Allometric relationship

We aimed to update the allometric relationship for the maximum dive duration on body mass in auks provided in Watanuki and Burger (1999), by adding new data obtained using electronic time-depth recorders. The confidence interval for the mass exponent (0.22-0.62) for maximum dive duration in auks included both the value of 0.30 predicted from the traditional oxygen store/usage hypothesis and is very similar to the value of 0.38 predicted from the 'updated' allometric relationships for oxygen use during diving and muscle oxygen stores, but not the value of 0.735 reported previously (Watanuki and Burger 1999). Seabirds, including auks, consume very low levels of oxygen during long dives (Bevan et al. 2002, Butler and King 2004, Niizuma et al. 2007, Ponganis et al. 1997), and it is the scaling of that minimal rather than average diving metabolic rate with body mass that is likely most relevant to extension of maximum dive duration. Our exponent of 0.42 is within the range of potential scaling exponents expected on a theoretical basis, and additional data on oxygen stores, especially plasma and lung/air sac volumes, and minimal diving metabolic rate of wild auks, is clearly needed to resolve any remaining discrepancy. Based on the agreement between our estimate and that expected on a theoretical basis, we suggest that the calculated exponent in Watanuki and Burger (1999) was over-estimated because some of the earlier data were unreliable. For instance, the maximum dive depth of 210 m recorded using a maximum depth gauge was later shown to be overestimated by roughly 33% (Elliott and Gaston 2009).

In contrast to maximum dive duration, average dive duration was independent of body mass. There is a large variation in dive duration among colonies (Sala et al. 2014) and individuals (Woo et al. 2008), and variation in average dive duration apparently reflects such ecological variation in local bathymetry, light levels and prey availability rather than physiological constraints.

5. ACKNOWLEDGEMENTS

We are grateful to Copeland Bird Observatory for providing logistics and generous support in the field. In particular, we thank Shane Wolsey, David Galbraith, Neville McKee and Philip McNamara. We thank George Dovekie for advice on field procedures. This work was funded by Merton College, Japan Students Services Organization and Department of Zoology (AS), and an NSERC Postdoctoral Fellowship (KHE). All work was conducted after ethical approval by the Northern Ireland Environment Agency (permissions and facilities), the British Trust for Ornithology (BTO permits: Perrins, 660; Shoji, 5939).

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Chapter 6

The foraging strategy of Manx Shearwaters: implications for dual foraging and pair-coordination

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Currently under review.

ABSTRACT

For iteroparous animals, allocating time and energy between their own survival and their offspring's is critical. In seabirds, provisioning strategies may reflect this allocation, while the distance between breeding sites and foraging areas may influence the decision. Nevertheless, few studies have explored the link between life history and foraging in the context of resource allocations. Studying foraging behaviour alongside food load rates to chicks provides a useful system to understand the foraging decisions made during parent-offspring conflict. Using simultaneously deployed GPS and time-depth recorders, we examined the provisioning strategies in free-living chick-rearing Manx Shearwaters *Puffinus puffinus*. Our results showed a bimodal pattern where birds alternated short and long trips. Short trips were associated with high feeding frequency and larger meals, whereas long trips appeared to be less productive for the young, suggesting that they were performed for self-feeding. Furthermore, while foraging locations largely varied, most foraging was carried out within 100 km of sea fronts. We further derive a simple model based on patch quality and travel time to show that birds should use a bimodal foraging trip duration to optimise feeding rates.

Key words: foraging strategy, bio-logging, GPS, diving

1. INTRODUCTION

Resource allocation between parents and their offspring during reproduction is a central issues in life-history theory (Ydenberg et al. 1994; McNamara and Houston 1997) and the outcomes of parent-offspring conflict are inextricably linked with fitness (Nur 1988). In iteroparous species, life-history theory predicts that individuals should balance the cost of their own survival and future reproductive success against investment in current reproduction (Stearns 1992). For instance, current parental effort may be increased in parents in good condition but decreased in parents in poor condition, so that they can maintain their own body condition.

Seabirds are on the extreme slow end of the life-history continuum: marine resources are generally patchily and scarcely distributed, and assumed to be unpredictable (but see Weimerskirch 2007), making it difficult for pelagic seabirds to regulate foraging patterns. However, a tight regulation of foraging schedule is critical in species with bi-parental care to ensure that energy demands of the offspring are met without over-feeding (Harris and Wanless 2011).

Some studies suggested that feeding rates in pelagic seabirds are fixed by inherent internal rhythms so that parents feed their offspring regardless of offspring condition (Ricklefs 1992; Hamer and Hill 1993). Other studies reported that parents show more flexibility in feeding rates than previously thought, so that they modify feeding patterns according to the offspring's condition (Hamer and Hill 1993; Bolton 1995; Weimerskirch 1995; Tveraa et al. 1998). Furthermore, sex-specific differences in chick-provisioning behaviour during the breeding season among monomorphic birds have been found in a number of species (*e.g.* Hamer et al. 2006; Elliott et al. 2010).

A dual foraging strategy, where parents alternate or mix short and long trips, is one example of how parental seabirds can regulate foraging patterns. During short trips, parents forage at a local oceanic shelf area to maximise offspring provisioning rates since the costs of commuting with a food load for the chick are kept low (Cuthill and Kacelnik 1990). On the other hand, during long trips parents can travel further to exploit inherently richer but more distant areas of deep oceanic water or seasonally stable sea fronts, where they can replenish their own reserves without paying the costs of repeated commuting (Matsumoto 2008) or food load carrying. A disadvantage of executing long trips for offspring feeding is that feeding rates to offspring are lower because of a longer commuting time (Chaurand and Weimerskirch 1994; Weimerskirch et al. 1994; Weimerskirch 1998). Furthermore, energetic or nutritional requirements often differ between parents and their young (Murphy 1996) and thus, foraging locations may vary depending on the intended recipient of food (Markman et al. 2004). A number of *Procelariiform* seabirds execute a bimodal foraging pattern; these include Thin-billed Prions *Pachyptilla belcheri* (Weimerskirch et al. 1994), Yellow-nosed Albatrosses *Diomedea chlororynchos* (Pinaud et al. 2005), Wandering Albatrosses *D. exulans* (Weimerskirch et al., 1994), Sooty Shearwaters *Puffinus griseus* (Weimerskirch 1998), Little Shearwaters *P. assimilis* (Booth et al. 2000), Cory's Shearwaters *Calonectris diomedea* (Granadeiro et al. 1998; Magalhaes et al. 2008), Streaked Shearwaters *C. leucomelas* (Ochi et al. 2010), Buller's Albatrosses *Thalassarche bulleri* (Stahl and Sagar 2006) and Blue Petrels *Halobaena caerulea* (Chaurand and Weimerskirch 1994), as do a number of *Alcids* (Little Auks *Alle alle*; Welcker et al. 2009; Brown et al. 2012; Jakubas et al. 2012) and *Sphenisciformes* (Little Penguins *Eudyptula minor*; Saraux et al. 2011, Adelie Penguins *Pygoscelis adeliae*: Ropert-Coudert et al. 2004). Yet dual-foraging strategies are not ubiquitous among seabirds (Phillips et al. 2009). Furthermore, factors affecting parents' decision to undertake a long or short foraging trip may be species-specific. Previous studies mainly focused on the frequency distribution of trip duration or the use of different foraging habitats, but few studies have connected those variables to meal mass, chick-feeding rates or foraging behaviour at sea (Phillips et al. 2009).

Manx Shearwaters (*Puffinus puffinus*) are widely distributed in the North Atlantic Ocean (Brooke 1990). This species shows a typical *Procelariiform* life-history pattern with a single-egg clutch and slow chick development that averages 70 days until fledging (Brooke 1990). The species exhibits bi-parental care during both the incubation and chick-rearing periods, and arrival at and departure from the colony only occur at night (Riou and Hamer 2008). Variation in foraging trip durations and foraging destinations during chick-rearing have been reported (Guilford et al. 2008), making shearwaters good candidates for testing foraging strategies from the standpoint of resource partitioning. The purpose of this study was to combine at-sea data (movement patterns and diving behaviour) and at-colony data (breeding schedule, meal mass delivered to young) collected from breeding shearwaters to test for and analyse dual foraging strategies in light of regulation of provisioning (*i.e.* fasting duration of offspring, chick-growth rates).

2. MATERIALS AND METHODS

Study site and birds

The study was carried out at Skomer Island (51°44'N, 5°17'W), Wales, UK, during a single breeding season (July-August 2013) to avoid potentially confounding effects of inter-annual environmental variability. All study birds were ringed as part of the long-term monitoring program carried out by Oxford University since 2006. Parents were sexed where possible by cloacal inspection during the laying period (Gray and Hamer 2001). Nests were visited daily to monitor breeding progress (laying dates, hatching dates, fledging dates where possible).

All chicks in the monitored burrows in the colony were weighed daily. To determine food load from parents to their chicks, we weighed chicks every evening at 8pm before Manx Shearwaters arrived at the colony and checked study burrows every 20 min through the night (typically between 23:00-04:00). To reduce disturbance, we used knock-down sticks at the entrance (Shoji and Gaston 2010), only checking nests when sticks were displaced. When we found an adult in a study burrow, we blocked the nest and left at least 20 min to allow parents to feed their young before weighing both parent and chick.

Foraging behaviour

To study the foraging behaviour of chick-rearing shearwaters, we simultaneously deployed 1Hz CEFAS G5 Time-depth recorders (TDRs) weighing 2.7 g, attached to a hand-made darvic ring on a leg, and GPS loggers (unpackaged i-gotU GT-120: Mobile Action, New Taiwan City, Taiwan) weighing 10-12 g, fitted dorsally to each bird using Tesa tape underlying a small group of contour feathers (Guilford et al. 2008) on 14 males and 8 females from the study colony for 1-7 successive foraging trips. Birds were taken from study burrows by hand through a short-access tunnel and weighed at device deployment and retrieval. Handling time for capture and retrieval was always less than 15 min.

Data analysis

All analyses were performed in R (R Development Core Team 2011). We quantified trip duration, total distance travelled, and foraging range (the maximum distance from the colony). All positional fixes were converted to metres using the Universal Transverse Mercator coordinate system. Horizontal ground speed was calculated from interpolated positions by using cubic splines of GPS position fixes. To monitor diving behaviour we used diveMove (Luque and Fried 2011), which corrected for device drift. We obtained dive depth, duration and surface pause duration for all dives and determined bouts based on sequential differences (Mori et al. 2001). Only dives deeper than 1 m were analysed because shallow dives are often associated with non-foraging behaviour such as bathing or socialising. Positions of seasonally stable fronts (Celtic Sea Front and Western Irish Sea Front) were obtained from the literature (Simpson and Hunter 1974) to examine effects of the foraging locations in shearwaters as shown in (Scales et al. 2014). We used an information theoretic approach to evaluate the relationship between (1) trip duration (response variable) vs. (2) locations, and provision rates (g per day), and number of dives per day, meal mass per trip and total number of dives (explanatory variables) per trip. All analyses were completed using linear mixed models with a maximum-likelihood fitting method allowing for inter-model comparisons by using package lme4 in R (Bates 2009). Data were collected more than once from individuals and so to account for pseudo-replication, individual identity was included as a random effect in the models (Buckley et al. 2003). Model selection was based on Akaike's information criterion (AIC) and ΔAIC from the null model (intercept-only). Means are presented as ± 1 standard deviation. We checked for deviations from normality and homoscedasticity by plotting fitted and observed values and residuals, and we log transformed variables when necessary.

Dual foraging modelling

We aimed to identify dual foraging in the Manx Shearwater by describing how food load size varies as a function of travel time by modifying the model presented in (Ropert-Coudert et al. 2004). When the travel time increases (from short to long), it is expected that the food load maximising provisioning rate should also increase (Charnov 1976) to balance energy gain against expenditure. When seabirds exhibit a dual foraging mode, it is likely that provisioning occurs during short trips, while self-feeding takes place during long trips: indeed, the cost of loading food is expected to increase with flight time and distance (Kacelnik 1984). Here, we used the Index of Patch Quality (IPQ) as a proxy for prey richness estimated based on the dive profiles (Mori et al. 2002; Shoji et al. 2014). Taking inspiration from (Ropert-Coudert et al. 2004), we examined how variation in travel time (foraging distance) affects the rate of energy gain by adults and chicks. We assumed that birds had a constant flight speed (derived empirically: see Fig S1) and that (i) patch quality, measured on the IPQ scale, is gained during six hours of foraging; (ii) the amount of foods that adults can bring back to their young is equal to the 25 quality points on the IPQ scale; the time required to accumulate these 25 points is henceforth denoted TPQ_{25}. Daily energy gain for chicks ($EGFC_{\mathrm{day}}$) is inversely proportional to the time to gain (TPQ_{25}):

$$EGFC_{\mathrm{day}} = 25 / TPQ_{25}$$

In turn, the time to gain 25 IPQ points includes travel time t_T plus foraging time. Foraging time is inversely proportional to IPQ, as it is expected that prey are easy to forage in a high-quality patch, so that:

$$TPQ_{25} = t_T + 6 / IPQ$$

Altogether, we expect that $EGFC_{\mathrm{day}}$ is inversely proportional to t_T. From the empirical estimation of IPQ, we can then relate foraging strategy to both travel time and provisioning. As the choice of the constants (6 hours; 25 points) is arbitrary, we re-ran the model with constraints of 10 h and 50 points we examined the robustness of our predictions to these values.

3. RESULTS

We retrieved and successfully downloaded GPS and TDR data from 17 birds out of the 22 originally deployed – the other 5 birds returned without a GPS logger. GPS recorders logged 15 complete foraging trips from females and 29 complete foraging trips from males during chick rearing. Trip duration and total distance travelled per trip were highly correlated (r = 0.84, r^2 = 0.70, p < 0.0001). The distribution of foraging trip durations showed three peaks, with short trips lasting 1-3 days, medium trips lasting 4-7 days and long tips 8-11 days (Fig 1). Mean adult body mass was 417 ± 38 g (before) and 406 ± 30 g (after) each trip. Adult body mass was independent of trip durations (ΔAIC = 0.6) with body mass before short trips (416 ± 35 g), medium trips (406 ± 42) or long trips (437 ± 42 g), or after short trips (407 ± 28 g), medium trips (397 ± 30) or long trips (412 ± 44 g). Among these three modes in trip duration, shorter trips appeared to be significantly more productive as shown in Fig 2 because the provisioning rate (meal mass per day) was much higher for one or two day trips than for longer trips (ΔAIC = - 9.27; Fig 2). We confirmed the relationship by applying a robust linear regression and the trend remained the same: shorter trips increased provisioning rates ($p < 0.0001$), but medium ($p = 0.39$) and long trips ($p = 0.57$) were independent of provisioning rates.

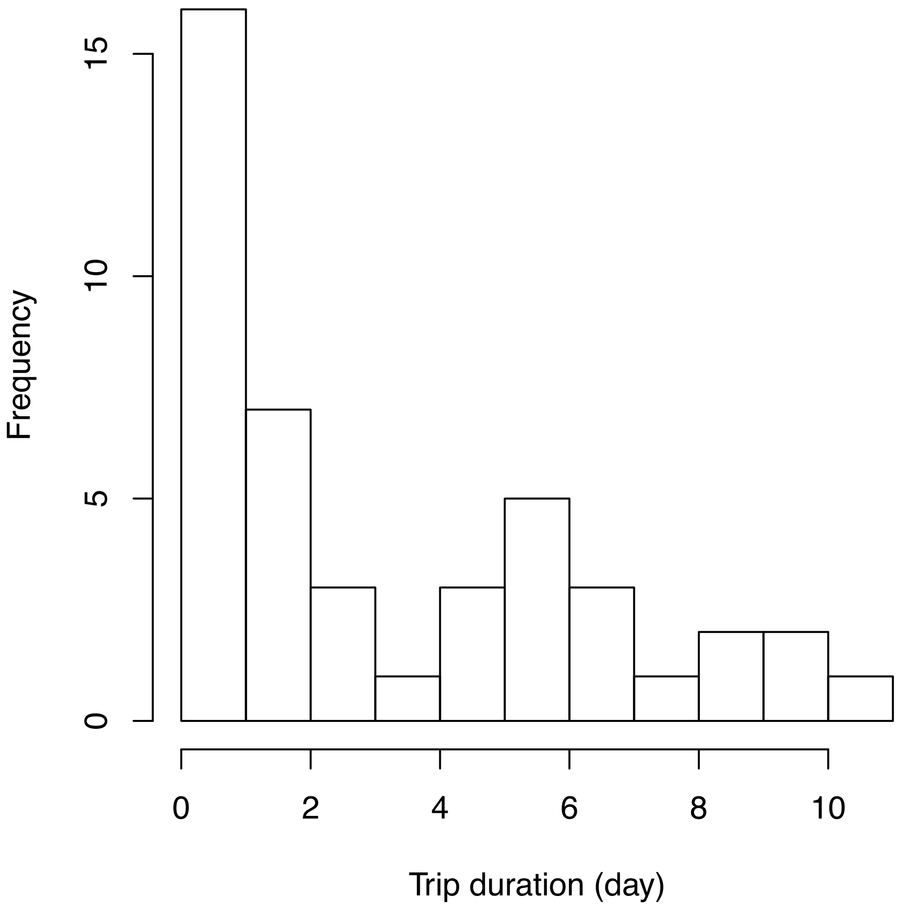


Figure 1. Frequency of trip duration during chick-rearing period in Manx Shearwaters.

