Behavioural adaptations to breeding in a long-lived pelagic seabird

James Evry
Wadham College and the Department of Zoology
University of Oxford

Thesis submitted for the degree of Master of Science by Research in Zoology

Trinity Term 2018

Behavioural adaptations to breeding in a long-lived pelagic seabird

James Evry

Wadham College

Thesis submitted for the degree of Master of Science by Research, Trinity Term 2018

Abstract

The traits of organisms evolve by natural selection to maximise fitness; however, we do not observe Darwinian Demons. This is because all organisms face various types of constraint, which ultimately limit fitness. Reproduction is inextricably linked with fitness, and constraints on reproduction have extensive implications for evolution and adaptation.

Two broad types of constraints on breeding are treated here. Firstly, breeding may be constrained by life-history trade-offs, perhaps most fundamentally in that current reproductive effort is constrained by its costs to future reproduction. Secondly, breeding may be constrained by the physical and ecological conditions and finite resources that are accessible from the breeding site, to which organisms may be tied to varying extents. The life-history and behaviour of animals are profoundly affected by these constraints, and they are especially influential in long-lived species.

This thesis examines behavioural adaptations to each of these types of constraint in a long-lived pelagic seabird: the Manx Shearwater, *Puffinus puffinus.* Firstly, I investigate how patterns of behaviour vary between sexes and populations in preparation for breeding and how this variation is related to the ecological and physiological constraints faced by the groups during breeding. Secondly, I test the responsiveness of parents to changes in offspring hunger during food provisioning and discuss the influence of constraint by costs to future reproduction. I tackle these questions using well-established biologging methods to remotely monitor behaviour in a natural and experimental setting.

Acknowledgements

This work was made possible by funding from the Biotechnology and Biosciences Research Council. The work would also not have been possible without the kind permission of the Skomer and Skokholm Islands Advisory Committee and the Copeland Bird Observatory.

I have been very fortunate to receive support from many people throughout my Masters. Thanks to Nancy del Carro, Martyna Syposz, Jessy Phillips, Ollie Padget, Jason Moss, Elisa Riera, Eddie Stubbings and Bee Beuche for providing both great assistance and company during the field season on Skomer. And to the many OxNav members gone before me who contributed to the long-term geolocator study that underpins my second chapter.

I want to thank Chris Perrins, Matt Wood, Tim Guilford, Annette Fayet, Sarah Bond and Ollie Padget for teaching me essential field skills.

Tim Guilford and Annette Fayet have also been instrumental in guiding my work, for which I am deeply grateful. I would particularly like to thank Annette, as without her kind and committed support I may never have crossed some of the motivational and intellectual hurdles that I encountered during this Masters.

Finally, I would like to thank my mum, dad and brother, and Sue, Andy and Liv, for all being there whenever I needed them.

Author Contributions

All work in this thesis is primarily my own.

Tim Guilford and Annette Fayet contributed to ideas and feedback on both data chapters 2 and 3, and Jay Willis to Chapter 2.

Long-term geolocator data used in Chapter 2 were collected by many individuals from the OxNav team over the past 10 years. To this dataset, I contributed to the deployment and retrieval of geolocators during the 2016 and 2017 field seasons.

Nancy del Carro, Martyna Syposz, Jessica Phillips and Annette Fayet assisted with the chick-swap experiment detailed in Chapter 2. TDR and GLS data used to validate foraging metrics were collected mainly by Jessica Phillips, although I also participated. Jessy kindly allowed me to analyse them for my study. RFID data were generously provided by Chris Tyson.

This thesis is dedicated to my late undergraduate tutor Ian Moore, whose good humour, dedicated teaching and contagious enthusiasm for biology I will always remember fondly.

Table of Contents

Chapter 1

General introduction

Introduction

Animal life-history strategies have been shaped by natural selection to maximise inclusive fitness within the limits imposed by ecological and physical conditions (Lack, 1954; West & Gardner, 2013; Williams, 1966). Since the resources available to an animal during its lifespan are limited, investment in one fitness-generating activity within its life cycle may be traded-off against other such investments in the future (Bell, 1980; Stearns, 1989). Perhaps the most fundamental example is the trade-off between current and future reproduction, which has played a significant role in the evolution of animal life-history strategies (Roff, 2002). Selection on animals to optimally allocate resources between current and future reproduction has extensive implications for animal behaviour, including parental care, foraging behaviour and breeding decisions, among others. Spatio-temporal variation in conditions can also alter the way in which current reproductive effort is constrained by costs to future reproduction within the lifetime of an animal (Erikstad et al., 1998; Roff & Fairbairn, 2007), and thus to maximise fitness, animals may employ behavioural systems to strategically adjust the way they allocate resources between current and future reproduction in the face of change, although how and to what extent animals do this is poorly understood.

In addition to constraints from costs to future reproduction, behaviour during breeding is constrained by the physical and ecological conditions and finite resources that an animal can access within a certain radius of its breeding site, to which species and individuals within species may be tied to different extents (Brooke, 2018; Clarke et al, 2006; Kappes et al., 2015; Patil et al., 2015; Pierotti & Annett, 1991; Shaffer et al., 2003; Travaini et al., 2001). The influence of an animal's breeding behaviour on fitness is likely to be most significant in long-lived species, in which each reproductive attempt represents a relatively small component of potential lifetime reproductive success (Roff, 2002). In such species, any negative impact of current reproduction on survival may have a magnified effect on lifetime reproduction, and hence the fitness costs of equal reproductive effort (i.e. the proportion of the total energy budget of an organism devoted to reproduction) are higher in long-lived species (Hirshfield & Tinkle, 1975). As a result, long-lived species are expected to show specific behavioural strategies to deal with these higher fitness costs of reproduction (Schultner et al., 2013), but much remains to be understood regarding the strategies employed by different species, the drivers underlying them and how they are adapted to changing conditions.

Seabirds as model species

Seabirds are excellent models to study behavioural adaptions to the constraints of breeding, in part because their breeding biology involves several well-defined and major constraints. Despite their pelagic habits, seabirds like all other birds can only breed on land. As a result, their breeding sites are often separated by significant distances from foraging locations at-sea, especially since food may be unpredictable and patchily distributed (Weimerskirch, 2007) or depleted near to breeding colonies (Ashmole, 1963). Foraging thus requires substantial commitments of time and energy to travel between the breeding site and foraging areas (Brooke, 2018). Linked to this is the problem that breeding duties restrict the amount of time that parents can spend away from the colony, effectively limiting the distance that seabirds can travel and the resources they can access (Orians & Pearson, 1979). The influence of these constraints is made more severe by the fact eggs and chicks are slow to develop, meaning that breeding seasons are long (Warham, 1990). Indeed, those of the albatrosses are the longest of any bird, and incubation alone can take as long as 81 days in the Royal Albatross *Diomedea epomophora* (Boersma, 1982).

Aside from being tied to land, breeding seabirds are heavily constrained in their breeding attempts by the high costs of increased investment in current reproduction on survival and future reproduction (Catry et al., 2013; Fayet et al., 2016; Shoji et al., 2015) and hence fitness. Despite encompassing a wide range of sizes, seabirds all have long lifespans, from the 27g European Storm-Petrel *Hydrobates pelagicus* which can live for over 37 years (BTO, 2018) to the 9kg wandering albatross *Diomedea exulans* which can live for over 50 years (Weimerskirch & Jouventin, 1987). Like other long-lived animals, seabirds breed many times and produce small or single-chick broods, meaning that each reproductive attempt represents only a small component of potential lifetime reproductive success. Therefore, even small impacts on survival can have large fitness consequences. Seabirds have evolved a range of behaviours that minimise the impacts of breeding on survival, such as foraging strategies to balance offspring demand against adult body condition (Erikstad et al., 1997; Shoji et al., 2015; Tyson et al., 2017), but much remains to be discovered.

The Manx Shearwater

The Manx Shearwater, *Puffinus puffinus,* is a common Procellariform (population 680,000-790,000, BirdLife International 2017 Species factsheet) with most of its global population breeding on islands around Britain, and smaller populations scattered on islands across the Northeast Atlantic (Brooke, 1990). The species overwinters in the South Atlantic off the coast of Argentina and undertakes an annual trans-equatorial migration of >10,000 km between these waters and the breeding grounds (Guilford et al., 2009; Kirk, 2016). Initial evidence for the extraordinary at-sea movements of Manx Shearwaters was limited, coming from localised at-sea surveys and recoveries of ringed birds washed ashore along migration routes and overwintering areas. In the last decade, the miniaturisation of tracking technologies has revolutionised our ability to study at-sea behaviour and made it possible to track breeding season foraging trips with high spatial and temporal precision using GPS loggers, or determine migration routes and overwintering locations using archival light and immersion loggers - here also referred to as geolocators. This advance in technology has led to an explosion in our knowledge of seabird movements and behaviour at sea (Brooke, 2018), including those of the Manx Shearwater (Dean et al., 2015; Guilford et al., 2009; Guilford et al., 2008). Despite this, a raft of questions on the at-sea activity of the Manx Shearwater remain unanswered.

To answer the research questions addressed in this thesis, I used geolocators to collect data on at-sea behaviour, both at fine temporal resolution over specific short periods within the breeding season, and for longer periods at a relatively coarser resolution. A significant portion of the data analysed in this thesis comes from a long-term dataset of geolocator data collected at multiple breeding colonies around the UK by a succession of researchers over the last 10 years, and to which I have added data for two years. Breeding data recorded consistently over the last 9 years at the Skomer breeding colony was also invaluable for my analyses. Where such data were not collected (e.g. at the Copeland breeding colony), the Skomer database was used to inform methods to infer key breeding parameters from geolocator data alone. It was possible to remotely and continuously monitor the at-sea and breeding behaviour of many birds through a relatively inexpensive and time efficient method, something that would have been impossible before geolocators.

Understanding the at-sea movements and behaviours of Procellariform seabirds such as the Manx Shearwater is important for several reasons. From a scientific perspective, there are numerous unanswered questions regarding life history strategies, at-sea behaviour and parental care. From another viewpoint, the study of Procellariforms is crucial to ensure the continued existence of these ocean wanderers, many of which are threatened with extinction (Phillips et al., 2016). Pelagic seabirds have also been shown to act as indicators of ocean health and ecological performance (Einoder, 2009), from which better knowledge of their at-sea and breeding activity is needed to inform marine conservation policy and enable the targeted mitigation of the human impacts on seas.

Aims

This thesis aims to investigate behaviour during the breeding season and address how it is adapted to maximise fitness in animals, with a focus on how behaviours are influenced by the constraints of current breeding duties which limit access to resources and constraints imposed by life-history trade-offs. Specifically, I will compare how patterns of behaviour vary between sexes and populations in preparation for breeding and assess how variation in these patterns is related to the different constraints faced by the groups during this period. I will also test the responsiveness of parents to changes in offspring hunger during food provisioning and discuss the influence of constraint by costs to future reproduction. Utilising a long-lived pelagic seabird as a study species, I tackle these questions using well-established biologging methods to remotely monitor behaviour in a natural and experimental setting.

References

Ashmole, N. P. (1963). the Regulation of Numbers of Tropical Oceanic Birds. *Ibis*, *103 b*(3), 458–473. https://doi.org/10.1111/j.1474-919X.1963.tb06766.x

Bell, G. (1980). The Costs of Reproduction and Their Consequences. *The American Naturalist*, *116*(1), 45–76. https://doi.org/10.1086/283611

Boersma, P. D. (1982). Why Some Birds Take so Long to Hatch. *The American Naturalist*, *120*(6), 733–750.

Brooke, M. D. L. (1990). *The Manx Shearwater*. London: T & A D Poyser.

Brooke, M. D. L. (2018). *Far From Land: The Mysterious Lives of Seabirds*. Princeton University Press.

BTO. (2018). BTO Bird Facts - Strom Petrel Hydrobates pelagicus. Retrieved September 28, 2018, from https://blx1.bto.org/birdfacts/results/bob520.htm

Catry, P., Dias, M. P., Phillips, R. A., & Granadeiro, J. P. (2013). Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: An experimental demonstration. *Ecology*, *94*(6), 1230–1235. https://doi.org/10.1890/12-2177.1

Clarke, J., Emmerson, L. M., & Otahal, P. (2006). Environmental conditions and life history constraints determine foraging range in breeding Adélie penguins. *Marine Ecology Progress Series*, *310*(1), 247–261. https://doi.org/10.3354/meps310247

Dean, B., Kirk, H., Fayet, A., Shoji, A., Freeman, R., Leonard, K., Guilford, T. (2015). Simultaneous multi-colony tracking of a pelagic seabird reveals cross-colony utilization of a shared foraging area. *Marine Ecology Progress Series*, *538*, 239–248.

https://doi.org/10.3354/meps11443

Einoder, L. D. (2009). A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research*, *95*(1), 6–13. https://doi.org/10.1016/j.fishres.2008.09.024

Erikstad, K. E., Asheim, M., Fauchald, P., Dahlhaug, L., & Tveraa, T. (1997). Adjustment of parental effort in the puffin; the roles of adult body condition and chick size. *Behavioral Ecology and Sociobiology*, *40*(2), 95–100. https://doi.org/10.1007/s002650050320

Erikstad, K. E., Fauchald, P., Tveraa, T., & Steen, H. (1998). On the Cost of Reproduction in Long-Lived Birds : The Influence of Environmental Variability. *Ecology*, *79*(5), 1781–1788.

Fayet, A. L., Freeman, R., Shoji, A., Kirk, H. L., Padget, O., Perrins, C. M., Verhulst, S. (2016). Carry-over effects on the annual cycle of a migratory seabird: an experimental study. *Journal of Animal Ecology*, *85*(6), 1516–1527. https://doi.org/10.1111/1365-2656.12580

Guilford, T. C., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., Perrins, C. M. (2008). GPS tracking of the foraging movements of Manx Shearwaters Puffinus puffinus breeding on Skomer Island, Wales. *Ibis*. https://doi.org/10.1111/j.1474-919X.2008.00805.x

Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., Perrins, C. M. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater Puffinus puffinus: insights from machine learning. *Proceedings of the Royal Society B*, *276*(1660), 1215–23. https://doi.org/10.1098/rspb.2008.1577

Hirshfield, M. F., & Tinkle, D. W. (1975). Natural selection and the evolution of reproductive effort. *Proceedings of the National Academy of Sciences of the United States of America*, *72*(6), 2227–2231. https://doi.org/10.1073/pnas.72.6.2227

Kappes, M. A., Shaffer, S. A., Tremblay, Y., Foley, D. G., Palacios, D. M., Bograd, S. J., & Costa, D. P. (2015). Reproductive constraints influence habitat accessibility, segregation, and preference of sympatric albatross species. *Movement Ecology*, *3*(1), 1–24. https://doi.org/10.1186/s40462-015-0063-4

Kirk, H. (2016). Thesis: Annual and individual patterns in the behavioural cycle of the Manx shearwater.

Lack, D. (1954). *The regulation of animal numbers*. Oxford: Clarendon Press.

Orians, G. H., & Pearson, N. E. (1979). On the theory of central place foraging. In D. H. Horn, R. D. Mitchell, & G. R. Stairs, (Eds.), *Analyses of ecological systems* (pp. 155–177).

Patil, V. P., Karels, T. J., & Hik, D. S. (2015). Ecological, evolutionary and social constraints on reproductive effort: Are hoary marmots really biennial breeders? *PLoS ONE*, *10*(3), 1–20. https://doi.org/10.1371/journal.pone.0119081

Phillips, R. A., Gales, R., Baker, G. B., Double, M. C., Favero, M., Quintana, F., Wolfaardt, A. (2016). The conservation status and priorities for albatrosses and large petrels. *Biological Conservation*, *201*, 169–183. https://doi.org/10.1016/j.biocon.2016.06.017

Pierotti, R., & Annett, C. (1991). Diet Choice in the Herring Gull : Constraints Imposed by Reproductive and Ecological Factors. *Ecology*, *72*(1), 319–328.

Roff, D. A. (2002). *Life History Evolution*. Sunderland: Sinauer Associates.

Roff, D. A., & Fairbairn, D. J. (2007). The evolution of trade-offs: Where are we? *Journal of Evolutionary Biology*, *20*(2), 433–447. https://doi.org/10.1111/j.1420-9101.2006.01255.x

Schultner, J., Kitaysky, A. S., Gabrielsen, G. W., Hatch, S. A., & Bech, C. (2013). Differential reproductive responses to stress reveal the role of life-history strategies within a species, 8–11.

Shaffer, S. A., Costa, D. P., & Weimerskirch, H. (2003). Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Functional Ecology*, *17*(1), 66–74. https://doi.org/10.1046/j.1365-2435.2003.00705.x

Shoji, A., Aris-Brosou, S., Culina, A., Fayet, A., Kirk, H., Padget, O., Guilford, T. (2015). Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biology Letters*, *11*(10), 20150671. https://doi.org/10.1098/rsbl.2015.0671

Shoji, A., Aris-Brosou, S., Fayet, A., Padget, O., Perrins, C., & Guilford, T. (2015). Dual foraging and pair coordination during chick provisioning by Manx shearwaters: empirical evidence supported by a simple model. *Journal of Experimental Biology*, *218*, 2116–2123. https://doi.org/10.1242/jeb.120626

Stearns, S. C. (1989). Trade-Offs in Life-History Evolution. *Functional Ecology*, *3*, 259–268.

Travaini, A., Donázar, J. A., Ceballos, O., & Hiraldo, F. (2001). Food habits of the Crested Caracara (Caracara plancus) in the Andean patagonia: The role of breeding constraints. *Journal of Arid Environments*, *48*(2), 211–219. https://doi.org/10.1006/jare.2000.0745

Tyson, C., Kirk, H., Fayet, A., Van Loon, E. E., Shoji, A., Dean, B., … Guilford, T. (2017).

Coordinated provisioning in a dual-foraging pelagic seabird. *Animal Behaviour*, *132*, 73–79. https://doi.org/10.1016/j.anbehav.2017.07.022

Warham, J. (1990). *The petrels: their ecology and breeding systems*. San Diego: Academic Press.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part II: Topical Studies in Oceanography*, *54*(3–4), 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Weimerskirch, H., & Jouventin, P. (1987). Population Dynamics of the Wandering Albatross , Diomedea exulans , of the Crozet Islands : Causes and Consequences of the Population Decline. *Oikos*, *49*(3), 315–322.

West, S. A., & Gardner, A. (2013). Adaptation and Inclusive Fitness. *Current Biology*, *23*(13), R577–R584. https://doi.org/10.1016/j.cub.2013.05.031

Williams, G. C. (1966). The Costs of Reproduction , and a Refinement of Lack's Principle. *The American Naturalist*, *100*(916), 687–690.

Chapter 2

Sex- and colony-specific strategies during pre-laying exodus in the Manx Shearwater

Abstract

In the interval between pre-breeding migration and egg-laying, Procellariform seabirds must replenish depleted body reserves in preparation for the upcoming breeding attempt. During this interval, males and females have asymmetric demands: the female must produce a large egg, which imposes additional energetic and nutrient demands, while the male must prepare body reserves for the first long incubation stint and may be constrained to remain near the colony by the need to defend the nest site from prospecting pairs. To meet these demands, all Procellariforms undertake a pre-laying exodus, usually involving a prolonged foraging trip for the female, and in some species, the male. A variety of sex-specific exodus strategies have been well documented in many species, however, relatively little is known about how exodus varies across different colonies within the same species.

In this study, a geolocator dataset spanning 10 years was used to characterise the pre-laying exodus in Manx Shearwater *Puffinus puffinus* from Skomer and Copeland – breeding colonies separated by 330 km in the seas off Britain. Exodus lasted an average of 21 days in Copeland females, significantly longer than in Skomer females by nearly three days. Geographical distributions during exodus were found to be markedly different between sexes within both colonies and between males from the two colonies, which mostly remained near to their colony, while females from the two colonies showed a high degree of overlap in their distribution along the continental shelf edge.

Behaviourally, there were both similarities and differences between sexes and colonies. Males visited land regularly at both colonies, but Skomer males visited land on a greater proportion of nights than Copeland males, which more often remained on land over the day. On Skomer, males increased their night-time visit frequency as the end of exodus approached,

whereas on Copeland there was no change in visit frequency over exodus. The mean amount of daytime allocated to flight did not differ between sexes or colonies, while females spent significantly more time resting and less time foraging compared to males, which was consistent across both colonies. Comparing within sexes between colonies, there were no differences in the amount of daytime allocated to different behaviours except that males from Skomer spent significantly more time resting at-sea compared to Copeland males. This may result from the Copeland males spending more time on land during the day, which they compensate for by being more active at-sea. Over the course of exodus, the amount of daytime allocated to different behaviours was relatively constant among males, whereas females dramatically increased time spent resting and reduced foraging and flight as the end of exodus approached, which may be explained by changing demands and flight/foraging efficiency as egg development proceeds.

Introduction

The energetic demands of organisms vary throughout the annual cycle (e.g. Green et al., 2009; Hegemann et al., 2012; Mugaas & King, 1981), and for migratory species, migration and reproduction are two of the most demanding stages. This is especially true in Procellariform seabirds, which typically undertake long-distance migrations and have protracted breeding seasons, involving long periods of fasting during incubation, time and energy-consuming commutes between the breeding colony and foraging grounds, and the need to catch enough prey to provision the chick while ensuring self-maintenance (Brooke, 2018). The long-term demands of migration and breeding can be so severe that costs carry-over between seasons, causing individuals to skip breeding in some years (Fayet et al., 2016; Shoji et al., 2015).

Between pre-breeding migration and egg-laying, Procellariforms remodel their physiology and replenish their body reserves in preparation for breeding (Arizmendi-Mejía et al., 2013). This is an important period, as body condition has a significant effect on breeding success (Chastel et al., 1995), and body condition sufficient for breeding must be achieved rapidly if there are benefits to early breeding (Perrins, 1966). At the same time, pair bonding, nest maintenance, territory defence, copulation and egg development occur (Warham, 1990). Egg development represents a significant added burden on the female. Procellariforms generally produce a single, large, slow-developing egg (around 15% of the female body mass in Manx Shearwater; Brooke, 1990), for which females must adjust their food intake to meet the additional energetic and nutrient demands, while carrying an increasingly heavy load that impairs flight and foraging efficiency (Williams, 2005; Witter & Cuthill, 1993). Meanwhile the male must prepare for a potentially long period of fasting, since the female usually returns to sea shortly after laying leaving the male to take the first long incubation stint (Warham, 1990).

To improve body condition before incubation and meet the demands of egg development, all Procellariforms undertake a pre-laying exodus, characterised by a period of absence from the breeding colony prior to laying (Brooke, 2018). The nature of exodus varies extensively between species in two major respects. Firstly, the duration of the exodus ranges from as little as two days in Shy Albatross *Thalassarche cauta* (Abbott et al., 2006) to as much as two months in Grey-faced Petrel *Pterodroma macroptera* (Imber, 1976). Secondly, the distance travelled during exodus varies dramatically between species, with some remaining within a few hundred kilometres of the colony while others travel thousands of kilometres from the colony. For example, Shy Albatross forage within 300 km of the breeding colony during their short exodus (Abbott et al., 2006), whereas Murphy's Petrel *Pterodroma ultima* travel up to 3800 km away from their colony (Clay et al., 2017).

Despite relatively little sexual dimorphism in most Procellariforms, sex-specific strategies during exodus are well documented, with significant variation in the magnitude and direction of these differences between species. In some species including Balearic Shearwater *Puffinus mauretanicus* (Guilford et al., 2012) and Manx Shearwater *Puffinus puffinus* (Guilford et al., 2009), the female departs the colony for a relatively long period while the male continues to visit the colony regularly, with the female travelling further from the colony than the male. In other species like Northern Fulmar *Fulmarus glacialis* (Macdonald, 1977) and Sooty Shearwater *Ardenna grisea* (Hedd et al., 2014), both the male and female depart the colony for relatively lengthy periods, but the male does so for a shorter duration and remains closer to the colony than the female. Finally, in some species, the male and female depart the colony for similar lengthy periods but the male travels further from the colony than the female, as in Barau's Petrel *Pterdroma baraui* (Pinet et al., 2012), Murphy's Petrel (Clay et al., 2017) and Chatham Petrel *Pterodroma axillaris* (Rayner et al., 2012).