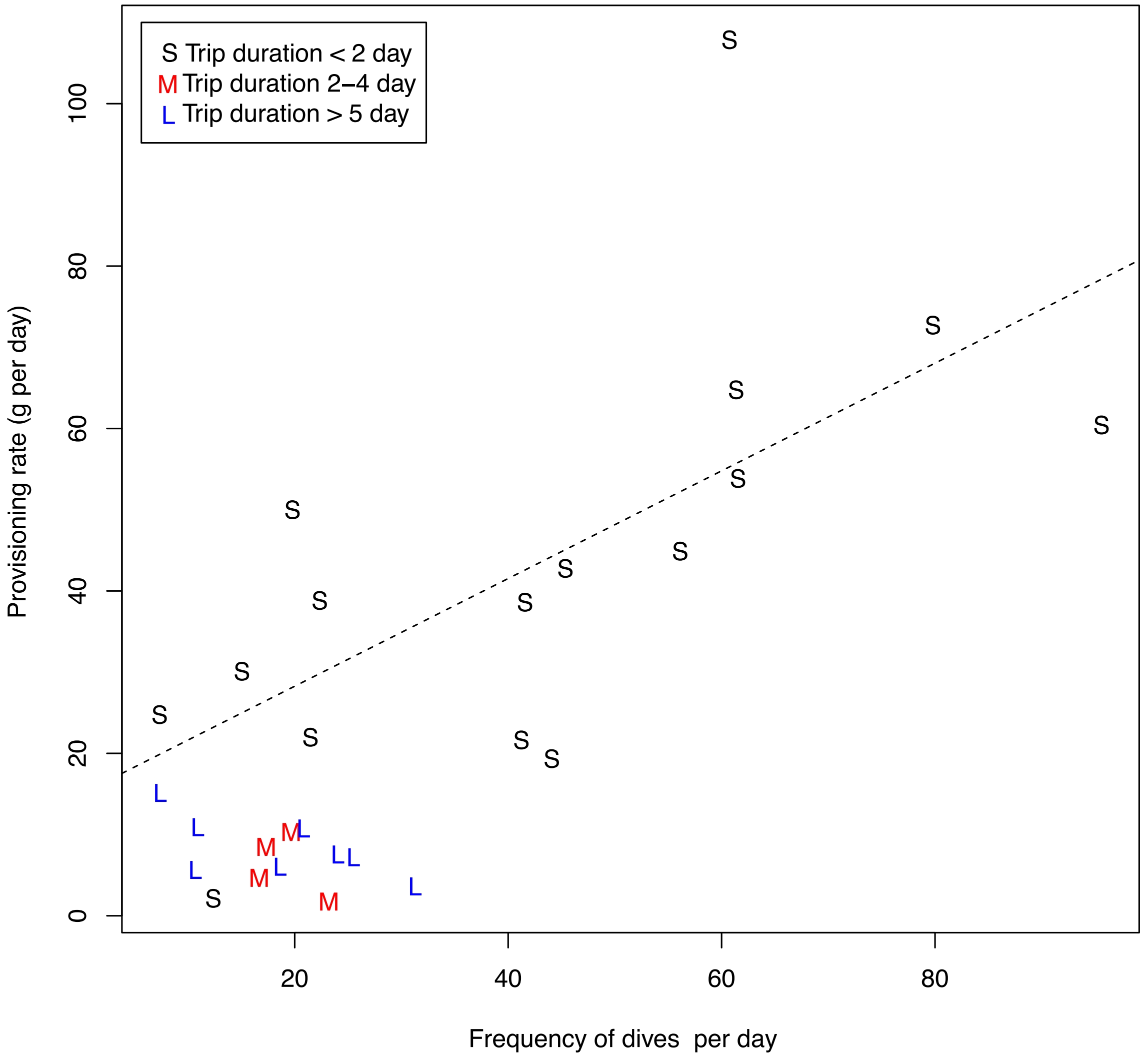
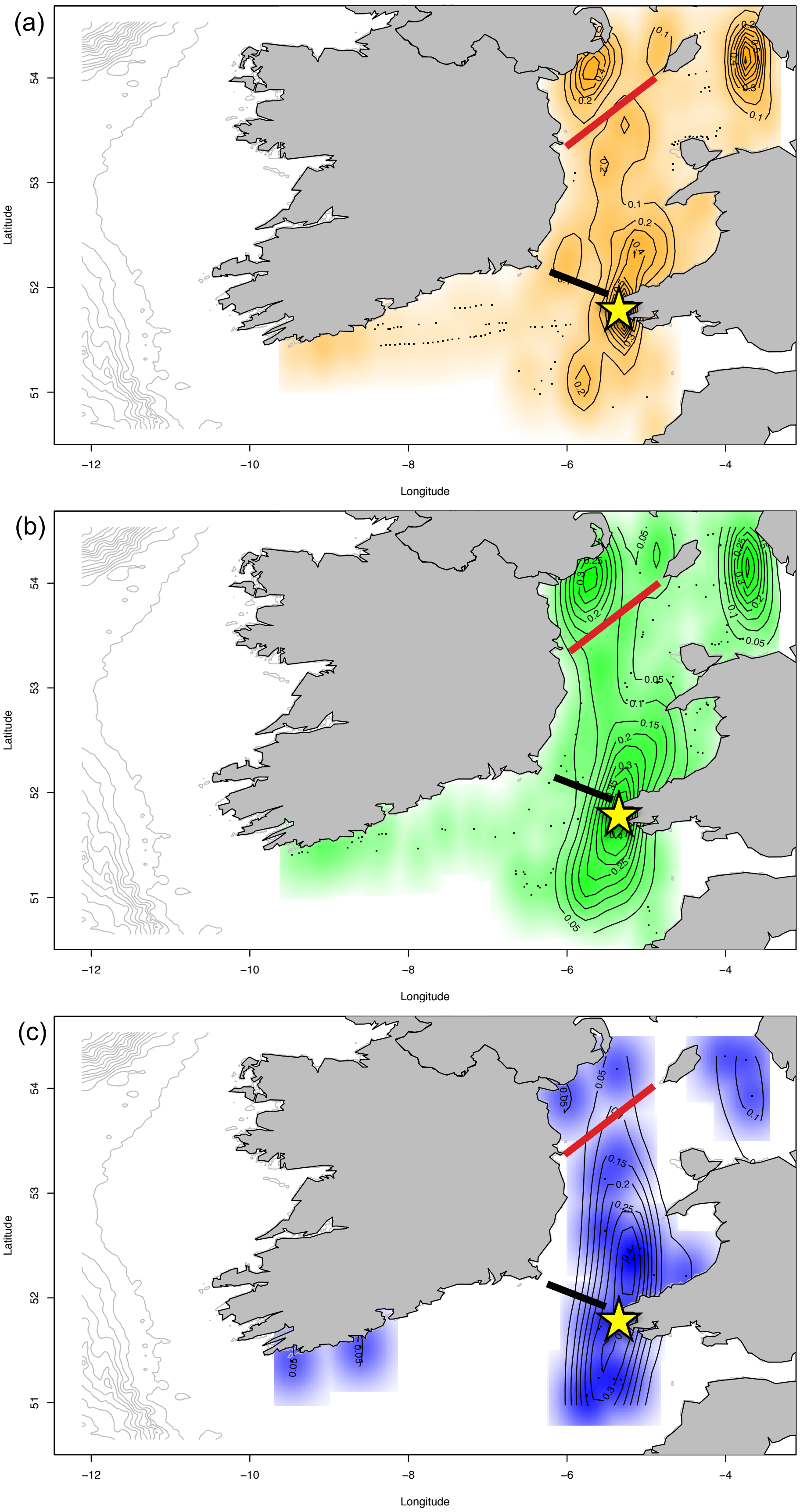


Figure 2. Distribution of provisioning rate (g per day) and frequency of dives (number per day). Each symbol indicates one trip. The dashed line is a trend line for S (short trip duration).

Figure 3 shows the contour maps of activity patterns in resting, flying, and foraging individuals. While both resting and flying behaviours were made at a wide range of locations (Fig 3a, b), foraging was more highly concentrated around the colony (Fig 3c). Distance (km) from dive locations (= foraging locations) to the colony showed a clear bimodal pattern (Fig 4a). In contrast, distance (km) from dive locations to front lines (as shown in Fig 3) showed a unimodal pattern (Fig 4b). The number of dives per trip increased slightly but significantly with trip duration (ΔAIC = - 13.37), while daily number of dives decreased with trip duration; shorter trips had higher number of dives per day (ΔAIC = - 5.70). The duration of foraging trips did not affect meal size per trip (ΔAIC = 1.68), but provisioning rate (g / day) decreased with trip duration. Daily chick growth rate (from hatching to the last meal) was 6.47 ± 5.22 g and the provisioning period was 63.67 ± 2.77 days (*n* = 15). The duration of the interval between subsequent feeds decreased after three days regardless of the starting condition, but at least half of these intervals were less than two days (Fig 5).

Figure 3. Contour plots of the kernel density distribution of divin and non-diving activity of chick-rearing Manx Shearwaters in 2013 during (a) rest (orange), (b) flying (green), (c) foraging (blue) are shown in black lines. Bathymetry lines are shown in light grey. Star indicates the position of Skomer Island. The approximate locations of the Irish Sea Front (red line) and Celtic Sea Front (black line) are shown on each map (Simpson and Hunter 1974).


(a)
(b)
(c)
Latitude
Longitude
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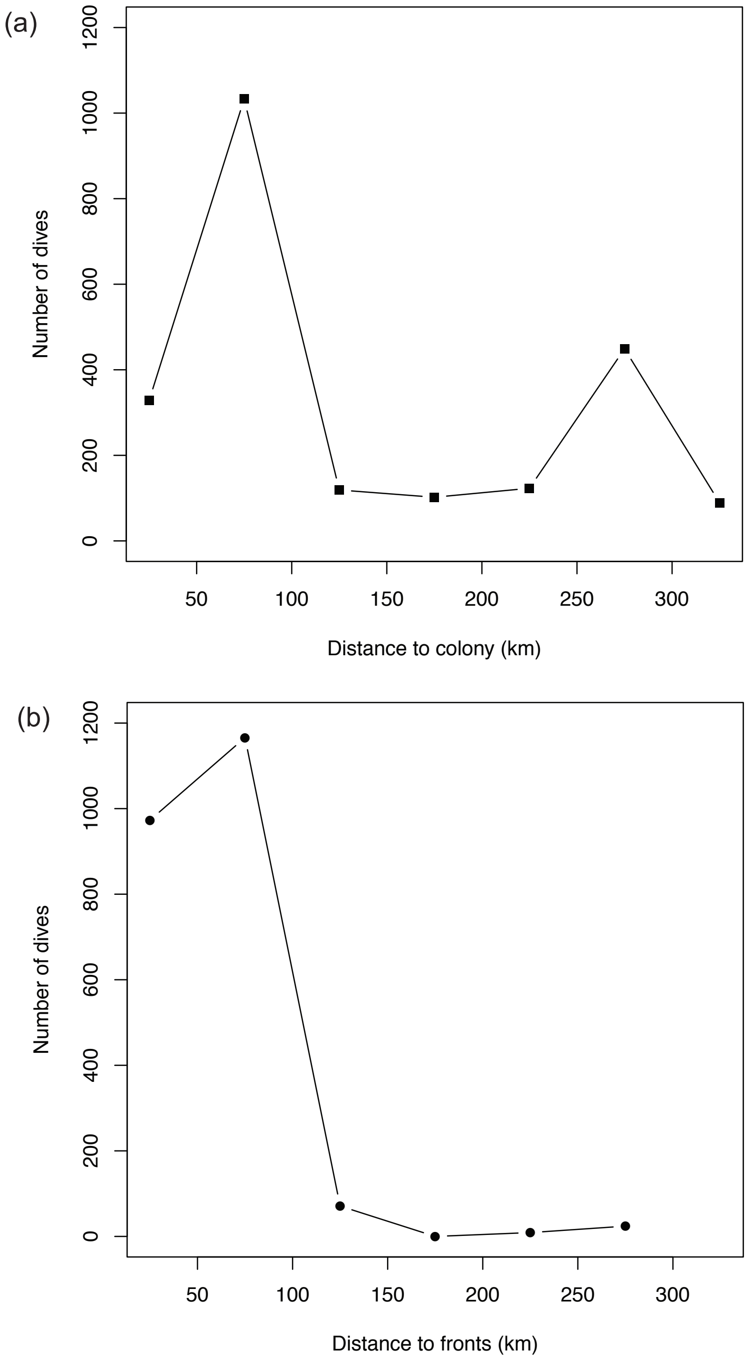

Figure 4. Distribution of the number of dives in relation to (a) the distance to fronts (km) at the dived locations and (b) the distance to colony (km) at the dived locations in Manx Shearwaters.

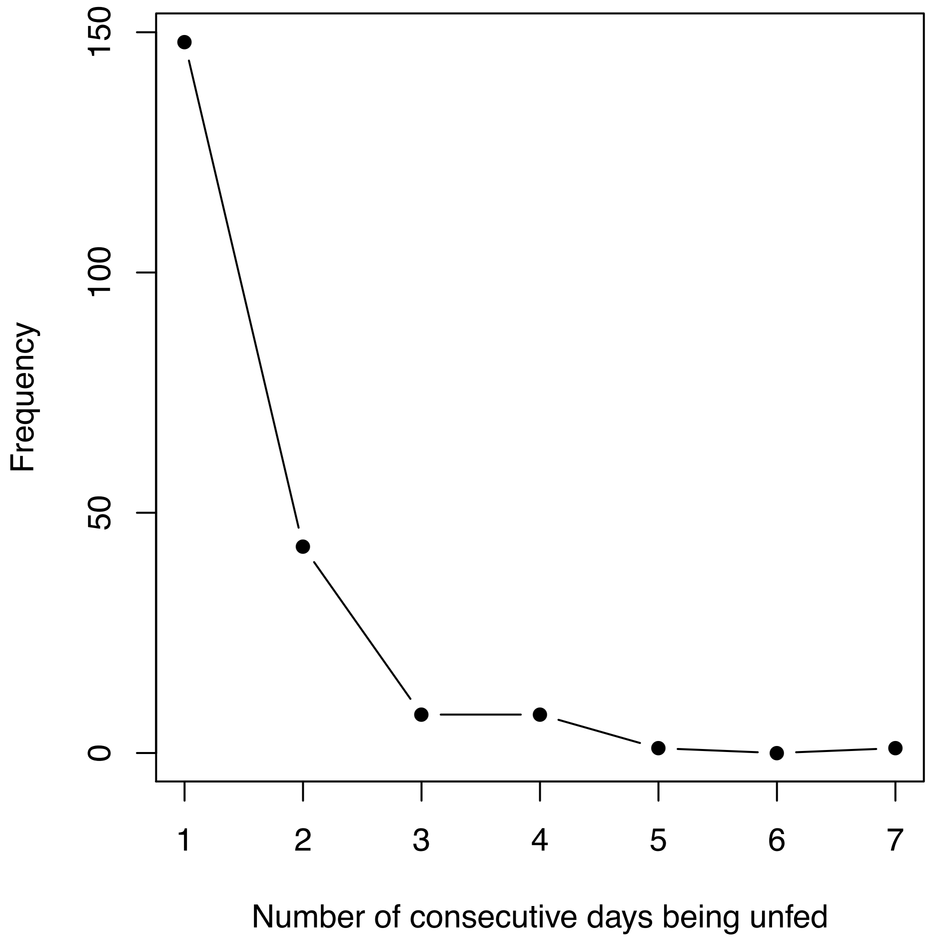

Figure 5. Frequency of the intervals between feeds to the chick (days).

Dual foraging modelling

In our data, Manx Shearwaters showed a tri-modal distribution of trip durations under visual inspection (Fig 1). To relate this foraging pattern to provisioning, we estimated daily energy gains for chicks ($EGFC_{day}$), which we plotted as a function of travel time in parallel with estimated IPQ. Our modelling results (Fig. 6) show that IPQ is indeed tri-modal as a function of travel time, as in Fig. 1, and that $EGFC_{day}$ is 50% of its maximum value only for short trips (< 10 hours; Fig. 6). Importantly, this result is robust to the choice of constants used in our modelling (Fig S2).