Although some Procellariform species breed in a single restricted area, others breed in multiple colonies that are geographically and ecologically distinct. Several studies have identified differences in breeding behaviour between individuals from different colonies, including differences in foraging trip duration and incubation stint lengths (for examples from Albatross species see Hedd & Gales, 2005). In contrast, relatively little is known about variation in exodus between colonies. Such knowledge is important because comparisons between colonies can be used to test how geographical and ecological factors shape exodus, whilst other factors that typically differ between species remain constant.

The current study aims to characterise the pre-laying exodus of Manx Shearwaters from two breeding colonies 330 km apart in the seas off Britain. Specifically, it aims to elucidate differences in exodus strategies between sexes and identify whether and how these strategies differ between colonies. The pre-laying exodus of Manx Shearwaters breeding on Skomer Island – one of the colonies studied here – has been studied previously for one season using geolocator data (Guilford et al., 2009) and over four seasons using a combination of GPS and geolocator data (Dean, 2012). These studies showed that female Manx Shearwaters from Skomer usually undertake a longer-duration exodus trip and travel further from the colony compared to males; females forage mostly around the continental shelf edge, while males mostly remain within 150 km of Skomer. When the female is absent from the colony, the male continues to visit the breeding burrow amid shorter foraging trips.

Here, this knowledge is extended by examining exodus from 10 years of geolocator data collected at the Skomer and Copeland Manx Shearwater colonies. The dataset of salt-water immersion and light data was used both to infer behavioural parameters and to estimate the geographical locations of Manx Shearwater on a twice-daily basis. Firstly, the colony-visiting behaviour of males was examined to test whether this behaviour varies over the course of exodus and between colonies. Secondly, the spatial distribution of birds during exodus was characterised and compared across sexes and colonies to identify whether birds from Copeland travel to the same or different areas compared to Skomer birds, and whether they too show spatial segregation of sexes. Lastly, temporal and spatial variations in behaviour during exodus were analysed to test whether males and females adjust their behaviour over the course of exodus and in different locations, and whether birds from different colonies show colony-specific behavioural strategies. This study is the first to identify how behaviour changes over the course of exodus in Manx Shearwater, and it is also the first to identify the exodus distribution of birds from the Copeland Islands, which show both similarities and differences to Manx Shearwaters breeding on Skomer.

Materials and methods

Study populations and geolocator deployments

This study is based on data collected between 2008-2017 from two breeding colonies of Manx Shearwater: one on Skomer Island off the Pembrokeshire coast of Wales (51°440 N, 5°190 W) and the other on Lighthouse Island in the Copeland Islands off the east coast of Northern Ireland (55°696 N, 5°525 W). Both colonies are part of a long-term tracking programme that has been ongoing since 2007. Breeding Manx Shearwaters were fitted with geolocators (from BAStrack and Migrate Technology) weighing 2.5 grams or less. Each device was attached with two lightweight cable ties to a plastic leg ring fitted around the tarsus. A metal BTO ring was fitted to the other tarsus so that individuals could be identified on recapture. Geolocators were normally retrieved and downloaded annually when birds were recaptured in their breeding burrows, but some were retrieved after as long as three years at-sea.

Field work was carried out with approval from the British Trust for Ornithology, the Skomer and Skokholm Islands Advisory Committee, the Countryside Council for Wales and the University of Oxford Local Ethical Review Committee. To minimise possible impacts on birds, handling time during deployment and retrieval of devices was kept to a minimum and did not exceed 10 minutes. The relative weight of geolocators ranged between 0.2%-0.8% of adult body weight, well under the suggested 3% limit (Phillips et al., 2003). Throughout the tracking project, impact assessments have been undertaken to compare the study population on Skomer (the most intensively monitored site) and an adjacent population of unmanipulated Manx Shearwaters. These showed no detectable negative impact of tracking and monitoring, including long-term geolocator deployment, on adult breeding success and survival in the Skomer study population (Shoji et al., 2015; Tyson et al., 2017).

Geolocator data

Electrical conductivity sensors on geolocators detected every three seconds whether they were immersed in salt-water, and devices recorded the number of immersed detections in 10-minute bins as a score of 0-200 (completely dry to completely immersed). The maximum ambient light intensity measured in each 10-minute bin was also recorded on geolocators, with light intensities clipped to a maximum of 64 lux.

All geolocator data processing and analysis was carried out in R 3.4.4 (R Core Development Team 2018). Pre-processing of raw geolocator data was first performed to: standardise data to a consistent format (that used by Biotrack devices); split each immersion and light trace into separate years; and to join trace sections that were recorded on the same bird in the same year but on separate deployments. In total, 364 distinct years were accounted for from Skomer birds and 156 distinct years from Copeland birds. Figure 1 shows an example of an immersion and light trace recorded for a complete year. Traces varied in completeness from two days to the full year (Supplementary Figure 1), and incomplete traces varied in which portions of the year they covered. Gaps were also present within some traces in which the geolocator battery died before the device was retrieved, or where a geolocator was not immediately redeployed after retrieval of a previous deployment.

With all geolocator data organised into distinct years, data were filtered to remove traces that lacked the potential to contain a full exodus period, leaving a subset of candidate exodus traces (hereafter referred to as candidate traces). Three filtering steps were used: (i) traces were removed if they did not contain any data from the potential period of egg laying, here defined as the 20th April – 6th June; (ii) traces were removed if egg lay date was known from monitoring records and was not contained in the trace; and (iii) traces were removed if they began during the incubation stage. For filtering, incubation was identified by visual inspection of immersion traces for the distinctive pattern of sequential multi-day dry periods interspersed with periods of mainly non-zero immersion scores (e.g. Figure 1).

Data were also filtered to remove traces that did not contain an incubation stage or a known lay date. Although such traces may have contained an exodus, it would have been impossible to identify the exodus from the immersion data since lay date could not be inferred without incubation (see methods below). For Skomer, 97 candidate traces from 59 individuals were identified from filtering the 364 original traces. Whilst for Copeland, 53 candidate traces from 30 individuals were identified from filtering the 156 original traces. These candidate traces formed the dataset for the remainder of the analysis.

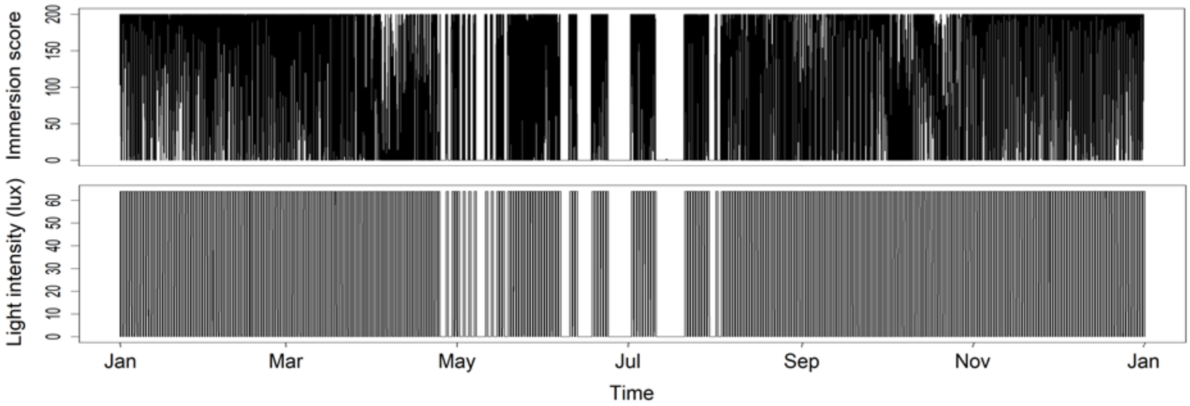


Figure 1. An example immersion and light trace from a female Manx Shearwater, FB05298, which bred on Skomer in 2009. Days spent at the colony can be identified as days that are dry and dark, since Manx Shearwaters remain in their dark burrow when on land during the day. Prolonged periods of dry-dark in June and July are incubation stints interspersed with foraging trips at sea. Periods on land in April and May show pre-laying visits to the colony.

Determination of sex

Sexing by cloacal inspection

Accurate determination of sex was essential, both because sex was required to identify exodus from immersion traces, and because comparisons between sexes were a key aim of this study. The Manx Shearwater is a sexually monomorphic species, and numerous attempts to identify diagnostic plumage and biometric differences between males and females have been unsuccessful (Brooke, 1990). However, Manx Shearwaters can be accurately sexed by examining the cloaca of incubating birds immediately after their egg is discovered. At this time, the male cloaca appears small and pink, whereas the female cloaca appears swollen and chalky (Brooke, 1990). In this study, 48 individual birds from Skomer represented by 68 candidate traces were sexed by cloacal inspection. The remaining 11 individuals from Skomer were not sexed by cloacal inspection, and since the colony was not monitored during the laying period, none of the 30 individuals from Copeland were sexed by cloacal inspection.

Sexing by behaviour: colony attendance at the start of incubation

For individuals not sexed by cloacal inspection, sex was determined behaviourally from pairs of immersion traces simultaneously recorded on breeding partners. Initially, a method was trialled to determine sex by colony attendance at the start of incubation: if only one partner was on land on the first day of incubation, then this partner was labelled as female; if both partners were on land on the first day of incubation, then whichever partner returned to sea first was labelled as female. To enable this, time spent on land was classified in candidate traces as ≥3 hours of constant dry-dark, and behavioural traces were generated to show time spent on land vs. at sea. The first day of incubation was defined as the first day on land that was proceeded by a prolonged continuous presence on land in alternating shifts between partners (Figure 2).

The method was tested on 7 pairs of candidate traces recorded from 5 breeding pairs on Skomer, all of which had been independently sexed by cloacal inspection (Figure 2). For 6 pairs of traces (A-E, G) sexes determined behaviourally by colony attendance at the start of incubation matched those found by cloacal inspection. The remaining pair (F) were incorrectly sexed, as the female took the first long incubation stint even though the male was on land with the female for the first day of incubation (Figure 3).

The presence of a classification error in such a small sample of traces undermined the validity of the incubation attendance method to accurately determine sex. Indeed, it has been shown that even when both partners visit the colony simultaneously, they may not encounter each other in the burrow (Tyson et al., 2017). In addition, the method assumes that the male always begins incubating as soon as he finds an egg in his burrow, thought to be an adaptation to allow the female to return to sea to replenish her body reserves, which become depleted during the egg building process (Brooke, 1990; Dean, 2012). However, from personal observations at the Skomer study site, females occasionally take the first incubation stint even after males have visited and the egg has been present. In addition, most males (24/29 males from paired candidate traces) were found to visit land for at least one full day during exodus, and if this were to occur the day before the female returned to lay, then the male could be erroneously classified as the female. Given these limitations, the method was deemed unreliable, and an alternative method of behavioural sexing was used.