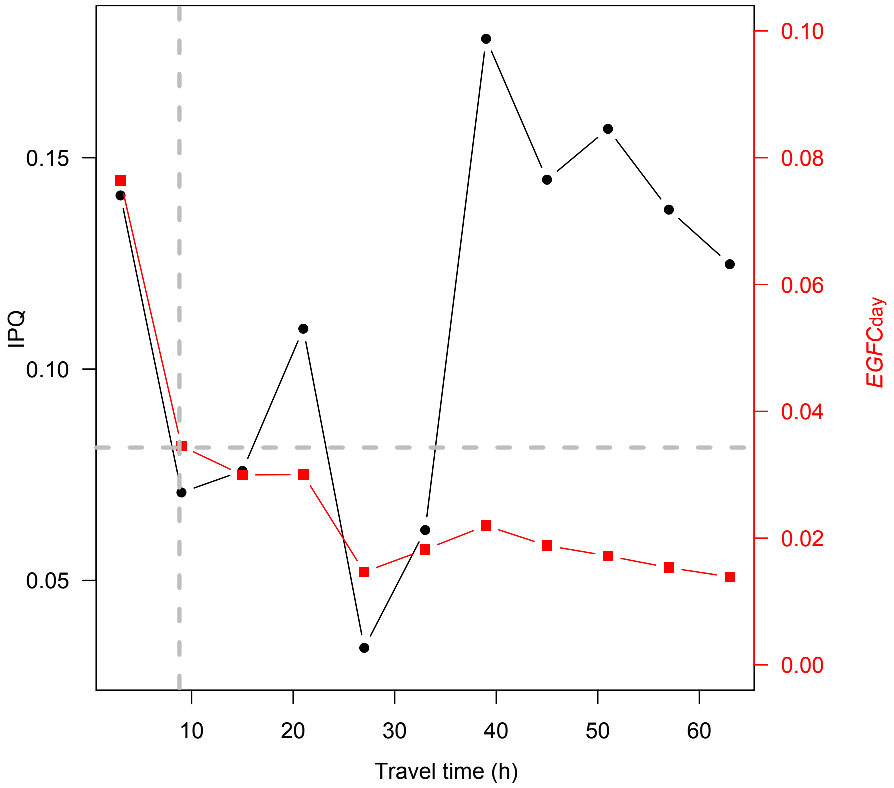

Figure 6. A model of dual foraging based on Index of Patch Quality (IPQ) in Manx Shearwaters. The black line indicates observed values of IPQ and the red line indicates the estimated daily energy gain for chicks ($EGFC_{\mathrm{day}}$), as a function of travel time (h). We assumed that birds had a constant flight speed and that (i) patch quality, measured on the IPQ scale, is gained during six hours of foraging; (ii) adults only bring back food when they have collected 25 points on the IPQ scale; the time required to accumulate these 25 points is denoted TPQ_{25}. Daily energy gains for chicks ($EGFC_{\mathrm{day}}$) is inversely proportional to the time to gain (TPQ_{25}). The horizontal grey line indicates the values of $EGFC_{\mathrm{day}}$ that were reduced to 50 % of the maximum value. The vertical grey line indicates where the $EGFC_{\mathrm{day}}$ crossed 50 % of the maximum value of $EGFC_{\mathrm{day}}$.

4. DISCUSSION

Central-place foraging theory predicts that animals should use distant foraging patches only when energy intake rate increases with distance from the colony (Charnov 1976; Ropert-Coudert et al. 2004). While variation in foraging trip duration is well known in pelagic seabirds, few studies have investigated its relationship with meal size to offspring in wild animals. Here, we show that Manx Shearwaters performed a dual foraging strategy in the sense that some trips (the short ones) were for chick provisioning while longer trips were for self-feeding (Fig 2). Shearwaters did not increase the meal size delivered to the chick with the travel time. Instead, young shearwaters gained more energy per time unit as adults brought more food back to the chick when they performed short trips. The average number of dives and meal mass delivered to chicks per day decreased with increasing trip length, so chicks did not benefit directly from longer trips. Foraging mode change-over was not initiated by parents reaching a critical lower body mass, but rather appeared to be coordinated, because chicks were constantly fed by parents (the interval between feeding was mostly one or two days) and chicks were rarely left unfed for more than three days (Fig 5). We speculate that such a dual foraging strategy is a consequence of a partner's long trip duration, suggesting that pair-coordination during chick-provisioning shapes foraging patterns, as is the case during incubation change-overs (Brooke 1990).

Some pelagic seabirds are known to employ a dual foraging strategy where parents alternate frequent short trips and a single long trip to meet the energetic demands of offspring while maintaining their own conditions (Granadeiro et al. 1998; Welcker et al. 2009). For example, Cory's Shearwaters use flexible foraging trip durations and parents increase body mass after long trips (Granadeiro et al. 1998). Here, shearwaters changed foraging areas between short and long trips, but in both cases, the foraging areas were highly restricted to an area close to the sea fronts (Fig 4). Thus, birds adjusted both trip duration and foraging locations in relation to the demands of their offspring or themselves. This raises the question as to why birds use two foraging patches instead of foraging only at a nearby patch, given that travel distance to those patches greatly differ. The area of the Irish Sea where shearwater parents performed long trips is known to be a “hot spot” for seabirds (Begg and Reid 1997), and lies to the north and west of the Irish Sea front (Pollock et al. 1997; Dean et al. 2012). Presumably, this region is highly productive and possibly better than the Celtic Sea. Indeed, IPQ is highest at the distant foraging area in this study. Thus, it is likely that birds increased travel distance to forage at this better foraging site during long trips. One potential explanation for a dual strategy is then that short trips lead to foraging near the colony, in areas highly exploited that lead to steady but average to low rewards; on the other hand, longer trips can be taken once chick provisioning is done to forage in farther areas, where fishing may become more unpredictable with distance but potentially of higher reward (Weimerskirch 2007).

In support of this explanation, our model illustrates that the net rate of gain per day decreases with distance and travel time for chicks, but increases for foraging parents themselves, suggesting an advantage of foraging near the colony for chick provisioning. However, we did not find that parents increased their body mass after long trips. Rather, the body mass was similar after both short and long trips. We do not have a definitive answer as to why parents did not increase their body mass if they performed long trips to maintain their own body condition.A possible explanation of this apparently contradictory result is that during long trips shearwaters foraged on better quality food (*e.g.* more oil), which would not have been immediately detectable using mass measurements alone (Einoder et al. 2013). Future studies could benefit from evaluating energetic content of prey throughout the chick-rearing period to examine whether variation in foraging strategies is associated with variation in prey quality.

5. ACKNOWLEDGEMENTS

We thank J. Roberts who dedicated time to the project during the 2013 field season. We also thank W. Whittington, J. Roden, N. Stevens, L. Yates and M. Mak, for assistance in the field, the Wildlife Trust of South and West Wales, the Countryside Council for Wales and B. Büche and E. Stubbings for logistic support. K.H. Elliott provided useful comments on the earlier version of the manuscript. Financial support came from Japan Student Services Organization (AS), the American Animal Behavior Society (AS), the University of Oxford Department of Zoology and Merton College (AS), the Natural Sciences and Engineering Research Council of Canada (SAB). All work was conducted after ethical approval by the Countryside Council for Wales, the Skomer Island Advisory Committee, and the British Trust for Ornithology (BTO permits: Guilford, 5311; Perrins, 660; Shoji, 5939).

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7. SUPPLEMENTARY MATERIALS

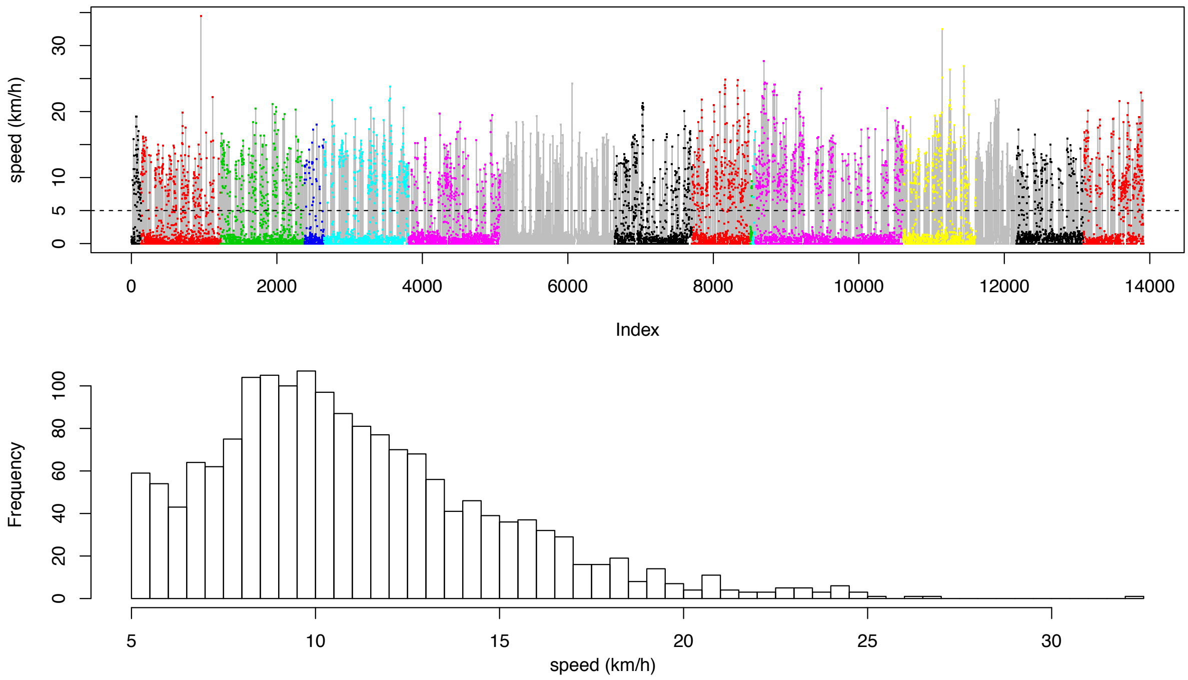

Figure S1. Manx Shearwater movement speeds. (A) Trace of speeds recorded by the GPS loggers. Individual birds are identified by alternating colours. (B) Distribution of horizontal surface speed during foraging trips of Razorbills on a log10 scale (*N* = 17 birds, *n* = 44 trips; only speeds exceeding 5 km/h are considered – see broken horizontal line in panel A). The black broken line in (A) indicates the cut-off value of 5 km/h used as a flight threshold in this study.

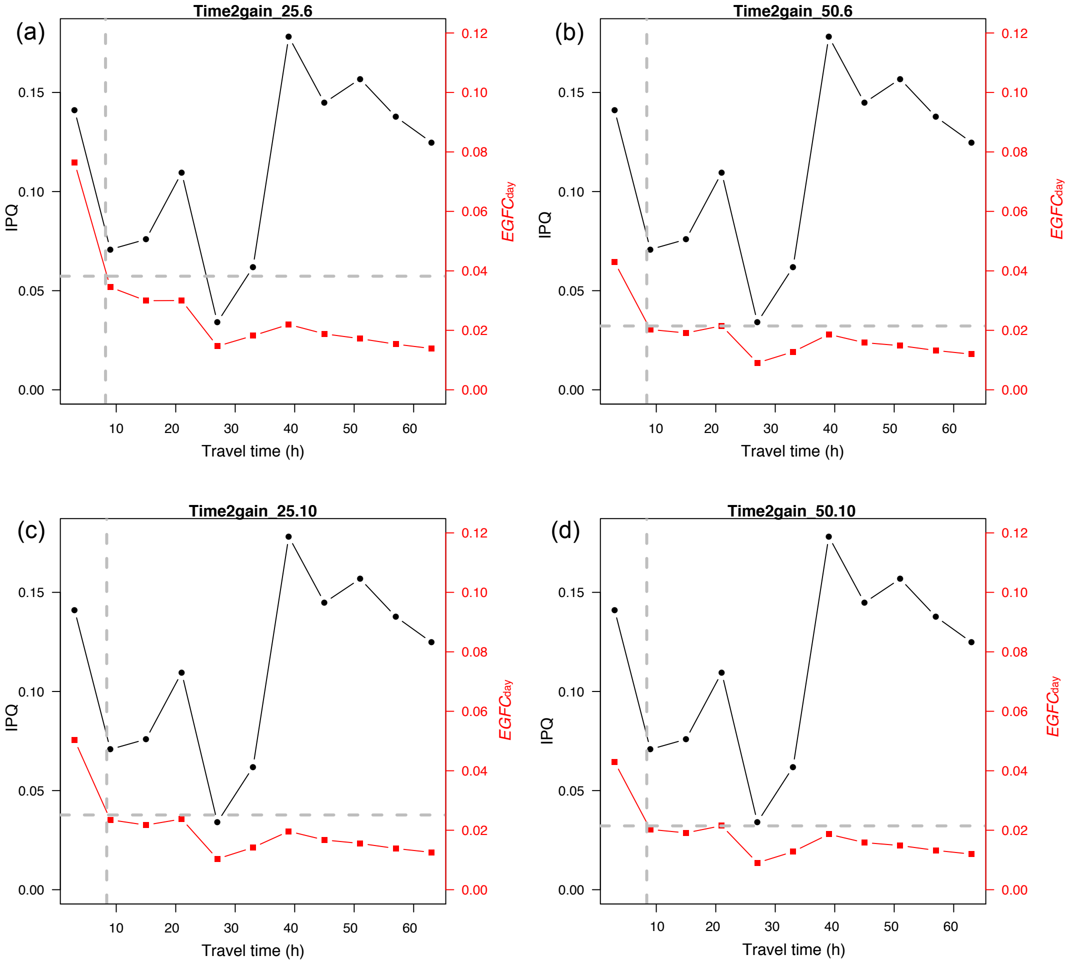

Figure S2. A model based on Index of Patch Quality (IPQ) for the dual foraging in Manx Shearwaters. Black lines indicate observed values of IPQ and red line indicates estimated daily energy gain for chicks ($EGFC_{day}$), as a function of travel time. We assumed that birds had a constant flight speed and that (i) patch quality, measured on the IPQ scale, is equivalent to six hours of foraging; (ii) adults only bring back food when they have collected 25 points on the IPQ scale; the time required to accumulate these 25 points is henceforth denoted TPQ_{25}. Daily energy gains for chicks ($EGFC_{day}$) is inversely proportional to the time to gain (TPQ_{25}) (a). As the choice of constant is arbitrary, we presented our choice for the time to gain of 25 points as well as 50 points. Similarly, we presented that patch quality, measured on the IPQ scale, is equivalent to six hours of foraging as well as ten hours of foraging: (a) TPQ_{25} with six hours of foraging; (b) TPQ_{50} with six hours of foraging; (c) TPQ_{25} with ten hours of foraging; (d) TPQ_{50} with ten hours of foraging. Horizontal grey lines indicate the values of $EGFC_{day}$ that were reduced to 50 % of the maximum values. Vertical lines indicate that where the 50 % of the maximum value of $EGFC_{day}$ crossed the lines of $EGFC_{day.}$ (a). As the choice of constant is arbitrary, we presented our choice for the time to gain 25 points as well as 50 points. Similarly, we presented that patch quality, measured on the IPQ scale, is equivalent to six hours of foraging as well as ten hours of foraging: (a) TPQ_{25} with six hours of foraging; (b) TPQ_{50} with six hours of foraging; (c) TPQ_{25} with ten hours of foraging; (d) TPQ_{50} with ten hours of foraging. Horizontal gray lines indicate the values of $EGFC_{day}$ that were reduced to 50 % of the maximum values. Vertical lines indicate that where the 50 % of the maximum value of $EGFC_{day}$ crossed the lines of $EGFC_{day.}$

Chapter 7

Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird

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Currently in Revision.

ABSTRACT

Conventional life-history theory suggests that intra-specific variations in reproductive performance are generally due to individual quality or age/experience. However, how the timing of inter-seasonal events, and patterns of non-breeding season behaviour, affect reproductive performance in wild animals is poorly known. Here, we examine these issues in a long-lived migratory seabird, the Manx shearwater (*Puffinus puffinus*). Individual breeding performance can be predicted from the previous breeding season phenology (measured directly), and is linked to clear differences in over-winter behaviour patterns (flying, resting, foraging, inferred ethoinformatically from on-board telemetry data). Furthermore, parental investment in one year influences breeding success the next, a carry-over effect reflecting the trade-off between current and future reproductive success. These findings demonstrate that carry-over effects from one breeding season affect activity in the following non-breeding period which in turn shapes the reproductive decisions in the next breeding season.

Key words: phenology, migration, machine-learning, adaptive boosting, data de-noising, multi-event capture-mark-recapture model

1. INTRODUCTION

Individual variation in both quality and reproductive performance (RP) offer critical insights into evolutionary ecology. While conventional theories in vertebrates suggest that such variation is mostly due to age or experience, recent work suggests that some individuals perform better regardless of their age (*e.g*. Hamel et al. 2009). In particular, carry-over effects (where events in one season affect performance in the next) have been recognised to play a critical role in influencing individual RP (Harrison et al. 2011), but these can be especially hard to observe at the individual level in highly mobile species such as seasonal migrants. Previous studies on the determinants of RP focused either on the timing (*i.e*. phenology) of events such as winter migration (Catry et al. 2013), or on diet (Sorensen et al. 2010) and hormone levels (Sanderson et al. 2014) during the non-breeding period (*e.g*. Inger et al. 2010; Eikenaar and Schlaefke 2013). However, how the interaction between phenology and wintering behaviour affects RP has, to our knowledge, never been explored.

To assess the outcome of this interaction in a wild animal, we combined direct breeding season observations of RP with an ethoinformatics approach (Freeman et al. 2013) to year round daily activity data monitoring from on-board data loggers carried by adult Manx Shearwaters (*Puffinus puffinus*), small pelagic long-distance migrants, between 2009 and 2014. We show how both the timing of events in the annual cycle and winter at-sea behaviour help to predict RP.

2. MATERIAL AND METHODS

The study was conducted on birds breeding on Skomer Island, UK (51°44’N, 5°17’W), which hosts the world’s largest Manx Shearwater colony (Perrins et al.

2012) between 2009 and 2014. During this six-year period, study burrows were visited daily during the breeding season to monitor both breeding progress and success. Geolocators (British Antarctic Survey; Biotrack Ltd: 20 × 9 × 5.5 mm; mass 1.5-2.4 g, approximately 0.3% of mean 450g body mass), with saltwater-immersion logging capability, were deployed on and recovered from adult Manx Shearwaters resulting in five consecutive periods of recorded migratory behaviour (2009-10, 2010-11, 2011-12, 2012-13 and 2013-14). Geolocators were attached to custom-made darvic leg-rings (Freeman et al. 2013). Only experienced breeders (those that had raised a young prior to the first observation period) were included (Table S1).

The non-breeding at-sea activity and phenology were analysed from the date of departure from the colony at the end of the breeding season to the date of return at the start of the next breeding season. Behaviours and their phenology during migration and winter were determined in two ways. First, saltwater-immersion data were used to quantify the proportion of time spent in flight ([immersion] = 0 AU or arbitrary units for 10 min) during daytime, to determine when individual flying activity increased or decreased over the course of each winter. Breakpoints were found by performing piecewise linear regressions for proportion of flight time *vs*. date; breakpoints (number and positions) were determined by the bootstrap restarting algorithm implemented in the segmented R library (Muggeo 2003). Second, inferred flight phenologies were then validated against arrival and departure dates based on geolocator-recorded light intensity data. Similar analyses were performed for resting behaviour ([immersion] = 200 AU for 10 min) and putative foraging-related activity (intermediate immersion values) (McKnight et al. 2013) – for each bird for each year. Breeding events were recorded directly at each nest.

To examine the predictive power of phenology on individual RP, we employed a supervised machine-learning algorithm based on adaptive boosting (Freund and Schapire 1996). The classifier was trained on a set of features to predict individual RP as one of these three categories: “CHICK” (egg hatched), “EGG” (egg failed) or “SKIP” (no egg was found). Nine features were included; we considered both prior- and post-breeding phenology (laying, hatching and fledging dates), as well as migratory phenology as extracted above (dates of colony departure, arrival at wintering grounds, departure from wintering grounds and colony arrival). The SAMME algorithm (Zhu et al. 2009) was used as prediction on > 2 (3 here) categories. The classifier’s accuracy was determined by a 10-fold cross-validation, where the algorithm is trained on nine tenths of the data, the last decile being used to compute a confusion matrix and the procedure repeated for all ten subsets. This process was repeated 1,000 times to assess the sampling distribution of classification accuracy.

To understand how wintering behaviour affects RP, we analysed behavioural patterns based on saltwater-immersion data. Because these data show high-frequency variability, a de-noising procedure was first used to extract nonlinear trends without any reference to breakpoints identified above. To this effect, a time-series additive decomposition was performed to extract nonlinear trends for each track. Cumulative distributions of de-noised data were then extracted and averaged for “CHICK”, “EGG” or “SKIP”. The Kolmogorov-Smirnoff test was used to assess significance. Year-to-year reproductive data can also be summarised as a transition matrix giving the frequencies of RP state changes from one year to the next. To this effect, sample size was expanded also to include an additional 88 individuals (47 males, 41 females) whose breeding progress and breeding performance were monitored, but which had not been tracked with Geolocators. Multi-event capture-mark-recapture (MECMR) models (Pradel 2005) were used to estimate transitions rates among “SKIP”, “CHICK”, “EGG” and “DEAD” (= not recaptured). Survival rates were either constant or varying as a function of state and/or time; the best transition rate model was identified using Akaike Information Criterion with small sample correction (details in ESM).

3. RESULTS

Geolocator data were successfully retrieved for a total of 111 bird-seasons (over two successive seasons between 2009-2014): 97 from birds which raised a chick, 11 that failed during incubation and 3 that failed to lay in the season preceding the tracked non-breeding period. Breeding success of study birds (0.72 ± 0.09 SD) was similar to that in an adjacent unmanipulated plot (0.63 ± 0.07 SD; Büche et al. 2013).

(a) Adaptive boosting extracts RP information from wintering phenology

With the classifier trained on the whole data set, we found that hatching and laying dates in the previous year were the two most important features used for classification, explaining ~40% of the information extracted (Fig 1). The 10-fold cross-validation error rate stood at 37.84% (Table S2), which is (i) smaller than expected by chance, indicating our model had predictive power ($P < 0.0001$; Fig S1) and (ii) shows that all three prior events, hatch date, lay date, and fledge date in this order, are the most important and reliable predictors of RP (Fig 1).

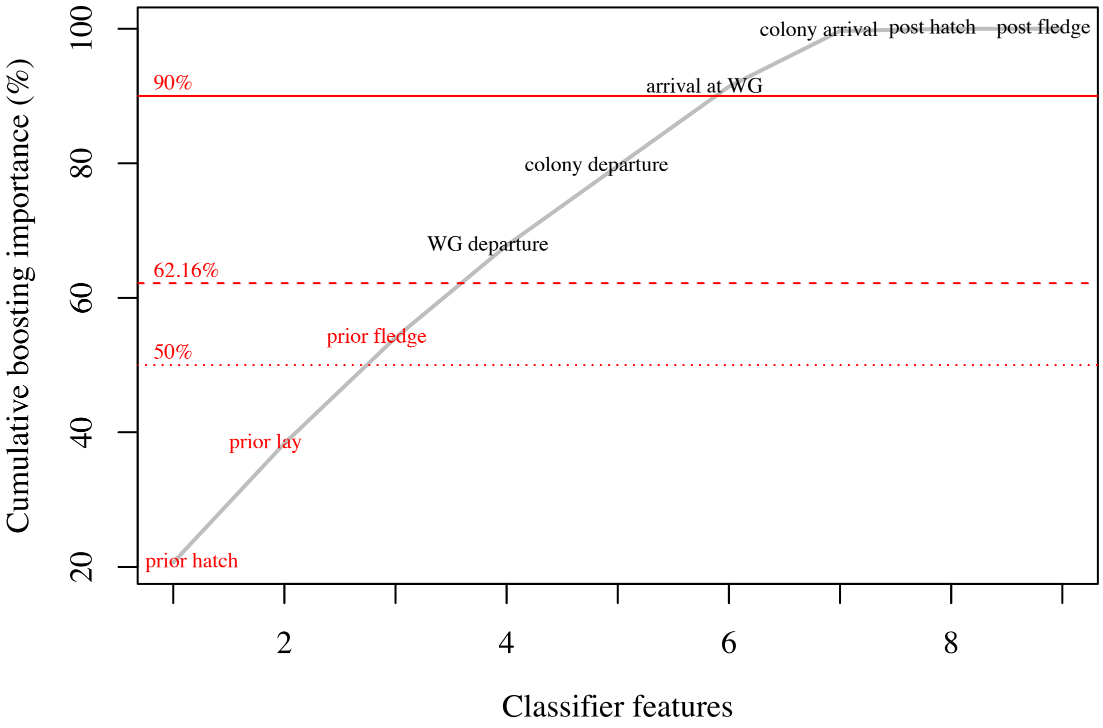

Figure 1. Ranking of classifier features according to their cumulative importance. The SAMME algorithm gave most importance to prior events, labelled in red. The ten-fold cross-validation success rate of the classifier is at 62.16%; all features above this value, labelled in black, have negligible predictive power with respect to RP.

(b) Winter behaviour *vs*. breeding performances

Individual saltwater-immersion data showed some trends, among high-frequency variation (Fig S2). Our de-noising procedure (Fig S3) revealed an activity-based segregation between breeders and non-breeders (Fig S4). This pattern was confirmed by extracting the corresponding empirical cumulative distribution by activity according to RP (Fig 2). All comparisons proved significant at the 1% level, even after applying the conservative Bonferroni correction. Birds that skipped breeding in any given season (a minority) had a previous winter that was marked by more flying (Fig 2a), less resting (Fig 2b) and much more foraging (Fig 2c) than birds that invested in reproductive behaviour. On the other hand, those who hatched a chick had had a winter essentially marked by low foraging (Fig 2c). No sex effects were detected ($P > 0.01$).

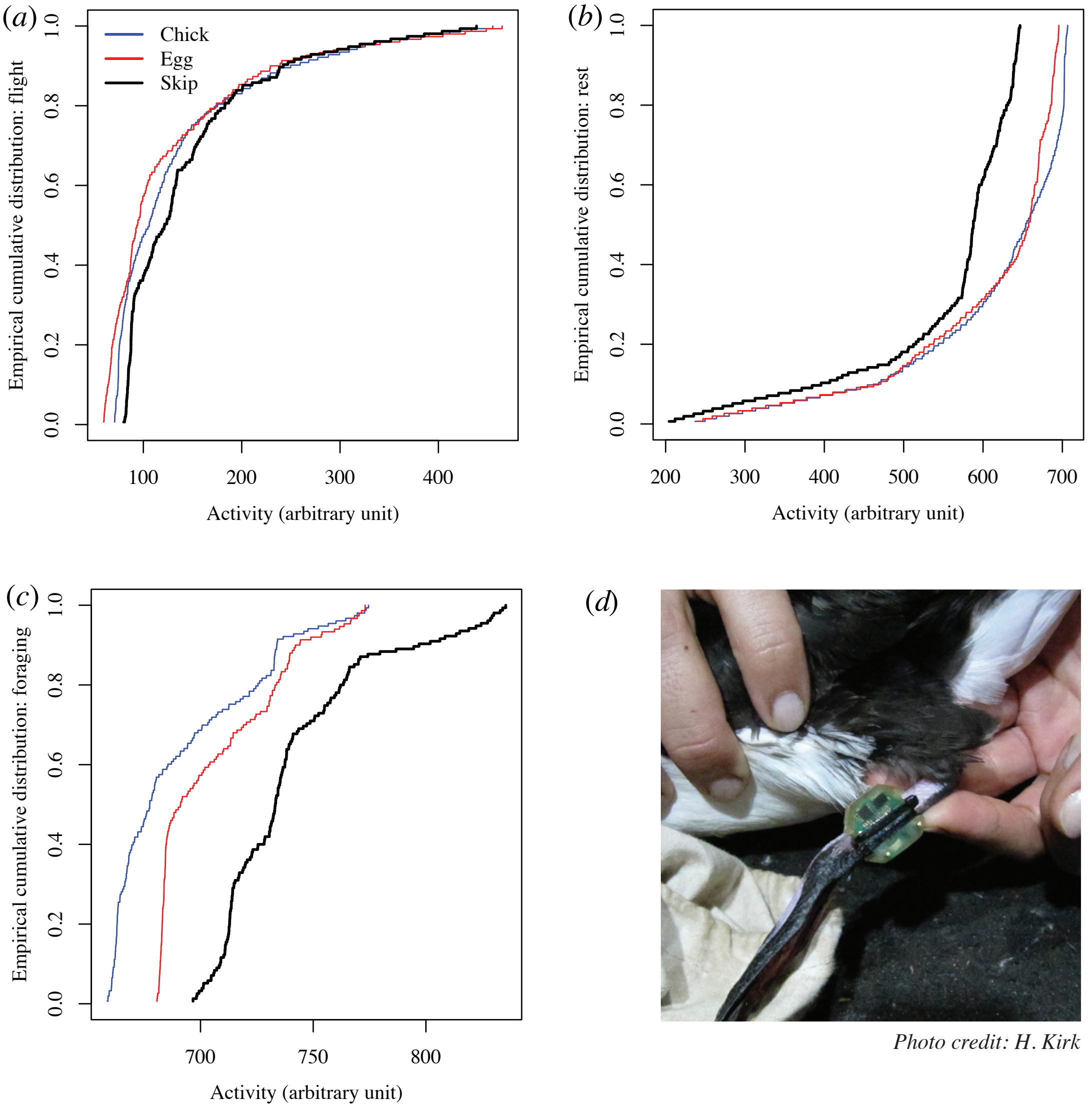

Photo credit: H. Kirk

Figure 2. Activity-based segregation between three RP categories represented in blue (birds with a chick), red (egg failed) and black (skipped breeding). Empirical cumulative distributions of mean activity patterns are represented for (*a*) flying, (*b*) resting and (*c*) foraging times, (*d*) a picture of a Manx Shearwater with a geolocator on its leg.

(c) Long-term reproductive strategy and carry-over effects

Year-to-year reproductive results summarised as a transition matrix giving the frequencies of RP state changes from one year to the next show that birds that skipped breeding were less likely to fail or skip in the following year (Table S3).

For both sexes, there was strong support for models in which transition rates were state-dependent, indicating that current breeding states influence the subsequent states (Table S5-S6). For the probability of being a successful breeder, skipped birds had the highest chance (0.79, lower CI: 0.36: upper CI: 0.96) followed by failed birds (0.61, lower CI: 0.33: upper CI: 0.83), with successful birds the lowest (0.57, lower CI: 0.45: upper CI: 0.69: Table S7-S8).

4. DISCUSSION

We used data from year-round on-board activity loggers (6 years, >100 individuals) to monitor remotely behaviour patterns at sea, and the timing of individual breeding and migratory events, in a long lived migratory seabird, the Manx Shearwater. We confirm empirically the existence of chained relationships between the seasons, with compelling evidence for links between previous breeding phenology, winter at-sea behaviour, and subsequent breeding performance.

First, we find that shearwaters occasionally skip breeding, and that when they do they go on to have a significantly better RP in the following season. This shows that release from the cost of breeding in one season carries over into enhanced future success. Over two consecutive years however, successful breeders had a higher RP than skipped birds, so that the result of winners for long-term is depending on the long-term frequency of the two-states. Second, birds that skip breeding show predictably higher activity (most probably higher foraging effort) in the previous winter (see also (Kazama et al. 2013)), which suggests that they are attempting to compensate either for the own poor condition or poor foraging conditions encountered in winter. In either case, whatever causes increased over-winter activity carries over into an effect on breeding success in the following season. Timing differences in breeding one year are also significantly related to RP in the next, with earlier egg laying, chick hatching, and fledging, all predicting greater RP in the following season as early birds do always better as shown in (Brooke 1990).

Our MECMR models provide strong support that not only the current breeding state affects the subsequent breeding states, but also the amount of current investment negatively and significantly affects subsequent breeding states. This carry-over effect reflects the apparent trade-off between current and future success as predicted by life-history theory (Williams 1966).

5. ACKNOWLEDGEMENTS

We thank: all volunteers who provided us with excellent help at Skomer; B. Dean, P. Collins, J. Roberts; the Skomer wardens, C. Taylor, B. Büche, E. Stubbings; and B. Sheldon for sharing insightful comments. All procedures were approved by the Skomer and Skokholm Islands Advisory Committee, BTO and CCW.

Funding statement

AS received financial support through JASSO, Merton College and the Department of Zoology at Oxford University. SAB was supported by NSERC. The Wildlife Trust of South and West Wales provided generous in-kind support.

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7. SUPPLEMENTARY MATERIALS

Table S1. Number of individuals tracked. A total of 108 birds were tracked between 2009 and 2014; three of them were tracked for > 1 season, which is why 111 bird-seasons were observed.

Migration year	Number of individuals
2009-2010	14
2010-2011	23
2011-2012	12
2012-2013	24
2013-2014	38

Table S2. Confusion matrix demonstrating the performance of the adaptive boosting algorithm. Results are based on a ten-fold cross-validation experiment. CHICK indicates individuals that successfully had a chick, EGG indicates individuals that failed breeding during incubation and SKIP indicates individuals that skipped breeding.

		Observed		
		CHICK	EGG	SKIP
Predicted	CHICK	56	15	16
	EGG	6	13	2
	SKIP	2	1	0

Table S3. Observed transition matrix in RP on the extended sample for (a) female and (b) male.