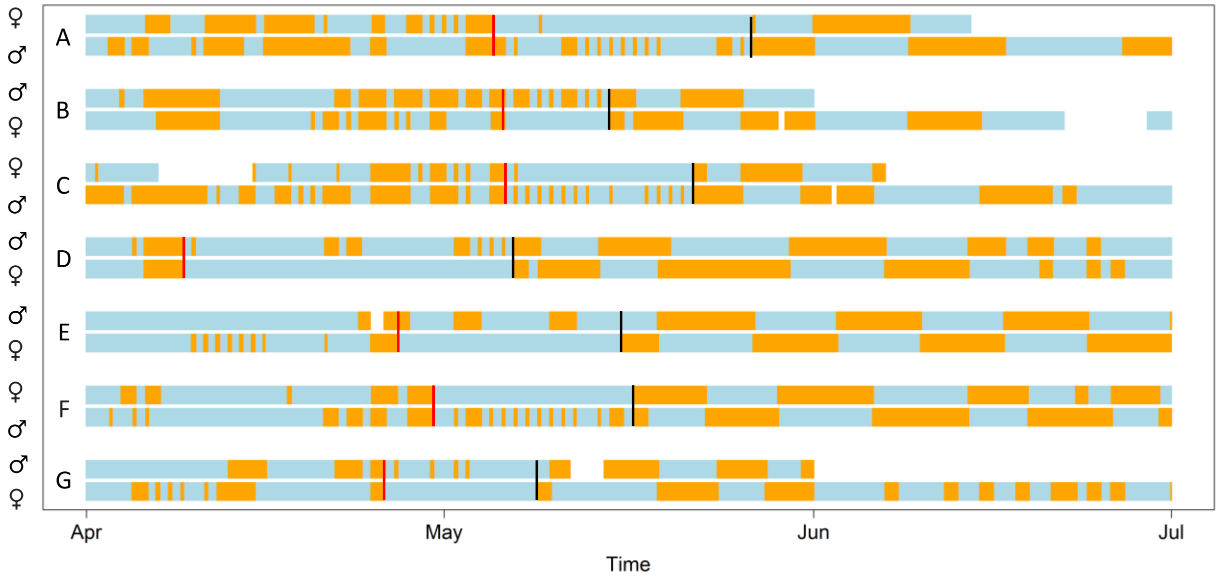


Figure 2. Paired behavioural traces for the seven breeding pairs (A-G) from Skomer that were sexed by cloacal inspection, with sex shown to the left of each trace. Light blue segments indicate time at sea, and orange segments indicate time at the colony. White gaps in some traces are the result of gaps between separate geolocator deployments. The first day of incubation is shown by vertical black lines. The last day before incubation when both partners were on land is shown by vertical red lines. Through the incubation attendance method, sex was correctly determined (i.e. matched sex determined by cloacal inspection) for pairs A-E and G, whilst pair F was incorrectly sexed. Through the pre-laying attendance method, sex was correctly determined for all individuals.

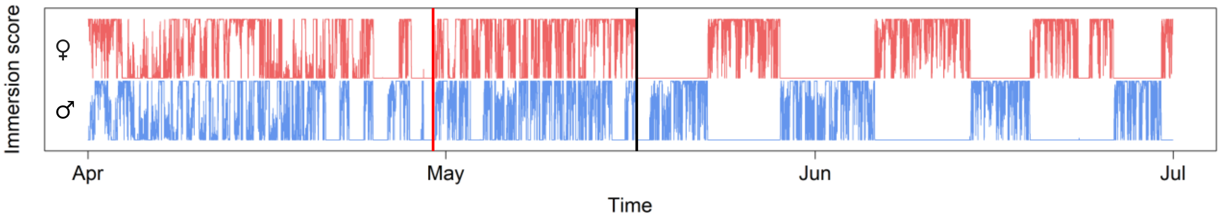


Figure 3. The paired immersion traces used to generate the behavioural traces for breeding pair F shown in figure 2. The start of incubation is marked by the vertical black line. The last day before incubation when both partners were on land is shown by vertical red lines. Although both the female (upper red trace) and male (lower blue trace) are on land on the first day of incubation, the female remains at the colony to take the first incubation stint while the male returns to sea to forage. Sex was incorrectly determined by the incubation attendance method, but correctly determined by the pre-laying attendance method.

Sexing by behaviour: pre-laying colony attendance

For Manx Shearwaters that had not been sexed by cloacal inspection, Kirk (2016) developed a technique to infer sex from pre-laying behaviour identified in immersion traces, based on a similar method applied in Balearic Shearwaters (Guilford et al., 2012). The method utilised differences in colony attendance between males and females during the pre-laying exodus, when the female departs the colony for upwards of 10 days while the male visits the colony during his partner's absence, often regularly (Brooke, 1990). Here, the start of exodus was defined from paired geolocator traces as the last full day that both partners spent on land together before incubation, and the end of exodus was defined from paired geolocator data as the start of incubation (incubation defined as previously described). Looking specifically at the exodus period for each bird in a pair, the individual that visited land with the highest frequency was identified as the male and the other as the female (Figure 2).

Using a feature of the pre-laying exodus to determine sex raises the concern that bias could be imposed, especially since comparisons of exodus between sexes were a key feature of this study. However, no bias should occur so long as the method accurately determines sex. Several lines of evidence support the use of pre-laying attendance as a highly accurate method to determine sex, and hence the validity of its use in this study.

Firstly, from monitoring burrows at breeding colonies and from GPS and geolocator tracking of individuals during pre-laying exodus, it has been firmly established that the male Manx Shearwater visits the colony during exodus whilst the female is absent (Brooke, 1990; Dean, 2012; Guilford et al., 2009). Secondly, the method has been tested previously on geolocator data from 31 individual Manx Shearwaters, and sex determined by pre-laying attendance matched sex determined by cloacal inspection in all cases (Kirk, 2016). Finally, the method was tested on the same 7 pairs of immersion traces that were used to test the incubation attendance method, and the sexes determined by pre-laying attendance matched those determined by cloacal inspection for all 7 pairs (Figure 2). Given the weight of evidence supporting the accuracy of the method, pre-laying attendance was used to behaviourally determine sex for all simultaneously recorded breeding partners which were not sexed by cloacal inspection.

Among Skomer birds, 7 pairs of candidate traces from 4 breeding pairs of Manx Shearwater were sexed solely by inspection of paired immersion traces. For the 3 breeding pairs that were recorded in 2 separate years, the assigned sexes matched between years. The 8 individuals sexed by inspection of paired immersion traces were represented by 23 candidate traces. Combined with candidate traces from individuals sexed by cloacal inspection, a total of 91 candidate traces from Skomer were successfully assigned a sex. 3 individuals from Skomer represented by 6 candidate traces were not sexed, since there were no candidate traces from their breeding partners*.

Among Copeland birds, 15 pairs of candidate traces were recorded from 11 breeding pairs / 21 individuals: 2 pairs were recorded in 2 separate years, 1 pair was recorded in 3 separate years, and 1 individual was recorded in 2 separate years but with a different partner in each. For individuals sexed repeatedly in different traces, the assigned sex was the same in every case. Since no birds were sexed by cloacal inspection on Copeland, all 21 individuals were sexed by inspection of paired immersion traces and were represented by 44 candidate traces. 9 individuals from Copeland represented by 9 candidate traces were not sexed, since there were no candidate traces from their breeding partners*.

*Due to reduced reliability of identifying exodus for a single trace without knowledge of its sex, an individual was not sexed behaviourally if there was no candidate trace from the breeding partner. Since sex was required for later stages of the analysis, candidate traces from birds of unknown sex were dropped from the analysis.

Identification of exodus periods

Exodus periods were identified differently for males and females. For females, exodus was defined as the period between the last full day on land before incubation begun (which coincided with the male's presence on land in all 29 paired candidate traces e.g. Figure 2) and the day on which the egg was laid. For males, exodus was defined as the period between the last full day on land before incubation that coincided with the female (this could only be determined from paired candidate traces) and the first visit to land when the egg was present, which usually corresponds to the first incubation stint because male procellariforms typically start incubation as soon as they discover an egg in their burrow (Warham, 1990). Using these definitions, two key dates were required to identify the end-date of exodus: (1) for males, the start date of their first incubation stint, and (2) for females, the egg lay date.

Identification of exodus end-dates from lay dates identified in the field

During the laying period on Skomer, most study burrows were monitored daily to record when an egg first appeared. A record of this data has been kept for Skomer study burrows since 2009, from which lay dates were found for 52 candidate traces. These dates defined the end of exodus in female candidate traces (n=25), while the first visit to land on or after the lay date (determined from geolocator data) defined the end of exodus in male candidate traces (n=27). The remaining 39 candidate traces from Skomer lacked lay dates as their burrows were not monitored daily, and all 44 candidate traces from Copeland lacked lay dates as Copeland burrows were not monitored during the laying period. For these candidate traces, the dates of the key breeding events were inferred from immersion traces.

Identification of exodus end-dates from paired candidate traces

Firstly, paired candidate traces recorded simultaneously on breeding partners were used, with lay dates identified as the date on which incubation begun. As before, the first day of incubation for paired traces was defined as the first day on land that was proceeded by a prolonged continuous presence on land in alternating shifts between partners (Figure 2). This was tested on 4 pairs of candidate traces from Skomer for which lay date had been recorded in the field. Lay dates inferred from paired candidate traces matched exactly those recorded in the field for all pairs, supporting the efficacy of the technique to accurately identify lay dates. The technique was used to infer lay dates for 10 pairs of candidate traces from Skomer and 15 pairs from Copeland for which lay dates had not been recorded in the field. These dates defined the end of exodus in female candidate traces, while the dates of the first visit to land on or after the lay date defined the end of exodus in male candidate traces

Identification of exodus end-dates from single candidate traces

For the remaining 19 candidate traces from Skomer and 14 candidate traces from Copeland that lacked lay dates, simultaneous candidate traces had not been recorded for the breeding partner and it was therefore not possible to classify incubation by a prolonged continuous presence on land in alternating shifts between partners. Instead, an algorithm was developed to identify incubation stints in single traces from the pattern and duration of visits to land, which (as before) were classified from candidate traces as ≥3 hours of constant dry-dark. The algorithm was refined using the 51 candidate traces from Skomer for which lay date had been determined by daily burrow monitoring. The algorithm classified incubation stints in the following way: (i) incubation stints could only be assigned between 27th April – 26th July, the window in which incubation can occur; (ii) periods of ≥3 consecutive days on land within the window were assigned as incubation stints; and (iii) if the earliest incubation stint was more than 14 days before the start the of the next stint, then the early stint was discounted as a pre-laying visit to land.

Using these parameters, the first incubation stint assigned by the algorithm matched the true first incubation stint determined from the known lay date in 22/24 female and 25/27 male candidate traces. For the other 4 candidate traces, the first incubation stint assigned by the algorithm matched the second true incubation stint determined from the known lay date, since each of the first true incubation stints in these 4 traces were only 2 days in length. Manx Shearwater incubation stints typically last upwards of 5 days, but they can be as short as 1-2 days (Brooke, 1978). A lower threshold of 2 or more days on land meant the algorithm correctly classified all first incubation stints in the 51 candidate traces with known lay dates, however, this threshold classified pre-laying visits to land as the first incubation stint in 5 candidate traces. As the best compromise, the threshold of ≥3 days on land was used in the final algorithm.

The start date of the first incubation stint assigned by the algorithm defined the end of exodus in male candidate traces. However, the start date of the first incubation stint assigned by the algorithm did not necessarily define the lay date (i.e. the end of exodus) in females. Female Procellariforms usually incubate their newly laid egg until the male visits the burrow and takes over incubation (Warham, 1990). If the male took over incubation and the female returned to sea in <3 days after the egg was laid, then the start date of the first female incubation stint assigned by the algorithm would not correspond to the lay date. If the male took over incubation and the female returned to sea in ≥3 days after the egg was laid, then the start date of the first female incubation stint assigned by the algorithm would correspond to the lay date. To distinguish between these two possibilities, a simple criterion was used to identify lay date from the first incubation stint assigned by the algorithm for female candidate traces: If the female visited land for ≥3 hours within 14 days of the start date of the first incubation stint, then this day was assigned as the lay date, otherwise the start date of the first incubation stint was assigned as the lay date. This method was tested on 24 candidate traces from Skomer females, comparing lay dates assigned from incubation stints to those recorded in the field. The lay dates matched for all candidate traces.

Using these methods to identify exodus end-dates from single traces, Incubation stints were assigned to 19 candidate traces from Skomer and 14 candidate traces from Copeland that lacked a known lay date and for which there was no candidate trace from the breeding partner. These included 6 candidate traces from Skomer females and 9 from Copeland females for which lay date was identified using the technique described above.

Identification of exodus start-dates from candidate traces

With the end dates of exodus identified for 91 candidate traces from Skomer and 44 candidate traces from Copeland, exodus start dates were identified. For females (Skomer: n=40; Copeland: n=24), the exodus start-date was defined as the last full day on land before the lay date. This was chosen on the basis that, from paired data from breeding pairs (n=29 pairs), the female's last full day on-land always coincided with the male also being on land for the full day, and this likely corresponds to when mating occurred (Dean, 2012). For males, the exodus start-date was defined as the last full day on land before the lay date that coincided with the female. This could only be determined for the 14 male candidate traces from Skomer and 15 male candidate traces from Copeland for which the partner candidate trace could be examined, since most males (24/29 males from paired candidate traces) visited land for at least one full day during exodus (range 1-7 days). This made it more difficult to reliably determine exodus start-date for single male candidate traces, as full-day visits to land during exodus must be distinguished from full-day visits to land at the start of or before exodus.