(a) Female

		Year y + 1 →			
		CHICK	EGG	SKIP	DEAD
Year y →	CHICK	39	14	8	18
	EGG	8	1	2	3
	SKIP	3	0	0	3
	DEAD	-	-	-	-

(b) Male

		Year y + 1 →			
		CHICK	EGG	SKIP	DEAD
Year y →	CHICK	39	16	6	19
	EGG	8	1	1	6
	SKIP	3	1	0	3
	DEAD	-	-	-	-

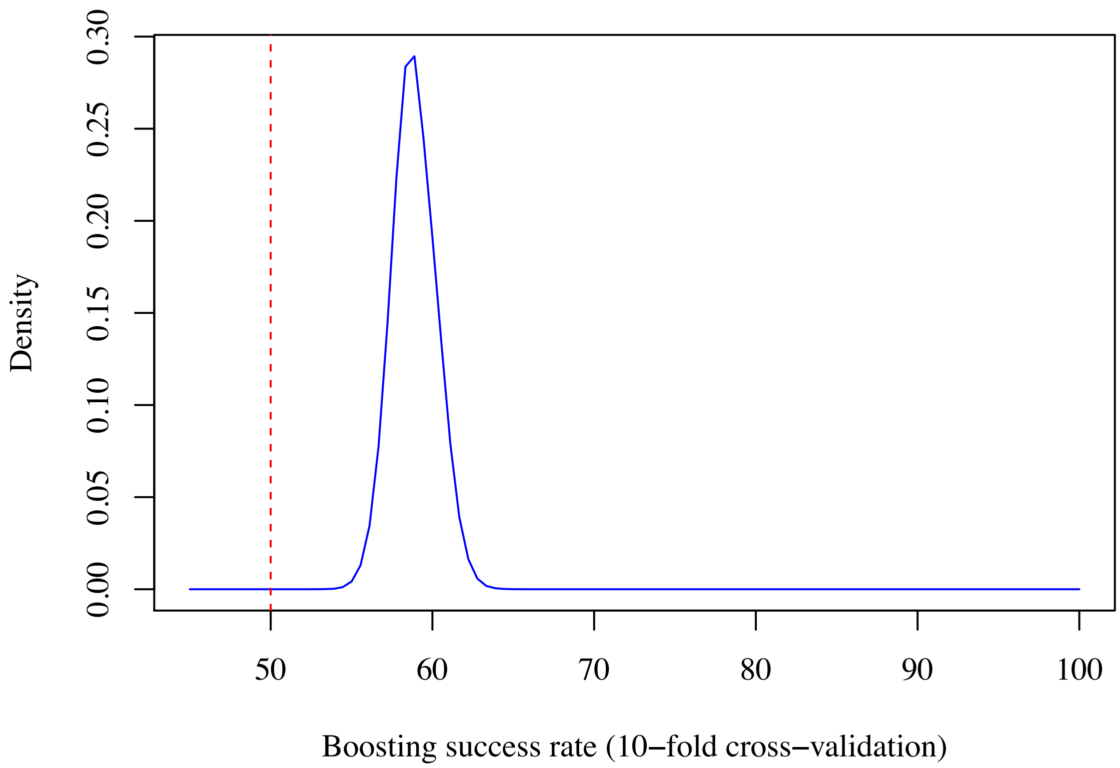
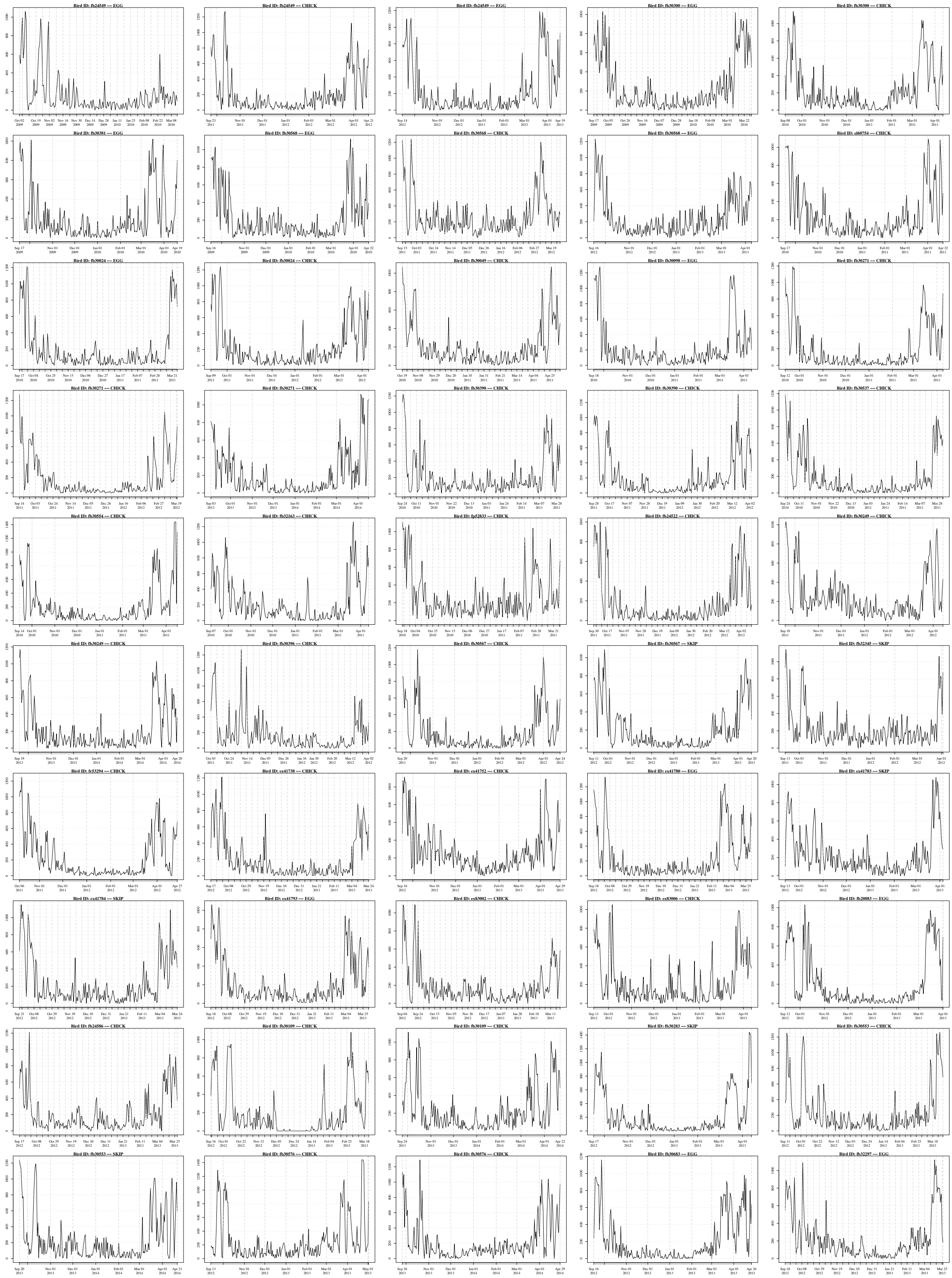


Figure S1. Sampling distribution of the success rate of the SAMME classifier assessed by ten-fold cross-validation. This distribution was obtained by running the cross-validation 1,000 times.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Bird ID: fb30300 --- CHICK
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Bird ID: fb30568 --- EGG
Bird ID: fb30568 --- CHICK
Bird ID: fb30568 --- EGG
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Bird ID: fb30024 --- EGG
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Bird ID: fb32163 --- CHICK
Bird ID: fp52833 --- CHICK
Bird ID: fb24522 --- CHICK
Bird ID: fb30249 --- CHICK
Bird ID: fb30249 --- CHICK
Bird ID: fb30396 --- CHICK
Bird ID: fb30567 --- CHICK
Bird ID: fb30567 --- SKIP
Bird ID: fb32345 --- SKIP
Bird ID: fr53294 --- CHICK
Bird ID: ex41738 --- CHICK
Bird ID: ex41752 --- CHICK
Bird ID: ex41780 --- EGG
Bird ID: ex41783 --- SKIP
Bird ID: ex41784 --- SKIP
Bird ID: ex41793 --- EGG
Bird ID: ex83002 --- CHICK
Bird ID: ex83006 --- CHICK
Bird ID: fb20883 --- EGG
Bird ID: fb24586 --- CHICK
Bird ID: fb30109 --- CHICK
Bird ID: fb30109 --- CHICK
Bird ID: fb30283 --- SKIP
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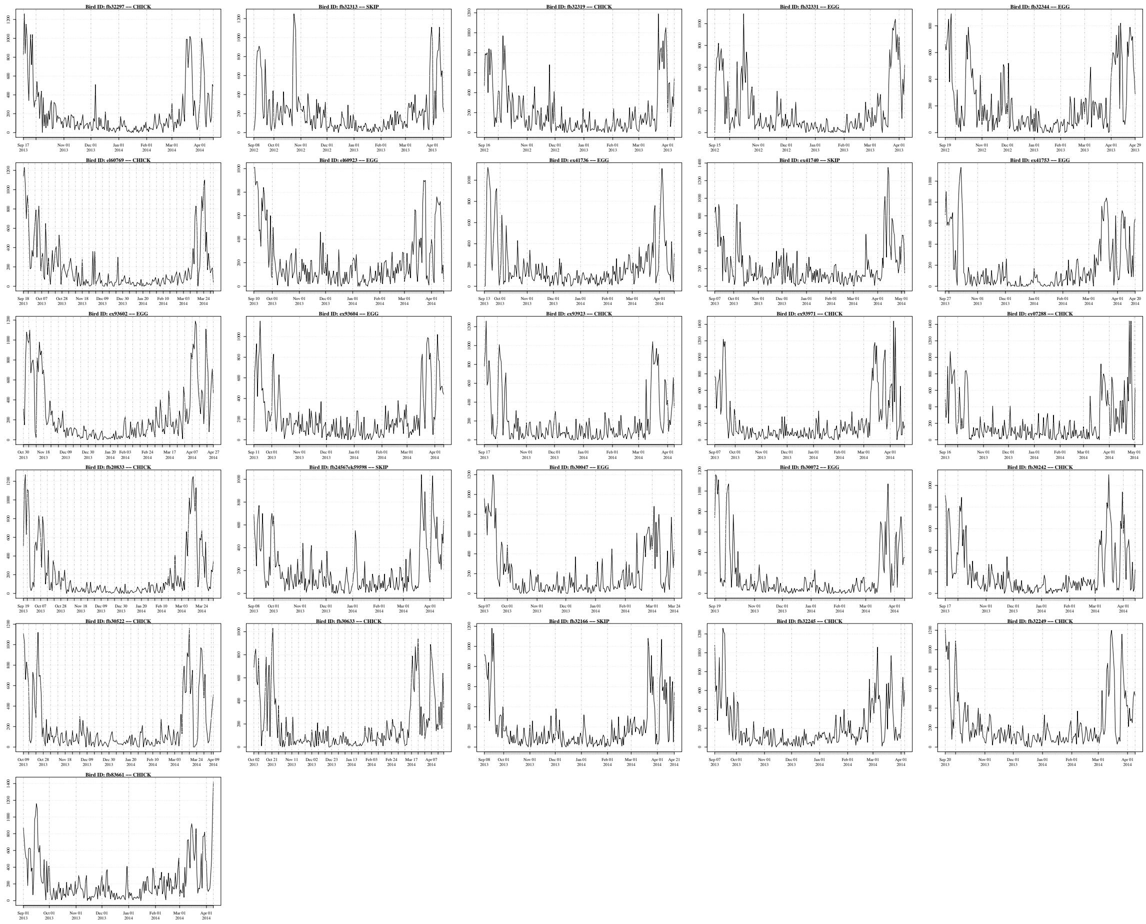
Bird ID: fb32297 --- EGG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Bird ID: ex41736 — EGG
Bird ID: ex41740 — SKIP
Bird ID: ex41753 — EGG
Bird ID: ex93602 — EGG
Bird ID: ex93604 — EGG
Bird ID: ex93923 — CHICK
Bird ID: ex93971 — CHICK
Bird ID: ey07288 — CHICK
Bird ID: fb20833 — CHICK
Bird ID: fb24567ek59598 — SKIP
Bird ID: fb30047 — EGG
Bird ID: fb30072 — EGG
Bird ID: fb30242 — CHICK
Bird ID: fb30522 — CHICK
Bird ID: fb30633 — CHICK
Bird ID: fb32166 — SKIP
Bird ID: fb32245 — CHICK
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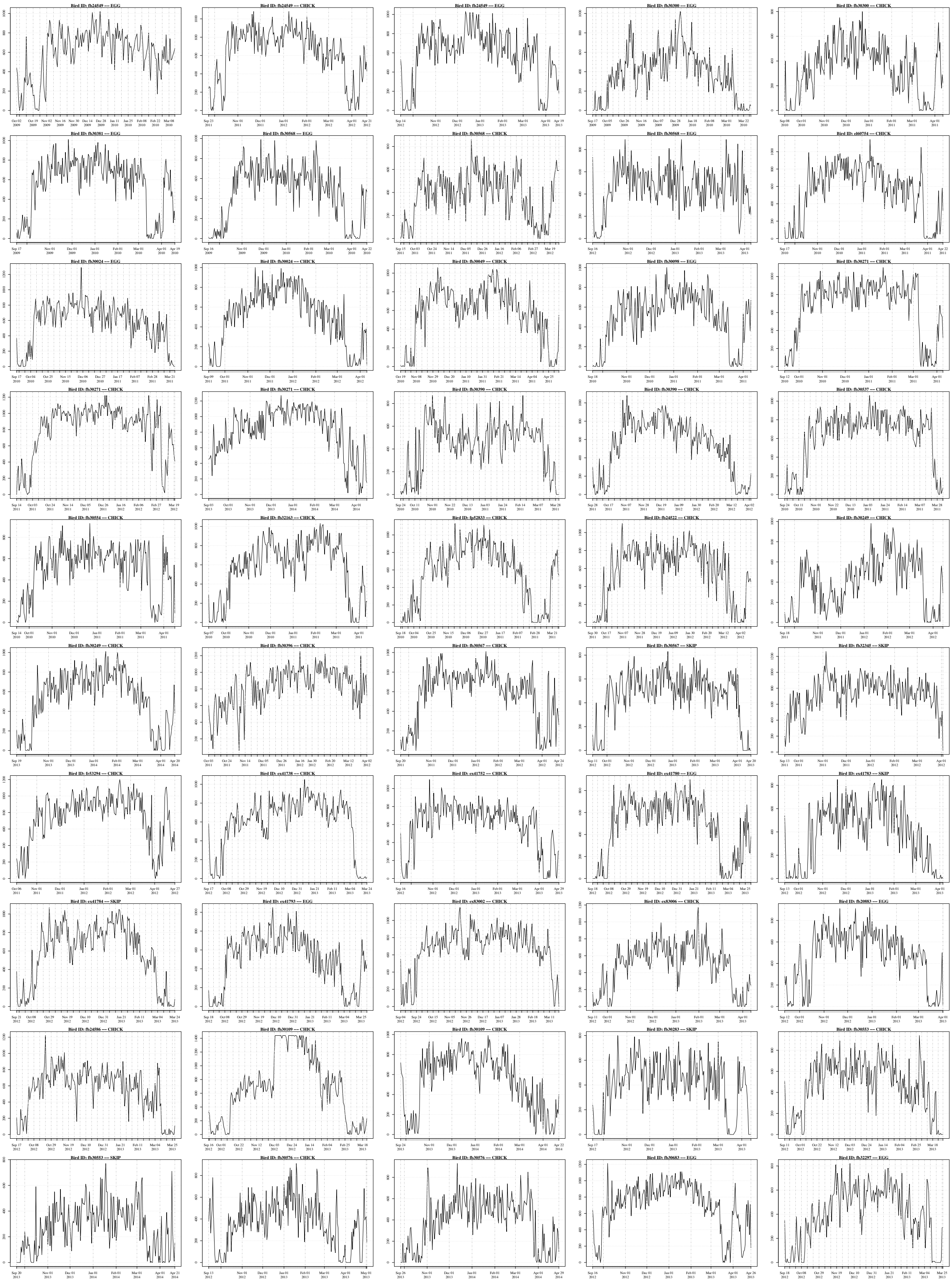
Bird ID: fb83661 — CHICK

Figure S2a. Flight patterns extracted from salt-immersion data for each bird. Level of activity is represented as a function of time. Individual RP is indicated.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Bird ID: el60754 — CHICK
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Bird ID: fb30567 — CHICK
Bird ID: fb30567 — SKIP
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Bird ID: ex41752 — CHICK
Bird ID: ex41780 — EGG
Bird ID: ex41783 — SKIP
Bird ID: ex41784 — SKIP
Bird ID: ex41793 — EGG
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Bird ID: fb30109 — CHICK
Bird ID: fb30109 — CHICK
Bird ID: fb30283 — SKIP
Bird ID: fb30553 — CHICK
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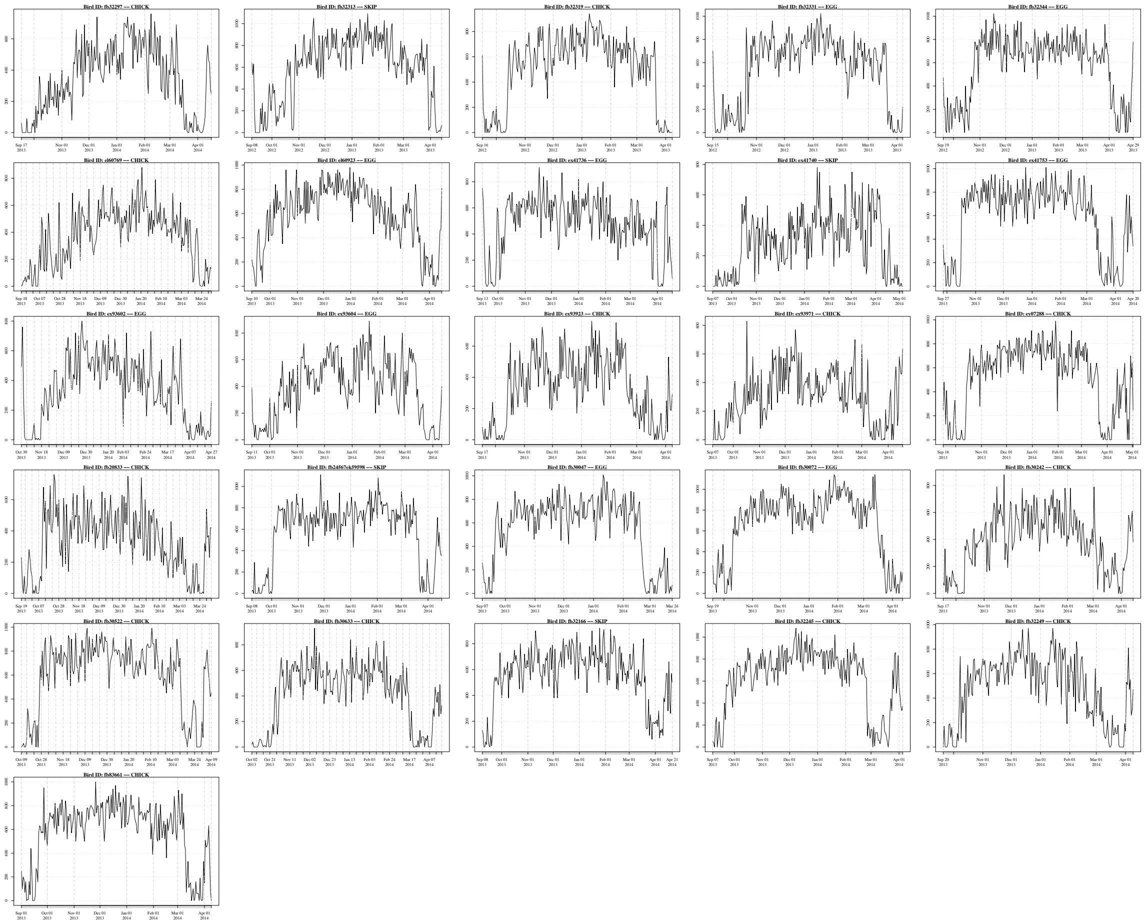
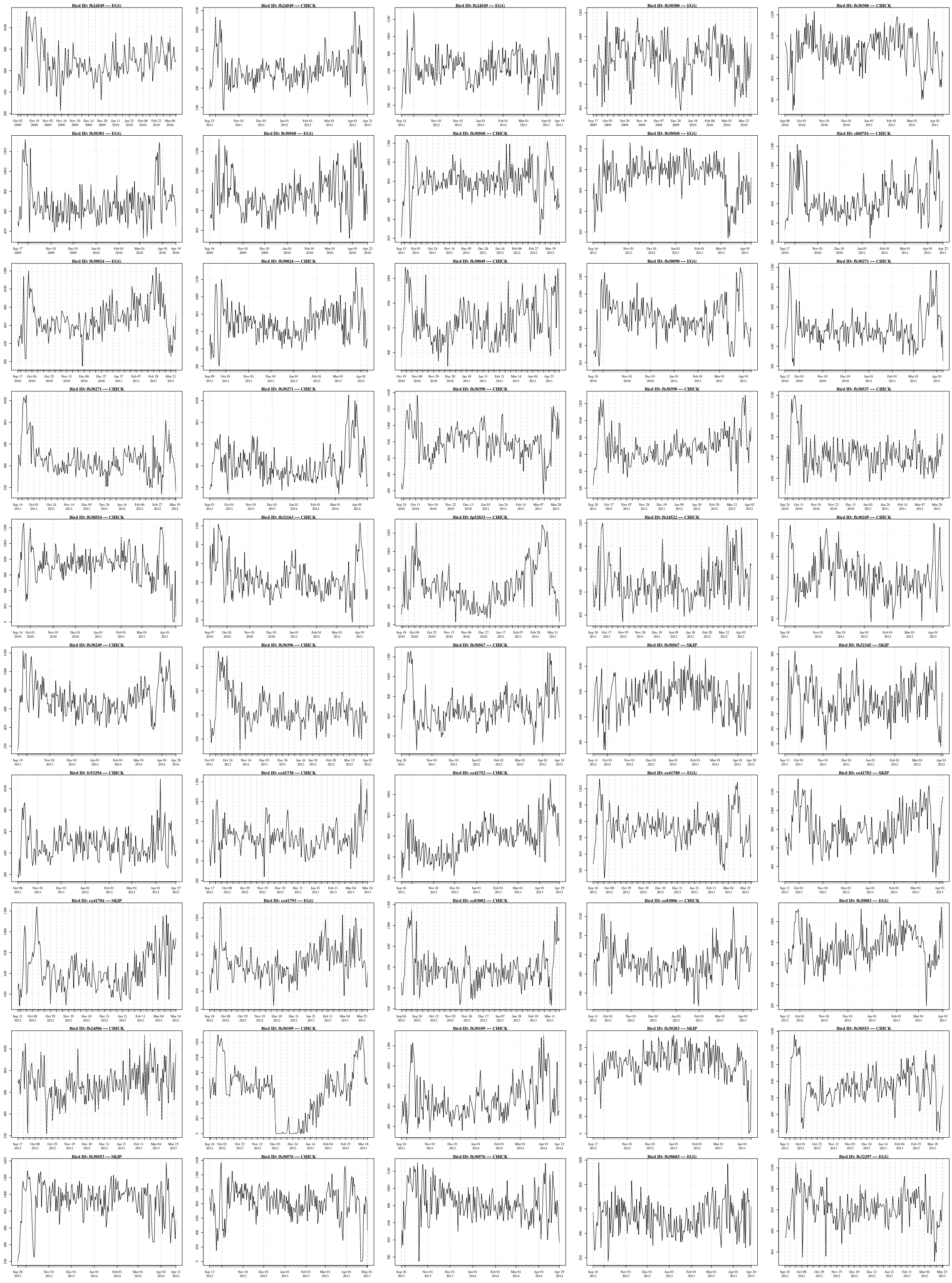


Figure S2b. Resting patterns extracted from salt-immersion data for each bird. Level of activity is represented as a function of time. Individual RP is indicated.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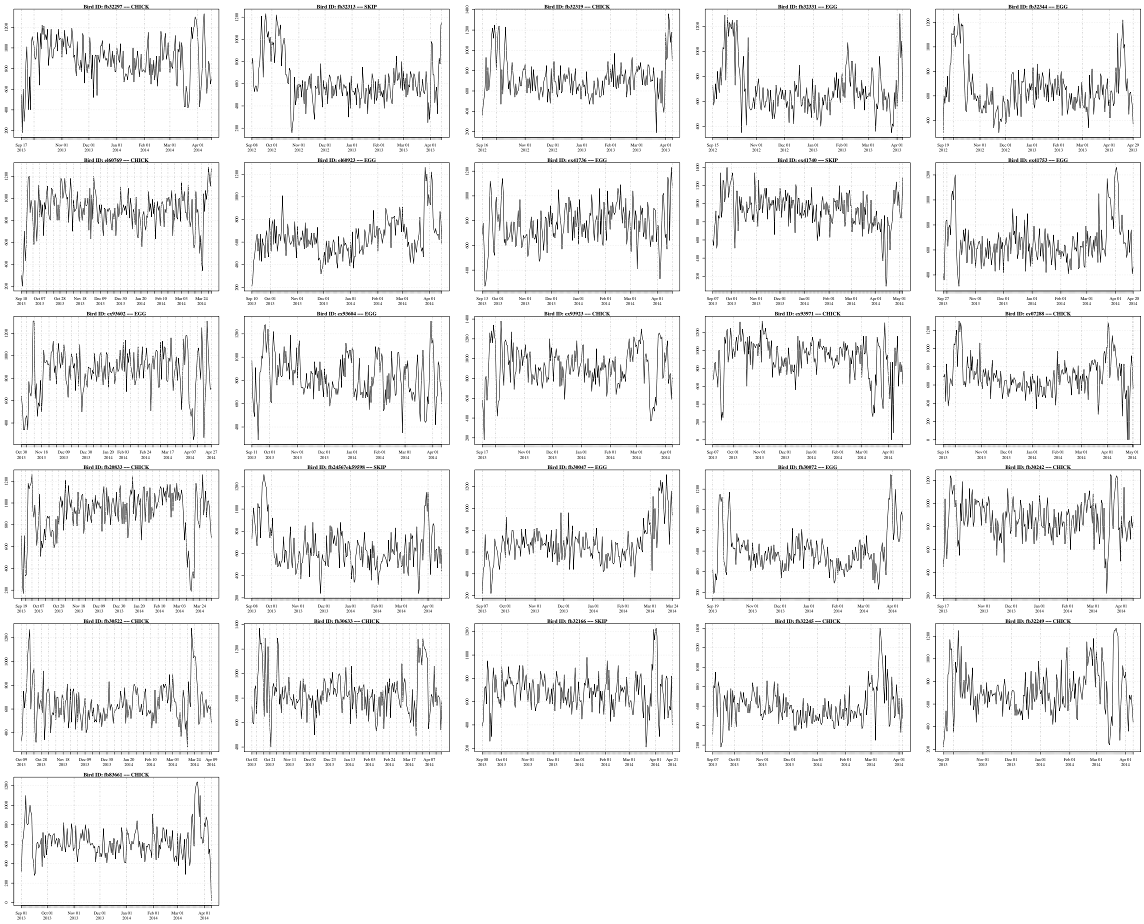

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Bird ID: fb30633 — CHICK
Bird ID: fb32166 — SKIP
Bird ID: fb32245 — CHICK
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Bird ID: fb83661 — CHICK

Figure S2c. Foraging patterns extracted from salt-immersion data for each bird. Level of activity is represented as a function of time. Individual RP is indicated.

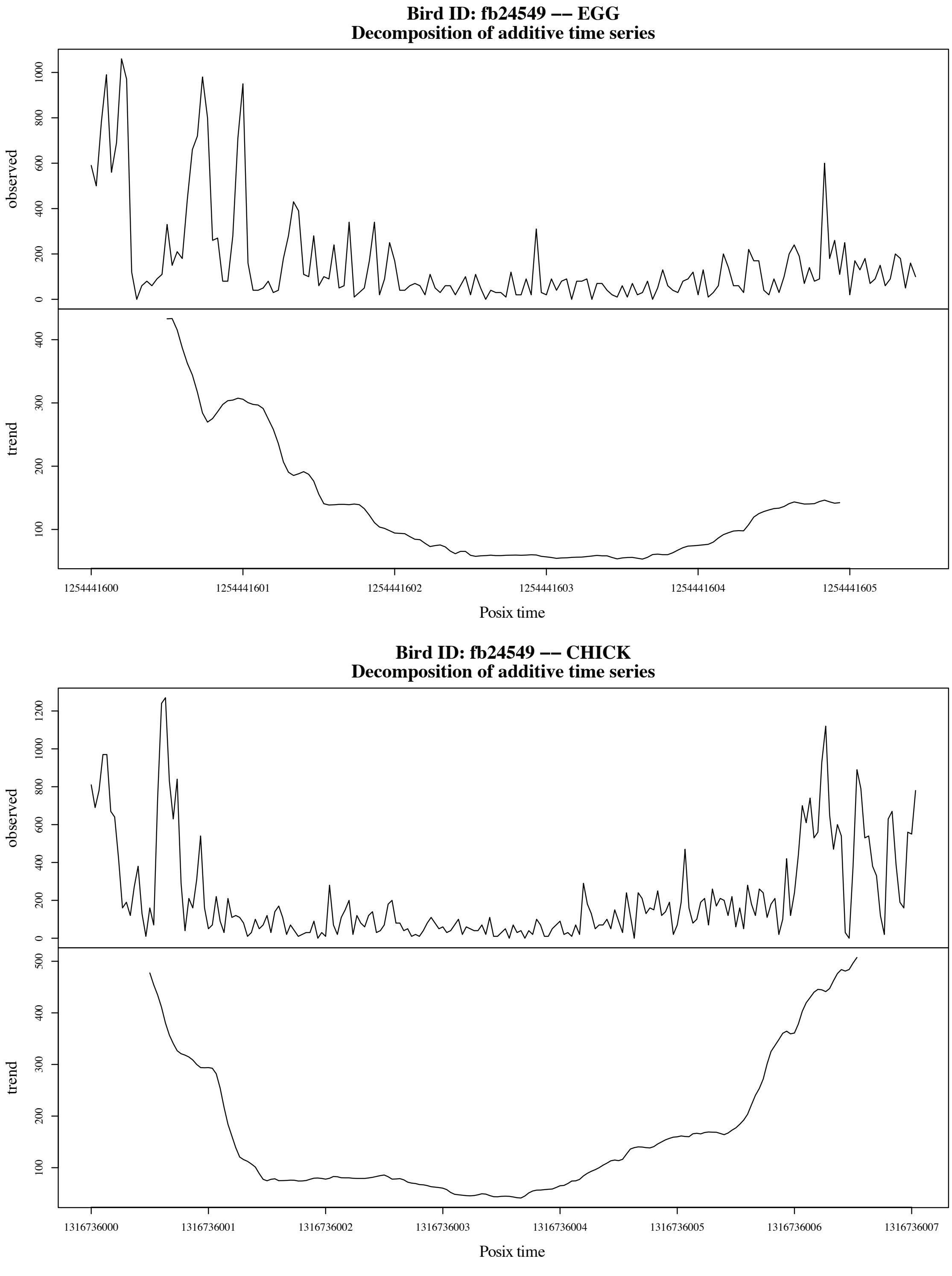

Figure S3. Two examples of data denoising by nonlinear trend extraction with additive time series decompositions.

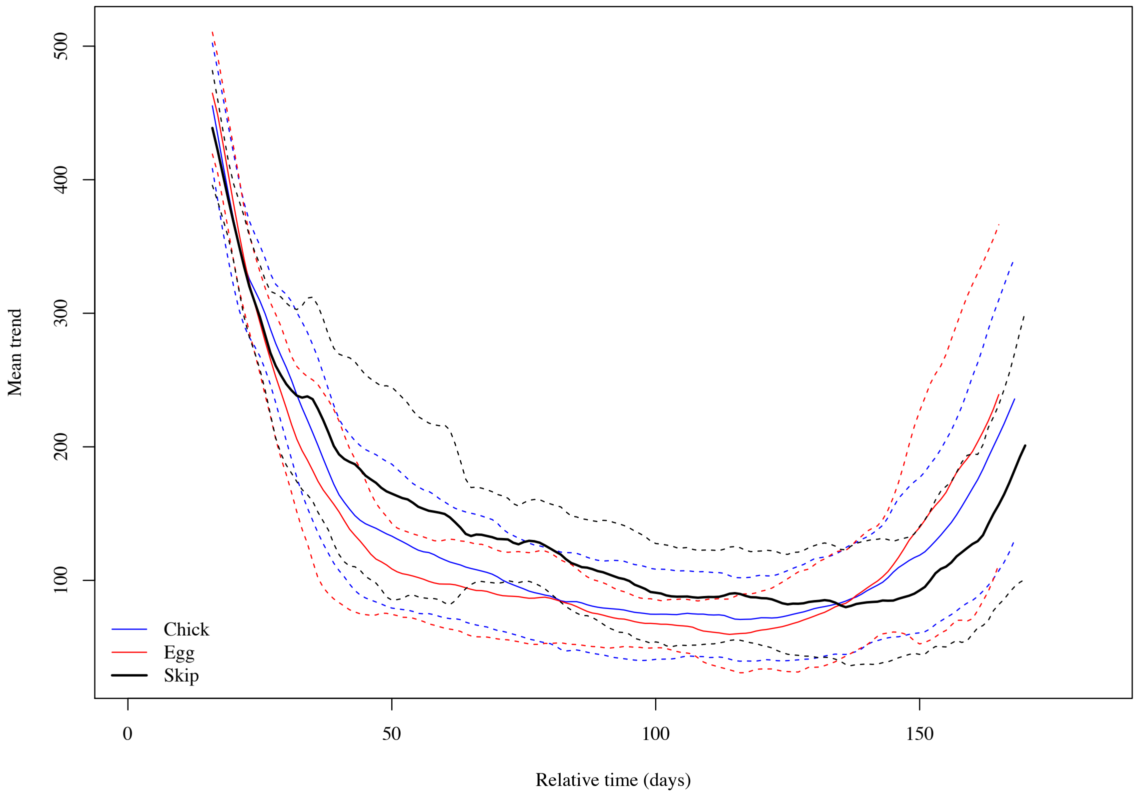

Figure S4a. Mean flying patterns obtained for birds with a chick (blue), egg failed (red) and for skipped birds (black). Mean values were obtained from activity plots presented in Fig 3a. Broken lines represent mean value ±1 SD.