For the 33/36 single male candidate traces from Skomer and 5/5 single male candidate traces from Copeland, the first full day on-land before a specific date (calculated as the end-date of the exodus minus 10 days for Skomer or 11 days for Copeland – the minimum duration of exodus among females for the respective colony) was used to define the exodus start-dates. For such males, the defined exodus possibly excluded early portions of the full exodus, since males are known to visit land during exodus, and any full-day visit to land prior to 10 / 11 days before the end of exodus would be classified as the start of exodus, regardless of whether this was the start of exodus or a visit to land during exodus. However, this limitation was preferred to an alternative higher threshold (e.g. the mean duration of female exodus), which would increase the likelihood of including pre-exodus periods within exodus. For analyses in which partial exodus might introduce bias, these exodus periods were excluded and only paired males (Skomer: n=14; Copeland n=15) were analysed. 3/55 single male candidate traces from Skomer were dropped from the analysis, since, the candidate trace begun fewer than 10 days before the end-date of exodus.

In summary, from 150 candidate immersion traces, 132 exodus periods from 76 individual Manx Shearwaters were identified, including 88 exodus periods from Skomer (40 females, 48 males) and 44 exodus periods from Copeland (24 females, 20 males). Of these, 29 pairs of exodus periods were simultaneously recorded for both partners of breeding pairs, consisting of 14 pairs from Skomer and 15 pairs from Copeland. A breakdown of the years in which exodus periods were recorded split by sex and colony is presented in Table 1.

Year	Males		Females		Yearly Totals
	Skomer	Copeland	Skomer	Copeland	
2008	5	0	4	0	9
2009	7	5	3	5	20
2010	4	5	3	6	18
2011	9	5	7	4	25
2012	6	0	5	0	11
2013	0	2	1	0	3
2014	4	0	9	2	15
2015	6	3	3	3	15
2016	7	0	4	1	12
2017	0	0	1	3	4

Table 1. Numbers of exodus identified from each island and sex by year.

Behavioural annotation

Behaviour at-sea

Immersion data were used to infer at-sea behavioural states for each 10-minute time bin. This is possible because different behaviours correlate with different salt-water immersion scores and patterns. In previous studies, high resolution biologging data (e.g. from GPS, dive loggers and accelerometers) have been used in combination with immersion and light data to annotate behaviour using various machine learning methods (Guilford *et al*. 2008, Dean *et al.* 2012, Freeman *et al*. 2013). In this study, a simple threshold method was used to classify immersion data into 3 behavioural categories: (i) resting at-sea, with an immersion score ≥96% wet; (ii) flying, with an immersion score ≤4% wet; and (iii) foraging, with an immersion score >4% wet and <96% wet. A similar annotation system was used by Fayet *et al*. (2016) on immersion data from Atlantic Puffins *Fratercula arctica*. In Puffins, foraging typically involves short flights interspersed with feeding from the water's surface and diving under the surface, leading to intermediate immersion scores. Manx Shearwaters forage in a broadly similar fashion, and the use of immersion data to infer behaviour in the species has been validated through co-deployments of geolocators, dive loggers and GPS (Dean et al., 2012).

Visits to land

In addition to behaviour at-sea, visits to the colony were classified from immersion data. Over-day visits to the colony were identified using the threshold of >75% dry scores per day. This threshold was validated by light levels during daylight hours that were equivalent to night-time light levels, since Manx Shearwaters remain in their burrow when they are on land during the day due to the high risk of predation on the surface (Brooke, 1990). Visits to land at night were more difficult to identify, as they must be distinguished from periods of night-time flight. Dean (2012) showed that Manx Shearwaters at-sea spent a large proportion (c.80-95%) of the night immersed during exodus, leading to the expectation that night time flight should be relatively short compared to visits to land, which may last most of the night (Brooke, 1990). Figure 4 shows the frequency distribution of different durations of continuous dry periods between civil dusk and civil dawn during exodus, from which it was clear that the lengths of visits to land and night-time flight overlapped very little. More than 50% short (<3 hour) dry periods occurred during nautical twilight, when Manx Shearwaters are known to be relatively active and make short flights between rafting on the water, whilst the long (≥3 hour) dry periods occurred mostly after nautical dusk and before nautical dawn, when Manx Shearwaters at-sea spend most time immersed (supplementary figure 2; Dean, 2012). Based on this, visits to land at night were identified as ≥3 hours of continuous dry.

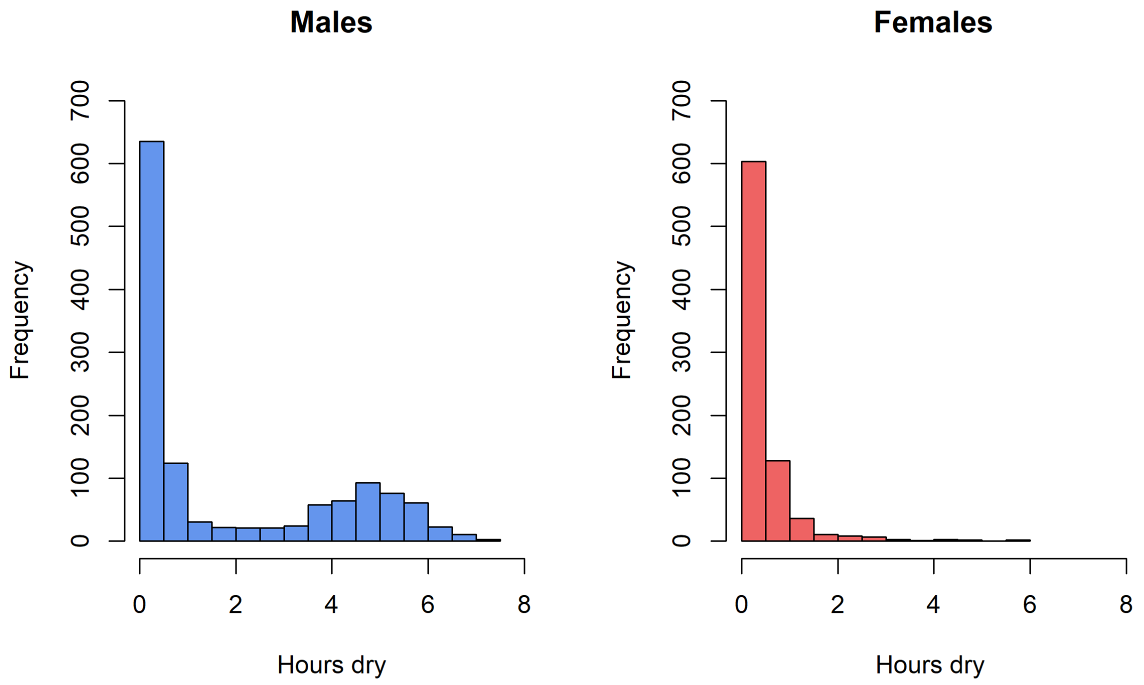


Figure 4. Histograms showing the frequency of durations of continuous dry data for each sex between civil dusk and dawn during exodus periods. Females usually do not visit land during exodus, and the high frequency of short (< 3 hour) dry periods are interpreted as periods of flight during twilight and night. Males are known to visit land during exodus, and here they show a bimodal distribution of durations of continuous dry periods. The high frequency, short (< 3 hour) dry periods are interpreted as short flights during twilight and night, while lower frequency, long (≥ 3 hour) dry periods are interpreted as visits to the colony.

Determining locations from light data

Light data were used to determine the locations of geolocators. Light-level geolocation requires twilight events (e.g. sunrise and sunset) to be defined using a light threshold to identify transitions between day and night. From the timings of these twilight events recorded by a known internal clock, latitude can be estimated by day length and longitude can be estimated by the times of sunrise and sunset.

All processing and analysis of light data was carried out using the GeoLight package in R. Firstly, the 'twilight' function was used to automatically extract times of dawn and dusk for each day using a light threshold of 3 lux. All twilight times were visually checked against each light curve to manually correct errors caused by irregularities in the light data. Secondly, the ‘coord’ function was used to calculate geographical coordinates for each pair of twilight events, generating a location for each midday and midnight. To do this, the sun elevation angle corresponding to the set light threshold must be inputted into the ‘coord’ function. To determine the best sun elevation angle, locations were calculated for multiple elevation angles between -8° and -2°, and for each angle, locations were plotted on maps of western Europe and the surrounding seas (Supplementary Figure 3). Maps were compared visually to qualitatively assess the plausibility of locations, specifically, the positions of clusters of Manx Shearwaters relative to their colonies and the overlap of cluster-centres with land. A single sun elevation angle of -5.5° was selected and used for all location calculations, which minimised implausible cluster centres over land. Although not used for the selection of the sun elevation angle, the value of -5.5° was further supported by the observation that location clusters of Skomer individuals qualitatively matched those found by GPS tracking of Manx Shearwater during exodus for an overlapping time period (Dean, 2012).

Locations were finally filtered to remove implausible locations that resulted from remaining light curve errors, or from significant clock faults. This was done by visually checking the tracks for each exodus period. Implausible locations were defined as tracks for which no single point fell within the -20° to 5° longitude and 40° to 60° latitude. In addition, individual points were removed if they were >1000km from the previous and subsequent positions. In total, final locations were retained for 41 male and 35 female exodus periods from Skomer, and 19 male and 20 female exodus periods from Copeland.

Kernel density estimation and mapping

Kernel density estimation was used to generate occupancy contours from the light-derived coordinate locations. This was carried out in ArcGIS 10.3 (ESRI), Geospatial Modelling Environment (GME, Spatial Ecology) and R. For each sex from each colony, coordinates were combined into a single csv file and point shapefiles were generated for each group. The point shapefiles were processed using the 'kde' function in GME to generate raster representations of kernel density estimates, with a bandwidth of 0.5° and a cell size of 0.1° to produce contiguous cores without over-smoothing. 75%, 50% and 25% occupancy contours were calculated from kernel density estimates using the 'isopleth' function in GME, and these final polygon shapefiles were imported to R for plotting. Base maps, including bathymetry data to illustrate the location of the continental shelf edge, were generated using the Marmap package in R, using data downloaded from the NOAA bathymetry database. Areas and overlaps of 25% occupancy kernel polygons were calculated using the 'area' and 'intersect' functions in the raster package in R. Percentage overlaps were calculated as the overlap area divided by the total area of both overlapping kernels.

Statistics

Statistical analyses were carried out in R. All means have associated standard error, unless otherwise stated. For comparisons of exodus metrics (exodus timings, visits to land, behaviours) between sexes and colonies, means were calculated for each exodus, and group means were calculated from these individual means to prevent longer exodus periods from carrying more weight e.g. the mean proportion of days spent on land for each exodus was calculated as the number of over-day visits to land divided by the total number of days in the exodus, and population means were computed from these values. Comparisons of exodus metrics were made using welch two-sample t-tests, to account for the unequal variance between groups. Multiple linear regressions were carried out using the ‘lm’ function in R for normally distributed data, and logistic regression was performed using the ‘glm’ function in R for binomially distributed data. To visualise temporal variation in behaviour over the course of exodus, days were aligned from the end of exodus, and for each day before the end-date, the mean number of hours spent in each behaviour during daylight was calculated and plotted with 95% confidence intervals to represent whether days were significantly different between sexes and colonies.

To visualise spatial variation in behaviour during exodus, 25% occupancy kernels were calculated from subsets of daily locations at which each behaviour was predominant. Each of these locations was weighted by the proportion of daylight (civil dawn to dusk) allocated to that behaviour, such that locations with 90% of daylight allocated to behaviour-x carried twice the weight of locations with 45% of daylight allocated to behaviour-x. The subset of daily locations in which behaviour-x was predominant consisted of all locations at which the ‘daily behavioural index’ for behaviour-x was greater than that of the other two behaviours. The behavioural index B for day i was calculated for each behaviour within each exodus e, using the formula: $B_{e(i)} = (b_{e(i)} – \min(b_e)) / (\max(b_e) – \min(b_e))$ where b is the proportion of daylight allocated to the specific behaviour. The daily behavioural index for each behaviour ranged from 0 to 1 within each exodus, therefore allowing predominant behaviour for each daily location to be determined relative to the baseline levels of behaviour within each exodus.

Results

Duration and timing of exodus

Mean duration, start-date and end-date of exodus were compared across colonies and sexes (Table 2). Exodus duration of males and females was similar within colonies, at 18.7 days (±1.48, n=14) and 18.3 days (±0.77, n=40) on Skomer, and 20.5 days (±0.90, n=15) and 21 days (±0.77, n=24) on Copeland, respectively (welch two-sample t-tests; Skomer: df=20, t=0.24, p=0.82; Copeland: df=31, t=0.38, p=0.71). Among males there was no significant difference in exodus duration between colonies (welch two-sample t-test; df=21, t=1.07, p=0.29), while exodus duration of Copeland females was 2.7 days / 15% longer than that of Skomer females (welch two-sample t-test; df=57, t=2.48, p=0.016).

Mean exodus start-date and end-date did not differ significantly across colonies or sexes (Table 2). Mean exodus start-date ranged from 27th April (±2.3 days, n=24) in Copeland females to 30th April (±1.5 days, n=40) in Skomer females (welch two-sample t-test; df=42, t=1.08, p=0.28), and mean end-date ranged from 17th May (±1.4 days, n=14) in Skomer males to 19th May (±2 days, n=15) in Copeland males (welch two-sample t-test; df=21, t=1.078, p=0.29). This concurs with a previous analysis of geolocator data which found no significant difference in lay date between Skomer and Copeland Manx Shearwaters (Kirk, 2016).

Visits to land during exodus

Visits to land during exodus were compared across colonies and sexes (Table 2). Manx Shearwaters only come ashore at night and usually return to sea before dawn, however they sometimes remain in the burrow over-day (here defined as between civil dawn and dusk). Females were not found at the colony over-day during exodus, as the last over-day visit before

Table 2. Comparing exodus metrics between islands for each sex. All values are population means, calculated from the means of each individual so that longer exodus periods did not carry more weight in calculations. Bracketed values are standard errors of the means.

Sex	Colony	Number	Duration of exodus (days)	Start-date	End-date	Proportion of nights spent at the colony	Duration of night-time visits to land (hours)	Proportion of days spent at the colony	Proportion of exodus spent on-land
Males	**Skomer**	14	18.7 (1.48)	28-Apr (1.9 days)	17-May (1.4 days)	0.66 (0.06)	5.47 (0.16)	0.09*[4] (0.02)	0.21 (0.02)
	Copeland	15	20.5 (0.90)	28-Apr (2.0 days)	19-May (2.0 days)	0.51 (0.04)	5.09*[3] (0.18)	0.18*[4] (0.02)	0.24 (0.02)
Females	**Skomer**	40	18.3*[1] (0.77)	30-Apr (1.5 days)	18-May (1.3 days)	0.01*[2] (0.003)	4.63 (0.52)	0 (0)	0.001 (0.0005)
	Copeland	24	21.0*[1] (0.77)	27-Apr (2.3 days)	18-May (1.8 days)	0.02*[2] (0.006)	4.04*[3] (0.36)	0 (0)	0.002 (0.0009)

Welch two-sample t-tests: [1] t=2.48, p=0.016; [2] t=2.12, p=0.041; [3] t=2.62, p=0.024; [4] t=2.59, p=0.015. Only a selection of statistically significant results is shown here, see main text for full test results of all comparisons.

Table 3. Number of days spent on land over-day during exodus.

Days on land	0	1	2	3	4	5	6	7
Skomer Males	5	1	5	1	1	0	0	1
Copeland Males	0	2	3	3	3	0	3	1

the lay date was used to define the start of their exodus. In contrast, some males were found to occasionally stay in the burrow over-day (Table 3). Copeland males were significantly more likely to remain in the burrow over-day at least once during exodus: 9/14 Skomer males spent ≥1 days on land while all Copeland males (n=15) spent ≥1 days on land (chi-squared test; df=1, χ^2=4.21, p=0.04). Copeland males also spent a greater proportion of days on land during exodus, with 9% (±2%, n=14) of days spent on land in Skomer males and 18% (±2%, n=15) of days spent on land in Copeland males (welch two-sample t-test, df=26, t=2.59, p=0.015).

Manx Shearwaters more often visit land at night and returned to sea before dawn (Figure 5). All males visited land on ≥4 nights during exodus (mean=10.7 ±0.76, n=29). In contrast, no female visited land on >2 nights during exodus (mean=0.2 ±0.06, n=64). 52 females did not visit land at all, 11 females visited land on 1 night, and 1 female visited land on 2 nights. Skomer and Copeland males visited land on 66% (±6%, n=14) of nights and 51% (±4%, n=15) of nights, respectively; although the difference was not significant (welch two-sample t-test; df=23, t=2.03, p=0.054). Skomer females visited land on 1% (±0.3%, n=40) of nights, significantly less than Copeland females which visited land on 2% (±0.6%, n=24) of nights (welch two sample t-test; df=31, t=2.12, p=0.042). Within each colony, females visited land on a significantly lower proportion of nights compared to males (welch two-sample t-tests; Skomer: df=13, t=10.5, p<0.001; Copeland: df=14, t=11.5, p<0.001).

The mean duration of night-time visits to land was similar between colonies within each sex (Figure 6). On average, Skomer male visits lasted 5.47 (±0.16, n=14) hours while Copeland male visits lasted 5.09 (±0.18, n=15) hours (welch two-sample t-test; df=26, t=1.55, p=0.13); Skomer female visits lasted 4.63 (±0.52, n=40) hours while Copeland female visits lasted 4.04 (±0.36, n=24) hours (welch two-sample t-test; df=5, t=0.93, p=0.39). There was no difference

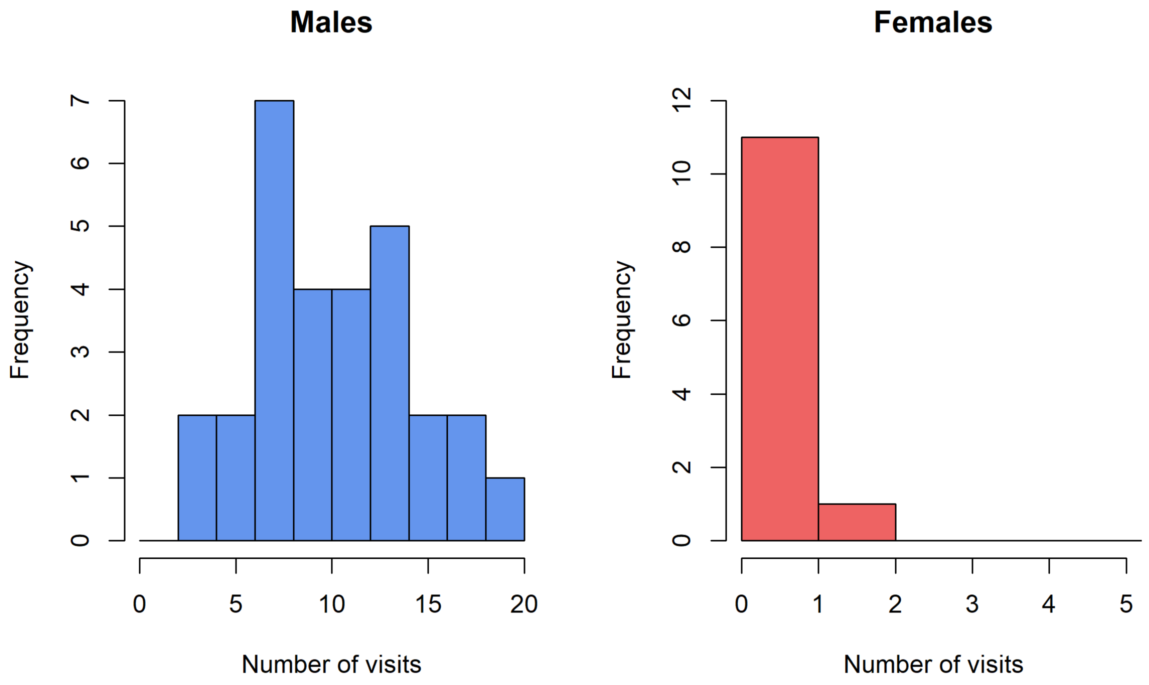


Figure 5. Frequency distributions for the number of ≥3-hour visits to land per exodus. All males (n=29) visited land on at least 4 nights during exodus. 52/64 females did not visit land, while 11/64 females visited land on 1 night and 1 female visited land on 2 nights.

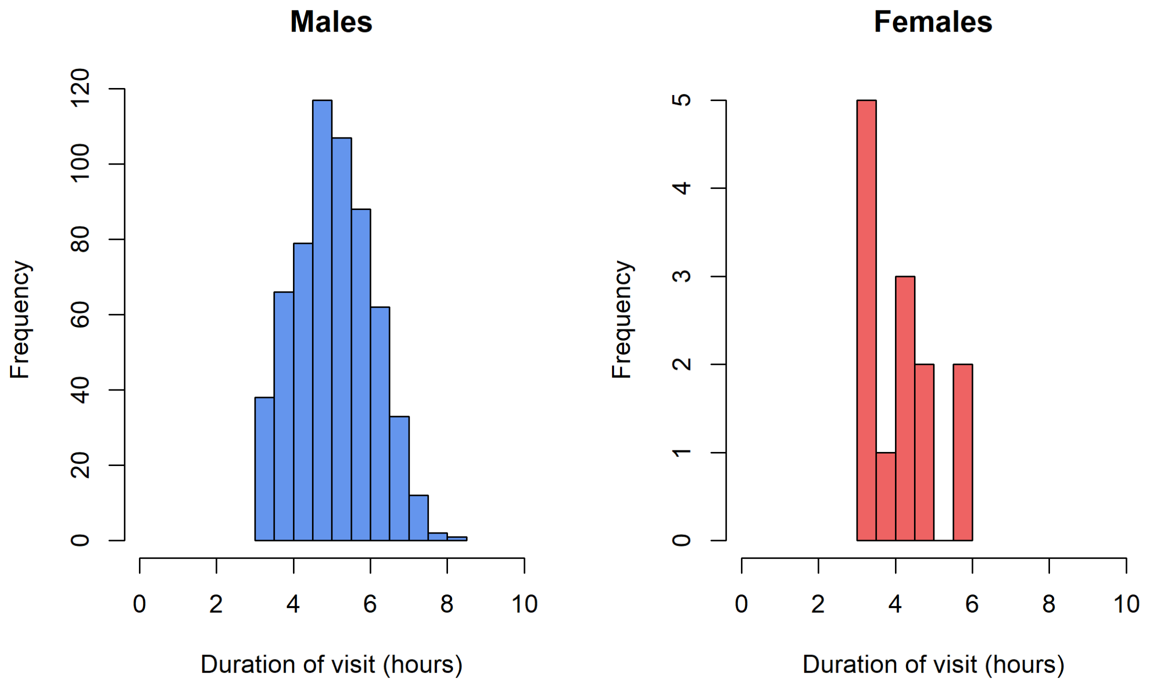


Figure 6. Frequency distributions for visit duration for all visits to land by males (n=605 visits) and females (n=13 visits) during exodus. Males spent a mean of 5.13 (±0.04) hours on land per visit, while females spent a mean of 4.21 (±0.28) hours on land per visit.

in the mean duration of night-time visits between sexes on Skomer (welch two-sample t-test; df=3, t=1.56, p=0.20), while Copeland male visits lasted significantly longer than Copeland female visits (welch two-sample t-test; df=10, t=2.62, p=0.024). Overall, Skomer females and Copeland females spent a similar proportion of their entire exodus on land, at 0.1% (±0.05%, n=40) and 0.2% (±0.09%, n=24), respectively (welch two-sample t-test; df=26, t=0.96, p=0.35), and Skomer males and Copeland males spent a similar proportion of their entire exodus on land, at 21% (±2%, n=14) and 24% (±2%, n=15), respectively (welch two-sample t-test; df=26, t=0.96, p=0.35). However, males from both colonies spent a significantly greater proportion of their entire exodus on land compared to their respective females (welch two-sample t-tests; Skomer: df=13, t=9.52, p<0.001; Copeland: df=14, t=11.0, p<0.001).