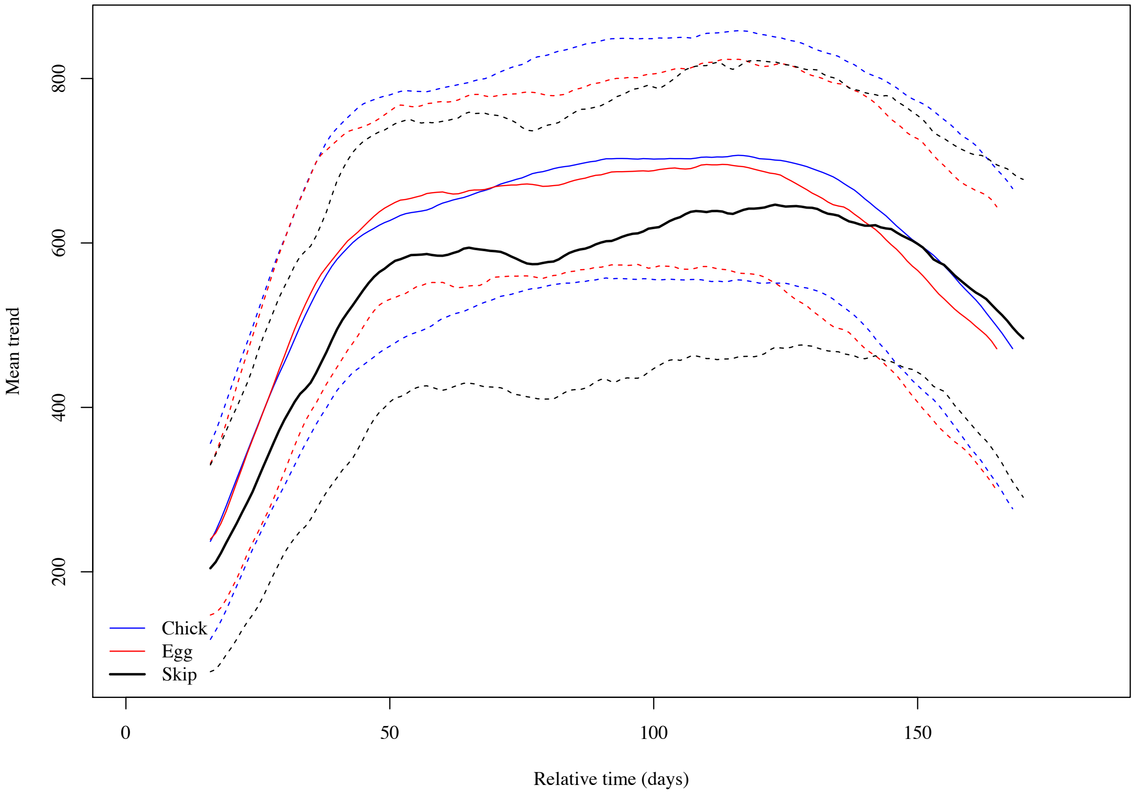

Figure S4b. Mean resting patterns obtained for birds with a chick (blue), egg failed (red) and for skipped birds (black). Mean values were obtained from activity plots presented in Fig 3b. Broken lines represent mean value ±1 SD.

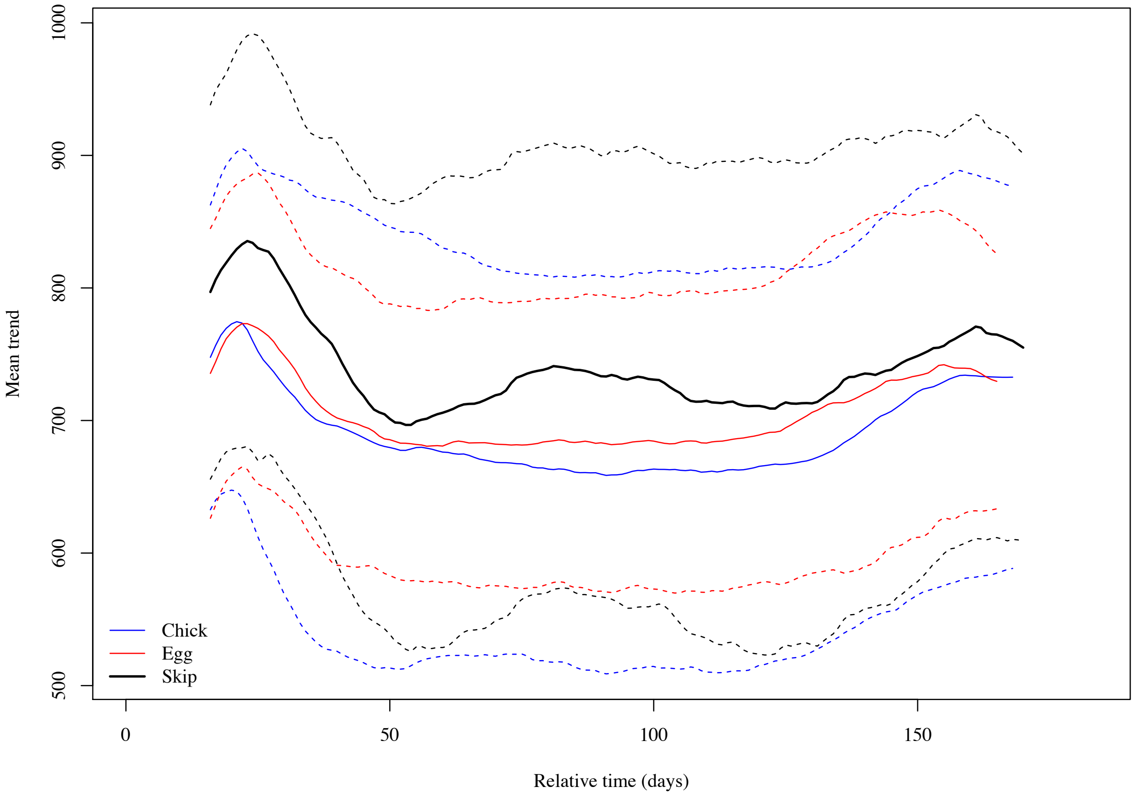

Figure S4c. Mean foraging patterns obtained for birds with a chick (blue), egg failed (red) and for skipped birds (black). Mean values were obtained from activity plots presented in Fig 3c. Broken lines represent mean value ±1 SD.

Multievent model framework for estimating state transition rates

Multieventcapture-mark-recapture (MECMR) is a modeling framework widely used to estimate state-dependent demographic rates of interest (e.g. survival) together with transition rates between different "states" individuals occupy (e.g. being infected or not), while explicitly accounting for imperfect (less than 1) and heterogeneous (biased) detectability of marked individuals, and uncertainty in the assignment of the state to an individual. Given their breeding status (i.e. skipped breeder, breeder with an egg, breeder with a chick), birds can be assigned to different state and multevent models provide an ideal framework for estimating transition rates (from state to state) and survival probabilities simultaneously in the same model. Furthermore, as different constraints can be imposed on state-dependent survival and transition parameters, multi-state models provide a rigorous method of evaluating the fitness consequences of transition rates.

In MECMR models, at each capture occasion individual can occupy one among a finite set of mutually exclusive states. Between subsequent capture occasions, individuals move independently between these states (Pradel 2005). However, state is not always possible to assign when an individual is captured. Thus, at each capture occasion, we observe and event rather than a state. Events are related to the true, but not necessarily known, state of the individual through a series of conditional probabilities (Pradel et al. 2008; Choquet et al. 2009b). The MECMR model we develop here uses four exclusive states that individual can occupy at each capture occasion (which is during the breeding season): (1) being breeder with a chick (state "CHICK"), (2) being a failed breeder, producing only an egg (state "EGG"), (3) skipped breeder (state "SKIP"), (4) dead (state "DEAD").

An individual can occupy only one state in a given breeding season. Transitions among these four states (i.e. "CHICK", "EGG", "SKIP, "DEAD") happen between two subsequent breeding seasons, with the state ‘DEAD’ being an absorbing state (a dead individual cannot move to another state). Transitions are modeled as a two-step process composed of the probability of survival over the annual time interval, followed by the probability of transitioning among live states. The recapture of the marked individuals is described in the event matrix, where an alive individuals (i.e. occupying alive state) can be either captured, or not captured. There are 4 possible events (coded between 1 and 0) we can observe. They are related to one or more real underlying states.

0 = individual is not captured (“DEAD”, “CHICK”, “EGG”, “SKIPPED”)
1 = individual is captured at the nest, but without an egg or chick (“SKIPPED”)
2 = individual is capture at the nest, and it produced an egg in that breeding season (“EGG”)
3 = individual is captured breeding at the nest, it produced a chick in that breeding season (“CHICK”)

We coded the capture histories of males and females using the event code. We treated females and males in the two separated analysis to avoid any problems related to non-independence between males and females (*i.e.* if they belong to the same breeding pair).

Specification of parameters and the model structure

Following notation in Pradel (2005) our model is defined with three types of parameters: (1) initial state probabilities, represented in a vector of probabilities, (2) transition probabilities involving: survival probabilities (ϕ), and between-state transition probabilities (ψ); and (3) recapture probabilities (p).

(ϕ) Survival probabilities

	SKIP	EGG	CHICK	DEAD
SKIP	y	-	-	1 - y
EGG	-	y	-	1 - y
CHICK	-	-	y	1 - y
DEAD	-	-	-	1

(ψ) Transition

	SKIP	EGG	CHICK	DEAD
SKIP	1 - y	y	y	-
EGG	1 - y	y	y	-
CHICK	1 - y	y	y	-
DEAD	-	-	-	1

(p) Recapture probabilities

	0	1	2	3
SKIP	1 - y	-	-	b
EGG	1 - y	b	-	-
CHICK	1 - y	-	b	-
DEAD	1 - y	-	-	-

Model covariates and model selection process

There is no specific goodness of fit (GOF) test for MECMR models. Thus, we assessed the fit of the general mark-recapture assumptions to our data by assessing the GOF of the single state Cormack-Jolly-Seber (CJS) model (Cormack). The CJS model assumes all animals present at the same sample occasion have equal future survival and recapture probabilities regardless of past history and capture in the current sampling occasion. These assumptions were tested using program U-SURGE (Choquet et al. 2009a). None of the components of the test returned significant results.

We considered four possibilities for the variation of each parameter (recapture, survival, transition): state (*i.e.* parameter varies according to a state individuals is), time (*i.e.* parameter varies in time), time + state, constant (parameter is the same for all individuals, and constant in time). We used a 3-stage model selection process (Grosbois and Tavecchia 2003): first we modeled recapture rates as constant, or as varying in relation to state, or time (yearly variation), while keeping survival and transition rates fully parameterized (state + time). Next, we used the best recapture rate model identified in the first state (i.e. the model with the lowest Akaike Information Criterion adjusted for overdispersal for small sample sizes ($QAIC_c$) correcting for overdispersion by including an estimate of model deviance (c-hat = model deviance/df) for the global model), to model survival rates as constant, or as varying in relation to state and time. Finally, with recapture and survival rates parameterized according to the best models identified above, we modeled transition rates as constant, or varying in relation to time and departure state (the state an individual transitions from). In total, we performed model selection on a candidate list of four different recapture, four different survival and four different transition rate models (Table S1). Model selection was based on QAICc (Anderson and Brnham 2002). Normarised QAICc weights (w*i*) were used as a measure of relative support for each model.

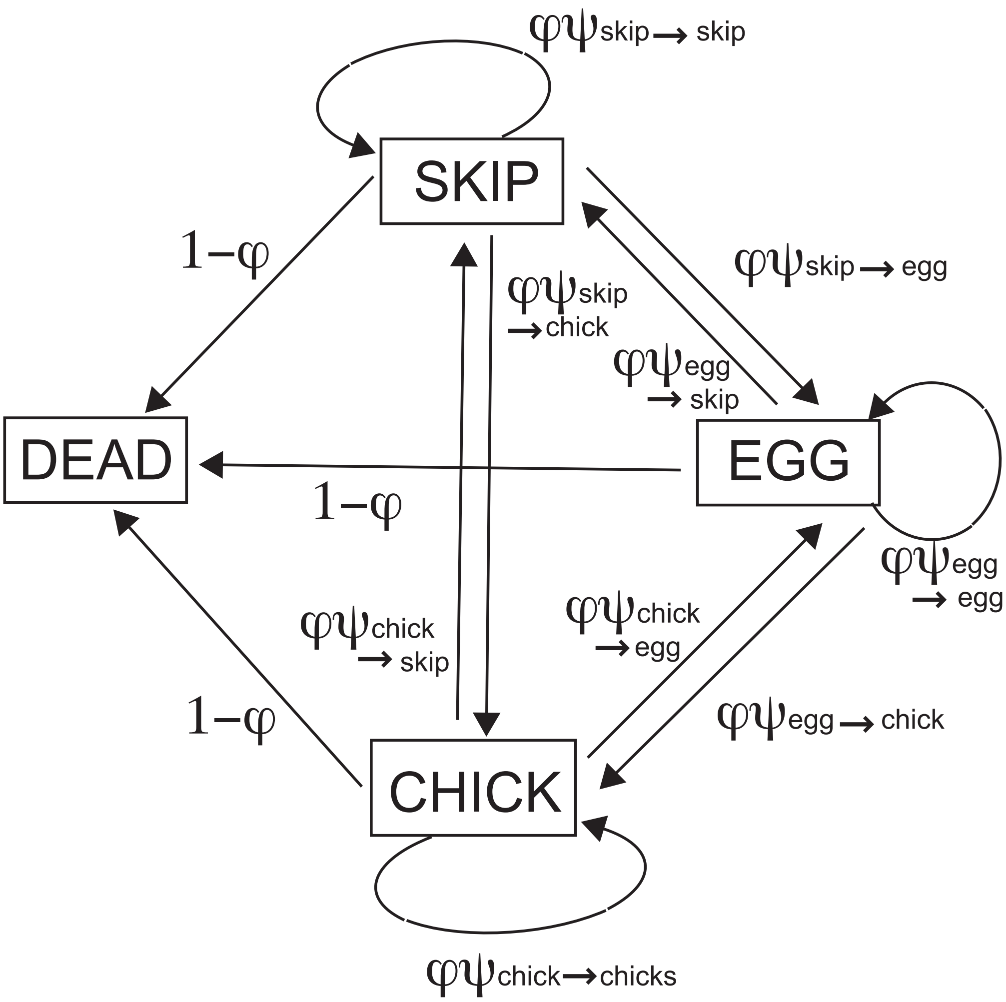

Fig S5. A diagram of the between-state transition process and the structure of the observation process used to estimate transition rates. RP (*t*): reproductive performance in year *t*, RP (*t*+1): reproductive performance in year *t* + 1. Chick: individuals that have a chick in a given year, Egg: individuals that failed breeding in a given year, Skip: individual that skipped breeding but stayed in a burrow in a given year. Dead: individuals that were not captured in a given year. ϕ: survival rate; Ψ: transition rate

Table S4. Model notation describing the recapture, survival and transition rate models included in the candidate list for multievent modeling of survival and transition rates in Manx Shearwaters.

Recapture	Survival	Between-state transition
state	Best model of recapture	Best model of recapture
t	state	Best model of survival
state + t	t	state
constant	state + t	t
	constant	state + t
		constant

Table S5. Summary results of the multievent mark-recapture analysis to estimate recapture, survival and transition rates between a given year and the following year in female Manx Shearwaters.

	Model Structure							
Parameter	p	Φ	ψ	*K*	dev	QAICc	Δ*i*	W*i*
Recapture rate (p)	**state**			**22**	**272.01**	**316.01**	**0.00**	**0.52**
	t			24	269.64	317.64	1.64	0.23
	state + t			26	265.78	317.78	1.77	0.22
	constant			20	281.51	321.51	5.50	0.03
Survival rate (Φ)	**state**	**constant**		**16**	**277.47**	**309.47**	**0.00**	**0.68**
		state		18	275.88	311.88	2.41	0.20
		t		20	273.39	313.39	3.92	0.10
		state + t		22	272.01	316.01	6.53	0.03
Transition rate (ψ)	**state**	**constant**	**state**	**12**	**289.27**	**313.27**	**0.00**	**0.76**
			t + state	6	303.58	315.58	2.31	0.24
			constant	11	302.40	324.40	11.13	0.00
			t	13	302.26	328.26	14.99	0.00

See Table S1 for model notation. K: number of estimable parameters, dev: deviance, QAICc: Akaike's information criterion for small sample sizes (QAIC$_c$) correcting for overdispersion by including an estimate of model deviance (c-hat = model deviance/df) for the global model, Δ*i*: the QAICc difference between the current model and the model with the lowest QAICc value, W*i*: Akaike weight, state: state dependent rates, constant: constant rates, t: time-dependent rates.

Table S6. Summary results of the multievent mark-recapture analysis to estimate recapture, survival and transition rates between a given year and the following year in male Manx Shearwaters.