Changes in visits to land over the course of exodus

Temporal variation in the duration and probability of visits to land was examined to test whether visiting behaviour changed over the course of exodus. Exodus periods were aligned from the end of exodus and the number of days before the end-date was treated as the explanatory variable. Only male visits were analysed due to the rarity of female visits.

Firstly, the effect of days before the end of exodus on the duration of night-time visits to the colony was analysed by separate linear regressions for Skomer and Copeland males*. Since night-duration decreased during exodus and could potentially influence visit-duration, night-duration was included as a covariate in the regression models. For both Skomer and Copeland males, night-duration had a significant positive affect on visit-duration, whilst only for Skomer males did days before the end of exodus affect visit-duration with a significant positive effect i.e. visit-duration decreased as Skomer males neared the end of exodus. Overall, the models incorporating night-duration and days before the end of exodus explained 27% of the variance in visit-duration on Skomer, and 34% of the variance in visit-duration on Copeland. Figure 7 shows how visit-duration and night-duration covaried with number of days before the end of exodus, and how these relationships differed between colonies. The duration of Skomer male visits was longer than Copeland male visits during the early stages of exodus but visit-duration converged towards the end of exodus (Figure 7).

*OLS multiple linear regression; Skomer: df = 150, intercept = 0.76 ±1.46 hours, night-duration effect estimate = 0.56 ±0.21 hours, p = 0.011, days before the end of exodus effect estimate = 0.056 ±0.017 hours, p = 0.001, adjusted R^2 = 0.267; Copeland: df = 145, intercept = -1.70 ±0.83; night-duration effect estimate = 1.00 ±0.13 hours, $p < 0.001$, days before the end of exodus effect estimate = -0.006 ±0.015 hours, p = 0.70, adjusted R^2 = 0.335.

Secondly, the effect of the number of days before the end of exodus on the probability of night-time visits to land was tested and compared between Skomer and Copeland males. The probability of visiting the colony on a night increased over the course of exodus in Skomer males, whilst there was no detectable change in Copeland males (Figure 8). Averaged across all nights during exodus for all Copeland males, individuals had a 0.52 ±0.03 probability of visiting land on a night, and there was no significant change in the probability with change in days before the end of exodus (logistic regression, effect estimate = 0.015 ±0.019, odds ratio = 1.015, p = 0.431). In comparison, averaged across all nights during exodus for all Skomer males, individuals had a 0.66 ±0.03 probability of visiting land on a night. For Skomer males, the probability of visiting land on a night increased significantly as the end of exodus approached (logistic regression; effect estimate = -0.078 ±0.022, odds ratio = 0.925, $p < 0.001$). From model estimations, Skomer males had a 0.49 ±0.052 probability of visiting land 20 nights before the end of exodus vs. 0.81 ±0.048 one night before the end of exodus.

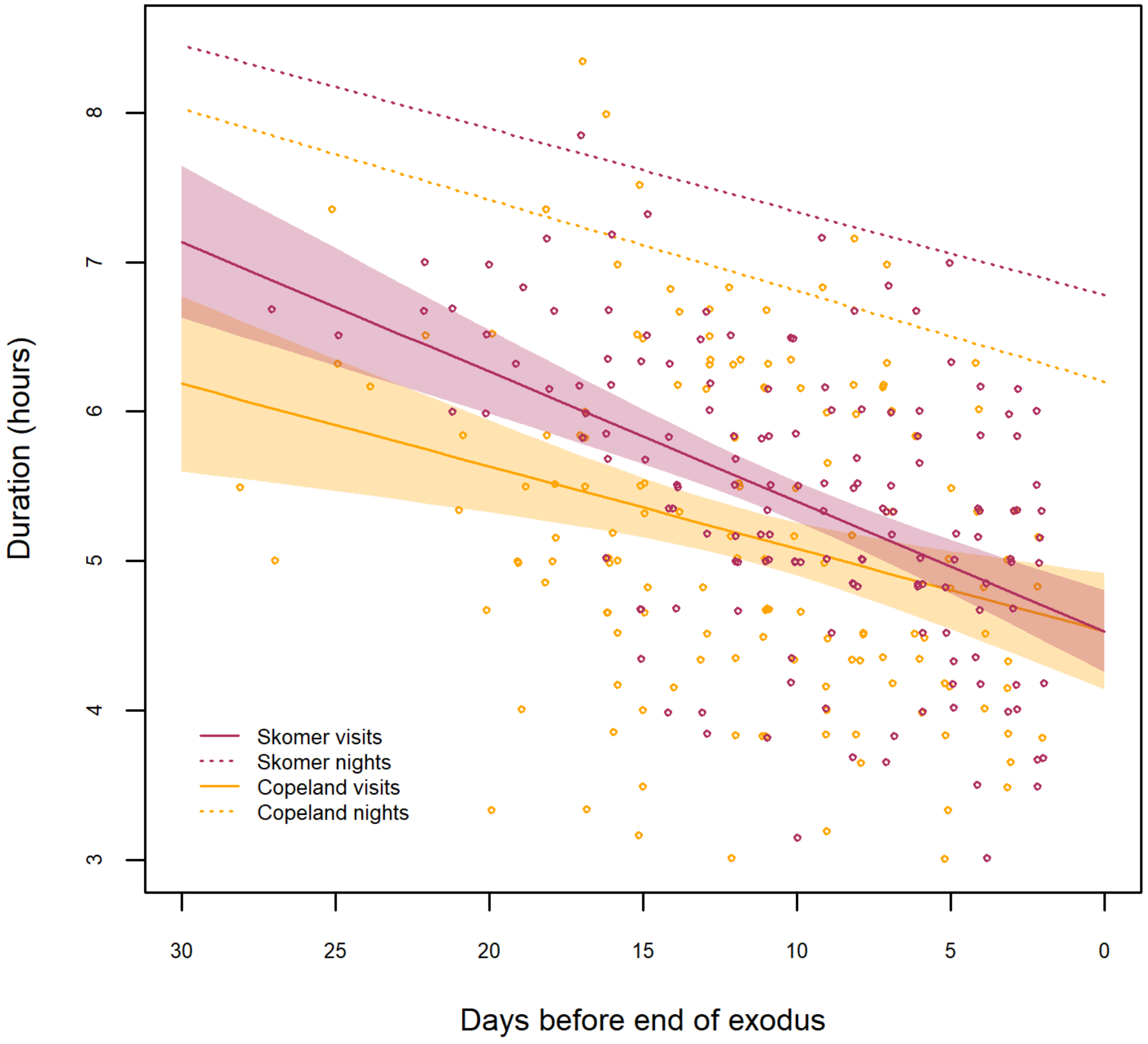


Figure 7. The relationship between the number of days before the end of exodus and the duration of night-time visits to land by males. Solid lines show linear regression model predictions of visit-duration explained by days before the end of exodus (shaded areas show ±2SE). Dotted lines show linear regression model predictions of night-duration explained by days before the end of exodus. At both colonies, visit-duration decreased as males neared the end of exodus, but this covaried with night-duration. On Copeland, the slope of visit-duration (0.055 ±0.016 hours/day) did not differ significantly from the slope of night-duration (0.061 ±0.008 hours/day), while on Skomer, the slope of visit-duration (0.087 ±0.012 hours/day) differed significantly by 0.031 hours/day from the slope of night-duration (0.056 ± 0.004 hours/day). Using multiple regression to control for night-length within each colony, there was no significant effect of number of days before the end of exodus on visit-duration in Copeland males, while there was a significant positive effect in Skomer males.

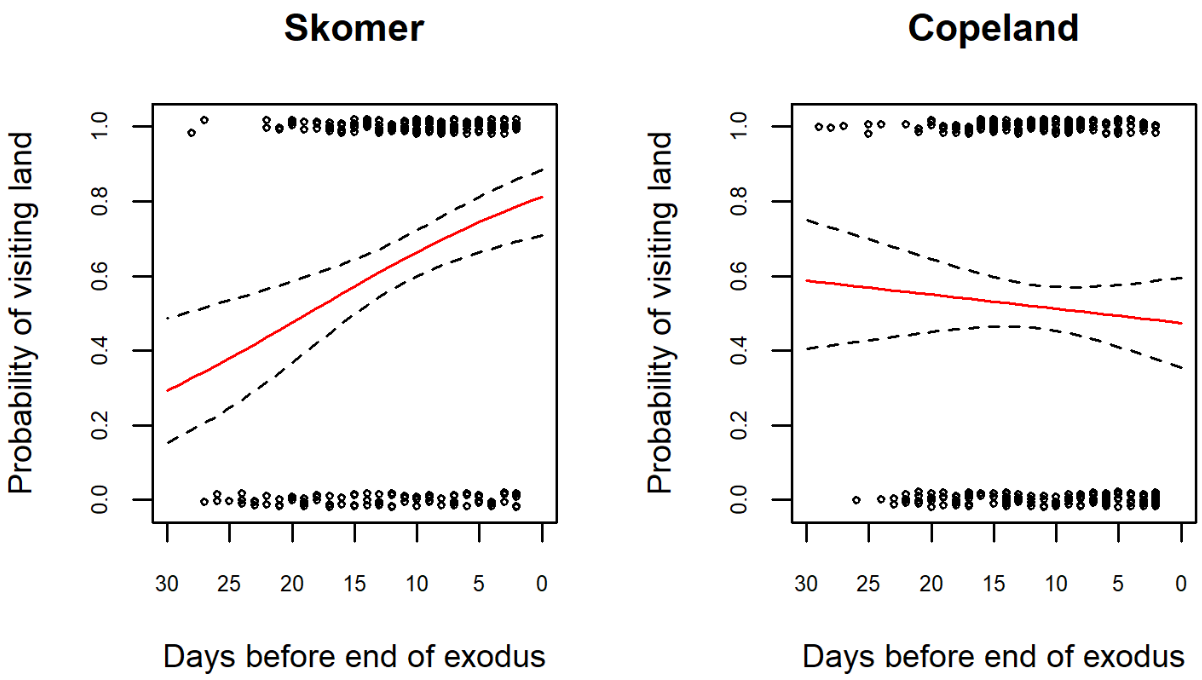


Figure 8. The modelled probability of visiting land at night among males is shown by the red lines, with 95% confidence limits shown by dashed lines. Points represent the outcome of every night for all individual males from each colony, 0 = no visit to land, 1 = visit to land. Skomer males show a significant increase in the probability of visiting land as the end of exodus approaches, whilst Copeland males show no significant change.

The spatial distribution of Manx Shearwaters during exodus

To identify general patterns in the spatial distribution of exodus trips, twice-daily locations were used to generate kernel density estimates for each sex within colonies. Occupancy kernels demonstrated similarities but also clear differences between sexes for both colonies (Figure 9). The 25% and 50% occupancy kernels showed single, tightly clustered distributions for Skomer and Copeland males, centred relatively close to their respective colonies in the Celtic and Irish Seas. However, males made infrequent distant trips west of Ireland, as shown by the subsection of the Skomer male 75% occupancy kernel adjacent to the edge of the continental shelf. 25% occupancy kernels highlighted two distinct areas for both Skomer and Copeland females: one area that overlapped with their respective male 25% occupancy kernels near to the colonies (69% overlap between Skomer males and females; 28% overlap between Copeland males and females), and one larger area to the southwest of Ireland over the continental shelf edge and the waters above the Porcupine Bight, where there was no overlap with respective male 25% or 50% occupancy kernels (Figure 9).

Between colonies, females from Skomer and Copeland showed relatively similar distributions to the southwest of Ireland with 41% overlap of 25% occupancy kernels in this area, although Copeland females displayed a more westerly limit in their distribution. In contrast, females from Skomer and Copeland showed more distinct 25% occupancy kernels near to the colonies, with only 16% overlap: Skomer females were centred relatively close to Skomer in the Celtic Sea off the southeast coast of Ireland, whilst Copeland females were centred further north and closer to Copeland, mostly in the Irish Sea to the east of Ireland. Males from Skomer and Copeland showed similar differences in their 25% occupancy kernels, with Skomer males mostly distributed within the Celtic Sea and Copeland males mostly distributed within the Irish Sea to the north, with only 8% overlap between 25% occupancy kernels.