	Model Structure							
Parameter	p	Φ	ψ	*K*	dev	QAICc	Δ*i*	W*i*
Recapture rate (p)	**constant**			**20**	**277.97**	**326.12**	**0.00**	**0.76**
	state			22	274.44	328.46	2.33	0.24
	t			24	274.90	335.02	8.90	0.01
	state + t			26	274.37	340.85	14.72	0.00
Survival rate (Φ)	**constant**	**constant**		**14**	**288.93**	**320.78**	**0.00**	**0.62**
		state		18	280.67	323.19	2.41	0.19
		t		16	286.46	323.54	2.76	0.16
		state + t		20	277.97	326.12	5.34	0.04
Transition rate (ψ)	**constant**	**constant**	**state**	**10**	295.53	317.48	**0.00**	**0.82**
			state + t	14	288.93	320.78	3.30	0.16
			constant	5	315.22	325.72	8.24	0.01
			t	9	308.67	328.25	10.77	0.00

See Table S1 for model notation. K: number of estimable parameters, dev: deviance, QAICc: Akaike's information criterion for small sample sizes ($QAIC_c$) correcting for overdispersion by including an estimate of model deviance (c-hat = model deviance/df) for the global model, Δ*i*: the QAICc difference between the current model and the model with the lowest QAICc value, W*i*: Akaike weight, state: state dependent rates, constant: constant rates, t: time-dependent rates.

Table S7. Initial state rates, transition rates and recapture rates and ± 95% Confidence Interval: CI for female Manx Shearwaters. Estimates were obtained from best-supported model in Table S3.

Parameters	Capture	To	Estimates	CI-	CI+	SE
Initial state	EGG	-	0.12	0.05	0.26	0.05
	CHICK	-	0.88	0.74	0.95	0.05
	SKIP	-	0.00	0.00	0.00	0.00
Transition rate	SKIP	EGG	0.00	0.00	0.00	0.00
	SKIP	CHICK	0.79	0.36	0.96	0.16
	SKIP	SKIP	0.21	0.04	0.64	0.16
	EGG	EGG	0.08	0.01	0.39	0.07
	EGG	CHICK	0.61	0.33	0.83	0.14
	EGG	SKIP	0.31	0.11	0.61	0.13
	CHICK	SKIP	0.22	0.13	0.35	0.05
	CHICK	EGG	0.21	0.13	0.32	0.05
	CHICK	CHICK	0.57	0.45	0.69	0.06
Recapture rate	EGG	-	1.00	1.00	1.00	0.00
	CHICK	-	1.00	1.00	1.00	0.00
	SKIP	-	0.46	0.24	0.71	0.13

Table S8. Initial state rates, transition rates and recapture rates and ± 95% Confidence Interval: CI for male Manx Shearwaters. Estimates were obtained from the best-supported model in Table S4.

Parameters	Capture	To	Estimates	CI-	CI+	SE
Initial state	EGG	-	0.06	0.02	0.18	0.04
	CHICK	-	0.89	0.77	0.96	0.04
	SKIP	-	0.04	0.01	0.15	0.04
Transition rate	SKIP	EGG	0.24	0.03	0.75	0.21
	SKIP	CHICK	0.76	0.25	0.97	0.21
	SKIP	SKIP	0.00	0.00	0.00	0.00
	EGG	EGG	0.09	0.01	0.45	0.09
	EGG	CHICK	0.81	0.48	0.95	0.12
	EGG	SKIP	0.09	0.01	0.45	0.09
	CHICK	SKIP	0.10	0.04	0.20	0.04
	CHICK	EGG	0.26	0.16	0.38	0.06
	CHICK	CHICK	0.64	0.52	0.75	0.06
Recapture rate	EGG	-	0.94	0.80	0.98	0.04
	CHICK	-	0.94	0.80	0.98	0.04
	SKIP	-	0.94	0.80	0.98	0.04

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Chapter 8

General Discussion

Introduction

This thesis provides us with a series of in-depth investigations of important aspects of foraging and reproductive strategies using a range of species in the wild. In the opening chapter of this thesis, I proposed that the aims of my research were (i) to examine the at-sea behaviour of free-ranging animals in respect to their life-history, and its consequence on the reproductive performance, and how at-sea behaviour during winter affects the subsequent breeding attempts, and (ii), to document the foraging behaviour of diving seabirds. In this final chapter, I provide a summary of findings from each chapter and an outline of future directions that remain to be explored.

Key findings and future directions

1. Why do central-place foragers increase their travel distance?

Classic foraging theory predicts that central-place foragers are expected to minimise transit time by using nearby foraging patches and following the most direct foraging trip path between the central-place (*i.e.*, their breeding colony) and prey patches (Baird 1991; Ydenberg et al. 1994; Saunders and Ydenberg 1995) in order to maximise foraging efficiency. Foragers are expected to use distant foraging patches only if net energy gain (*e.g.* quality and quantity) is higher than at nearby patches (Houston and McNamara 1985; Cuthill and Kacelnik 1990; Waite and Ydenberg 1996). In support of this prediction, previous studies found that the size of prey captured increases with the distance to the patch for many central-place foragers, including social insects (Martin and Vinson 2008), nesting songbirds (Hegner 1982; Carlson 1983; Kacelnik 1984; Krebs and Avery 1985) and colonial seabirds (Wanless et al. 1993; Ainley et al. 1998).

In a marine environment, resources are patchily and sparsely distributed and may be unpredictable, especially when the distance from familiar locations increases (Weimerskirch 2007). In this context, there are two possible scenarios explaining why central-place foragers extend their travel distance even though the costs of travel increase. First, foragers may encounter some difficulty in finding prey at nearby patches and thus have to extend their foraging range (and hence, their travel distance) to meet energy requirements for their young and themselves (in this case, prey may be depleted so that birds move to the next patch, but patch quality does not necessarily increase with travel distance). Alternatively, foragers extend their travel distance because either resource availability is high or prey quality is better further from the colony (in this case, patch quality increases with travel distance). While the former hypothesis has attracted more support by correlating trip duration and environmental conditions in marine animals (*e.g.* Davoren and Montevecchi 2003), the latter hypothesis has so far not been well tested empirically due to difficulty in obtaining prey patch quality at sea. In particular, relatively few studies have investigated whether foragers change their search strategy in response to environmental conditions. In Chapter 2, I assessed potential factors affecting travel distance from colony, in response to proximate environmental conditions, by using simultaneously co-deployed GPS loggers and time-depth-temperature recorders on chick-rearing Razorbills. I showed that Razorbills are capable of adjusting their foraging pattern in response to environmental conditions, and the distance that they travelled to foraging locations increased with sea-surface temperature. Furthermore, I showed that distant patches are better than those nearby as estimated by an indirect measure, the Index of Patch Quality (IPQ: (Mori et al. 2002), which is based on dive profiles.

The reason why travel distance is related to sea-surface temperature still remains to be explored, but a possible explanation may be that sea-surface temperature is related to higher prey abundance or quality. Irrespective of the actual cause(s), Razorbills are able to detect high quality patches and apparently balance energy gain and expenditure. But how do they find foraging patches? As flight costs in this species are extremely high compared to other seabirds (Elliott et al. 2013), Razorbills are expected to be penalised by extending their foraging distance so that they may be under strong selection to minimise transit costs. Thus, it is likely that they have a search strategy, but our knowledge of search strategies in marine animals is limited. Do Razorbills use a single rule for searching or do they use multiple rules depending on the context? If so, when and how might they change these rules? These are the questions addressed in Chapter 3.

2. How do birds flexibly search for food at-sea?

Optimal foraging models provide a theoretical framework predicting how animals should behave when searching for food. On the assumption that natural selection is likely to have produced efficient foragers, we may analyse foraging strategies in terms of how they help to maximise an energetic currency under environmental or life-history constraints. This can allow us to move towards understanding animals' optimal decision rules (Stephens and Krebs 1986). A limitation of this theory is that it was been developed and tested in small systems, and under controlled environmental conditions. In reality, environmental conditions fluctuate in both time and space, but such uncertainty is traditionally not accounted for by the model.

More recently Lévy flight foraging theory has been developed to extend the optimal foraging theory that is to optimise search efficiencies in free-ranging animals (*e.g.* Edwards et al. 2007; Sims et al. 2008; Humphries et al. 2010; Humphries et al. 2012; Sims et al. 2012; Regular et al. 2013). The basic idea underlying this hypothesis is that search is memory-less and a transition from scale-free to scale-specific motion can be interpreted as a transition from a resource-poor to a resource-rich environment. However, whether or not natural selection has favoured Lévy flight foraging in animals is still a matter of debate. Early studies were limited to species with small range of movement due to (i) technical problems (*i.e.* data were not accurate or low resolution) and (ii) motion types not being unequivocally described. As a result, early studies failed to provide sufficient evidence supporting the L*é*vy hypothesis (Edwards et al. 2007; Elliott et al. 2009). Recently, studies based on high resolution movement data and larger step lengths leant support to the hypothesis (Edwards et al. 2007; Sims et al. 2008; Humphries et al. 2010; Humphries et al. 2012; Sims et al. 2012).

The L*é*vy flight foraging hypothesis has focused on search patterns on a broad scale of animal taxa and the smallest system considered to examine the hypothesis is at the species level. However, animals have different constraints between breeding or non-breeding periods, and these constraints may affect search patterns. Nevertheless, to the best of my knowledge, there was no empirical data to test whether different breeding stages may lead to different search patterns in marine animals prior to my study. For example, do birds change searching rules when they have fewer constraints (*e.g.* less frequent commuting during incubation period) compared to when they have more constraints (*e.g.* more frequent commuting during chick-rearing period)? While environmental conditions are shown to explain movement patterns in some animals (Humphries et al. 2010; Sims et al. 2012), how individual characteristics such as breeding stage (*i.e.* incubation and chick-rearing) affect search pattern has been poorly explored. In Chapter 3, I examined how different breeding stages affect the search strategies by using simultaneously co-deployed GPS loggers and time-depth-temperature recorders on both incubating and chick-rearing Razorbills. I showed that Razorbills are able to adjust their feeding location in relation to resource availability, but that the potential mechanism underlying this adaptive behaviour is independent of breeding stage while the magnitude of flight reorientations was found to be scale-dependent.

The major limitation of this chapter is a lack of repeated measurements of trips from the same individuals. Although I attempted to obtain movement data from the same individuals for several trips, it was difficult to collect data repeatedly from the same individuals due to our choice of devices as well as the study system. It would be fascinating to examine the route similarity within individuals between incubation and chick-rearing periods, both within a single season and across several breeding years. For instance, I did not detect any connection between memory use and movement patterns in Chapter 3, but memory might have been used not to record the exact locations or paths, but just initial bearing. Alternatively, birds might have several context-dependent memories for different routes and places. We were unable to test these possibilities due to low-resolution GPS data. I propose that monitoring the same individuals for extended periods would benefit our understanding of search strategies, especially since there is growing evidence that animals use random walk patterns (Sims et al. 2008; Sims and Humphries 2012; Humphries et al. 2013; Regular et al. 2013) based on the assumption that they use memory-less search in the wild. Despite these limitations, my findings reveal that Razorbills are capable of adjusting their foraging location in response to resource availability, but use the same rule during incubation and chick-rearing periods even when the parental constraints are different. This suggests that Razorbills may be less susceptible to ongoing climate change thanks to their opportunistic foraging strategy compared to specialist seabirds such as the benthic feeders (*e.g. Cepphus*. spp.) presented in Chapter 5.

3. How do sympatric seabird species coexist at the most energetically demanding phase?

I still remember that when we were approaching Skomer Island by boat back in April 2012, I was truly amazed by the scenery as the whole island, as far as I could see, was covered by seabirds. Once I set foot on the island, all the way from the jetty to the research cabin was filled with busy puffins, and massive cliffs at the isthmus were densely occupied by countless

Common Guillemots and Razorbills while various gulls were flying above us. Seeing this I wondered, how could it be possible to have so many birds together? The competitive exclusion principle predicts that true competitors cannot stably coexist. Nevertheless, it is common to see seabird colonies where multiple (sympatric) species coexist even though they breed at the same time and apparently share the same prey species. If we assume that the prediction of the competitive exclusion principle is true, there are two explanations as to why sympatric species can coexist: either these species differ in resource use in time and/or space during breeding (so they are not true competitors), or populations may not be close to the carrying capacity yet - otherwise, these populations may be declining. Recent advances in technology are increasingly being used in field studies, allowing us to collect a large amount of biological data on a wide range of variables through archival bird-borne data loggers. Seabird foraging behaviour particularly benefits from the bio-logging techniques because it is difficult to observe them under water. However, our knowledge of seabird foraging behaviour is still limited to mostly large seabirds. Chapter 4 fills this information gap a little by describing the detailed foraging behaviour of chick-rearing Atlantic Puffins making it possible to examine how puffin foraging behaviour may differ from sympatric Razorbills. I show that foraging behaviour in both species is very similar, in contrast to the former hypothesis. It remains to be examined whether those species are close to carrying capacity and experience competition. However, the long-term population trend for Razorbills on Skomer is declining whilst puffins are stable (Büche et al. 2013), which suggests that Razorbills may be near carrying capacity. Alternatively, there is a possibility that the critical resource over which there is competition is not related to foraging, but this remains to be established. I further show that auks are not exceptions to the hypothesis that a trade-off between oxygen stores and oxygen utilization drives variation in dive duration. Across all auks species that are currently available including my Atlantic Puffin, Razorbill and Black

Guillemot data, the equation for maximum dive duration was $0.36M0^{.42}$ as similar to the prediction for small breath-hold divers.

4. Why do seabird parents switch between short and long foraging trips?

Dual foraging strategies have been shown in some seabirds (*e.g.* Ropert-Coudert et al. 2004) and it has been suggested that short trips are made for provisioning young while long trips are for self-feeding. However, few studies have investigated the relationship between trip duration and food load size. In Chapter 6 I show that chick-rearing Manx Shearwaters use a dual foraging strategy to switch foraging destinations, mixing between short and long trip durations while the majority of the foraging patches are close to ocean-front locations where the distances from the colony differ. This suggests that despite foraging destinations varying among trips, shearwater parents target potentially high quality patches close to fronts. A simple model I developed here formalises the conditions under which feeding for chicks or self will be adaptive for parents in relation to travel time and distance. Skomer Island is the largest Manx Shearwater colony in the world (Perrins et al. 2012) and this result may provide an explanation for why Skomer supports such a large number of shearwaters, because fronts are located at both nearby patches (Celtic Sea front) and distant patches (Irish Sea front).

Future research on dual foraging should aim to measure colony attendance patterns for both pair members throughout the chick-rearing period to examine whether males and females alternate short and long trips. My results suggest that they alternate foraging trip duration between pair members, but this needs to be confirmed by future investigation.

5. How do individual differences in phenology and behaviour result in enhanced reproductive performance at the population level?

As we expect for humans, we observe intra-specific variations in every aspect of animal biology. For instance, some animals are bigger/smaller or faster/slower than others. It is also true in migratory animals that there are variations in phenology, migratory routes, stop-over locations and wintering grounds (Lack 1968; Newton 2010; Guilford et al. 2011). In migratory birds, an individual that arrives early on a breeding site has commonly a higher success in reproductive performance than individuals that arrive late (Berthold 2001). This raises the question, why don't all birds arrive early? Generally, individual quality, often associated with age or experience, explains the variation, but this is not a fully satisfactory explanation. Chapter 7 provides an answer to this question: when an adult shearwater increases foraging behaviour during the non-breeding period, they are likely to skip breeding in the following breeding season. Furthermore, I found that there is a trade-off between current parental investment and future reproductive performance. In this case, skipping breeding benefits individuals in the long-term because lifetime fitness could potentially be higher than, for example, continuing breeding under poor conditions.

On the other hand, there are some individuals that constantly had a chick every year during our study period. It is not clear whether carry-over effects impact reproductive performance on some individuals (presumably poor quality ones) or on all birds, it may simply be that we did not observe it during the study period. I attempted to collect all available data from the same individuals over the course of 2-6 years, but by considering the longevity of this species (~ 55 years), our study period is too short to confirm this. It would be fascinating to examine the breeding success of an individual over its entire lifespan and to measure whether carry-over effects occur only for some individuals (presumably ones with poor quality) or for all birds (in which case we just did not observe any during the study period).

Concluding remarks

Like many at-sea behaviour studies of marine predators, my study is purely correlational. It is hard to manipulate free-ranging animals in the wild, which are sensitive to human disturbance, though it is possible to some extent (Catry et al. 2013; Jacobs et al. 2013). Studying the at-sea behaviour of marine predators is largely and more frequently relying on technological developments. This is because it is virtually impossible to observe, at least in the long-term, the natural behaviour of these animals. Since I started this thesis, the bio-logging techniques have been developed further so that data-loggers have become impressively small, light and inexpensive. We are now entering a new era in which the main challenge is to analyse data, rather than to collect it. Studying at-sea behaviour requires trying something very new and exploratory, even sometimes starting without proper controls or hypotheses. My thesis work has shown some ways to make use of bio-logging data to improve our understanding and unravel the ongoing mysteries of the at-sea behaviour of marine animals.

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