Exodus distributions of Manx Shearwaters from Skomer were consistent with previous findings from GPS data that demonstrated a similar segregation of males and females in the regions found here (Dean, 2012). This study is the first to identify exodus distributions for Copeland; males showed relatively distinct distributions compared to Skomer males but were similar in that they remained relatively local to the colony, while females showed broadly similar distributions to Skomer females, particularly along the continental shelf edge.

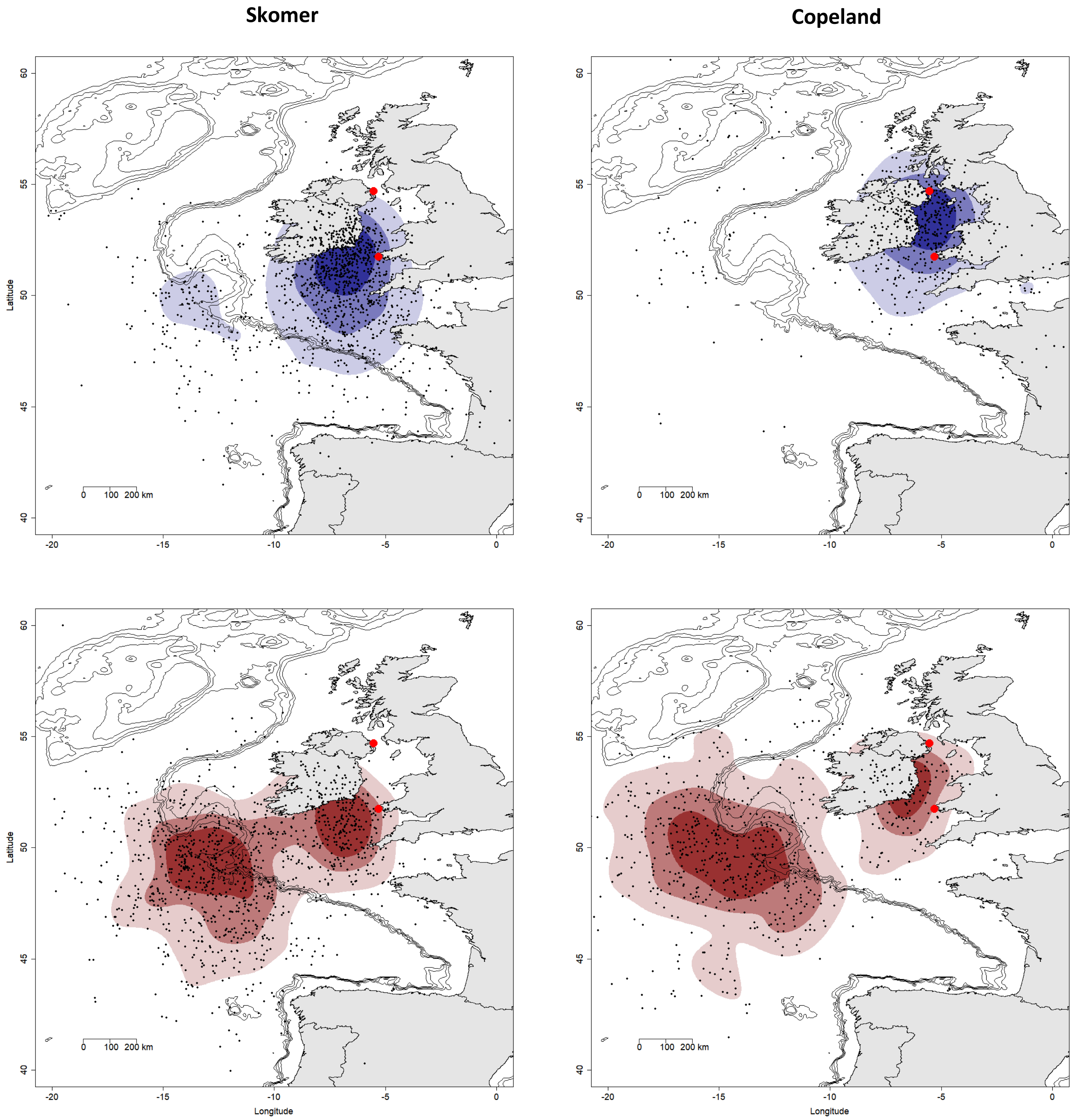


Figure 9. Locations of Manx Shearwaters during exodus for males (blue shading) and females (red shading) from Skomer (southern red circle) and Copeland (northern red circle). Shaded regions from light to dark represent 75%, 50% and 25% occupancy kernels. Black points represent light-derived locations of birds twice-daily during exodus. Contours at sea represent ocean depths from 500m to 2000m at 500m intervals.

Behaviour at-sea during the exodus

Behaviour at sea was classified using immersion score thresholds to categorise 10-minute time bins into flight, foraging or resting at-sea. For each exodus, two means were calculated for each behaviour: total time allocated to each behaviour during daylight over (i) the total number of days and (ii) the number of days spent at-sea (i.e. excluding days that were spent in the burrow). Population means were calculated from these values and the mean allocation of daytime to each behaviour (expressed in hours per day) was compared between sexes within colonies (Table 4) and between colonies within sexes (Table 5).

There were both similarities and differences in the mean allocation of daytime to different behaviours among sexes and colonies. Firstly, there were no significant differences in the allocation of daytime to flight between sexes within colonies (welch two-sample t-tests; Skomer: df=25, t=1.40, p=0.17; Copeland: df=29, t=1.22, p=0.23) or between colonies within sexes (welch two-sample t-tests; males: df=26, t=0.82, p=0.42; females: df=43, t=1.33, p=0.19), with means ranging between 2.7-3.5 hours of flight per day for all groups.

The mean allocation of daytime to foraging was similar between colonies for both sexes (welch two-sample t-test; males: df=26, t=0.14, p=0.88; females: df=40, t=0.88, p=0.38). In contrast, within both colonies males spent significantly more daytime foraging than females, both averaged over the total number of days (welch two-sample t-test; Skomer: df=17, t=2.17, p=0.044; Copeland: df=25, t=2.67, p=0.013) and over days spent at-sea (welch two-sample t-test Skomer: df=25, t=6.24, p<0.001; Copeland: df=24, t=6.66, p<0.001). Of Skomer birds, females spent a mean 7.07 ±0.14 hours foraging per day, while males spent an additional 0.79 hours / 11% longer foraging per day*, or an additional 1.55 hours / 22% more time foraging per day at-sea. Of Copeland birds, females spent a mean 6.84 ±0.22 hours foraging per day whilst males spent an additional 1.09 hours / 16% more time foraging per day*, or an additional 2.63 hours / 38% more time foraging per day at-sea.

The mean allocation of daytime to rest at-sea was different between sexes within colonies (welch two-sample t-tests; Skomer: df=27, t=5.04; p<0.001; Copeland: df=36, t=9.28; p<0.001). It was also different between Skomer and Copeland males, but similar between Skomer and Copeland females (welch two-sample t-tests; males: df=23, t=3.57; p=0.002; females: df=44, t=0.69, p=0.50). Of Skomer birds, females allocated the most time to rest at-sea, with a mean of 6.47 ±0.23 hours per day, while males spent 1.96 hours fewer / 30% less time resting per day*, or 1.47 hours fewer / 23% less time resting per day at-sea. Of Copeland birds, females also spent the most time resting at-sea, with a mean of 6.74 ±0.32 hours per day, while males spent 3.61 hours fewer or 54% less time resting per day*, and 3.02 hours fewer or 45% less time resting per day at-sea. Although Skomer and Copeland females allocated similar amounts of daytime to rest per day at-sea, Skomer males spent significantly more time resting per day than Copeland males: an additional 1.38 hours / 44% more time resting at-sea per day* than Copeland males, and an additional 1.72 hours / 46% more time resting at-sea per day at-sea than Copeland males.

* averaged over the total number of days in exodus.

Table 4. Comparing behavioural metrics between sexes for each island. Bracketed values are standard errors.

Colony	Sex	Number	Daytime flight (hours/day)		Daytime foraging (hours/day)		Daytime resting at-sea (hours/day)	
			Over total days	*Over days at-sea*	*Over total days*	*Over days at-sea*	*Over total days*	*Over days at-sea*
Skomer	**Males**	14	2.71 (0.25)	2.98 (0.31)	7.86*[1] (0.34)	8.62***[3] (0.21)	4.51 ±0.32***[5]	5.00**[7] (0.34)
	Females	40	3.12 (0.16)	3.12 (0.16)	7.07*[1] (0.14)	7.07***[3] (0.14)	6.47 ±0.23***[5]	6.47**[7] (0.23)
Copeland	**Males**	15	3.03 (0.31)	3.60 (0.32)	7.93*[2] (0.34)	9.47***[4] (0.36)	3.13 ±0.22***[6]	3.72***[8] (0.28)
	Females	24	3.51 (0.24)	3.51 (0.24)	6.84*[2] (0.22)	6.84***[4] (0.22)	6.74 ±0.32***[6]	6.74***[8] (0.32)

Welch two-sample t-tests: [1] t = 2.17, p = 0.044; [2] t = 2.67, p = 0.013; [3] t = 5.29, p < 0.001; [4] t = 5.64, p < 0.001; [5] t = 5.04, p < 0.001; [6] t = 9.28, p < 0.001; [7] t = 3.41, p = 0.002; [8] t = 7.49, p < 0.001.

Table 5. Comparing behavioural metrics between islands for each sex. Bracketed values are standard errors.

Sex	Colony	Number	Daytime flight (hours/day)		Daytime foraging (hours/day)		Daytime resting at-sea (hours/day)	
			Over total days	*Over days at-sea*	*Over total days*	*Over days at-sea*	*Over total days*	*Over days at-sea*
Males	**Skomer**	14	2.71 (0.25)	2.98 (0.31)	7.86 (0.34)	8.62 (0.21)	4.51*[1] (0.32)	5.00**[2] (0.34)
	Copeland	15	3.03 (0.31)	3.60 (0.32)	7.93 (0.34)	9.47 (0.36)	3.13*[1] (0.22)	3.72**[2] (0.28)
Females	**Skomer**	40	3.12 (0.16)	3.12 (0.16)	7.07 (0.14)	7.07 (0.14)	6.47 (0.23)	6.47 (0.23)
	Copeland	24	3.51 (0.24)	3.51 (0.24)	6.84 (0.22)	6.84 (0.22)	6.74 (0.32)	6.74 (0.32)

Welch two-sample t-tests: [1] t = 3.57, p = 0.016; [2] t = 2.87, p = 0.009.

Temporal variation in behaviour at-sea over the course of exodus

The amounts of time allocated each day to different behaviours were examined over the course of the exodus to test whether behaviour changed as the end of exodus approached. Exodus periods were aligned from the end of exodus and the mean number of hours allocated to each behaviour was calculated for each day.

Firstly, patterns in behaviours over time were compared between males and females pooled from both colonies (Figure 10). Among males, time spent in flight (Figure 10A) was relatively constant at 2.5–4 hours per day throughout the exodus. Females broadly matched males in their allocation of time to flight per day over the exodus, however, females showed a more distinct negative trend in flight per day towards the end of exodus, from a peak of around 6 hours per day 20-25 days before the end of exodus to a minimum of around 2 hours per day 1-5 days before the end of exodus. Overall, females tended to fly more than males at the start of exodus (17-25 days before the end-date) and marginally less than males for the remainder of the exodus (1-16 days before the end-date).

On every day during exodus males allocated more daytime to foraging than females, and less daytime to resting at-sea from 18 days before the end of exodus onwards. These results were consistent with the significant differences between sexes in mean daytime allocated to these behaviours averaged over the whole of exodus (Table 4). Over the course of exodus, the duration of daytime allocated to foraging (Figure 10B) and rest at-sea (Figure 10C) changed markedly over the course of the exodus among females. The duration of day time spent foraging was relatively constant at 7-8 hours per day for most of the exodus (8-25 days before the end-date) but decreased after this to a distinct minimum of around 5 hours per day 3 days before the end-date. This coincided with the day of minimum flight and maximum rest at-sea.

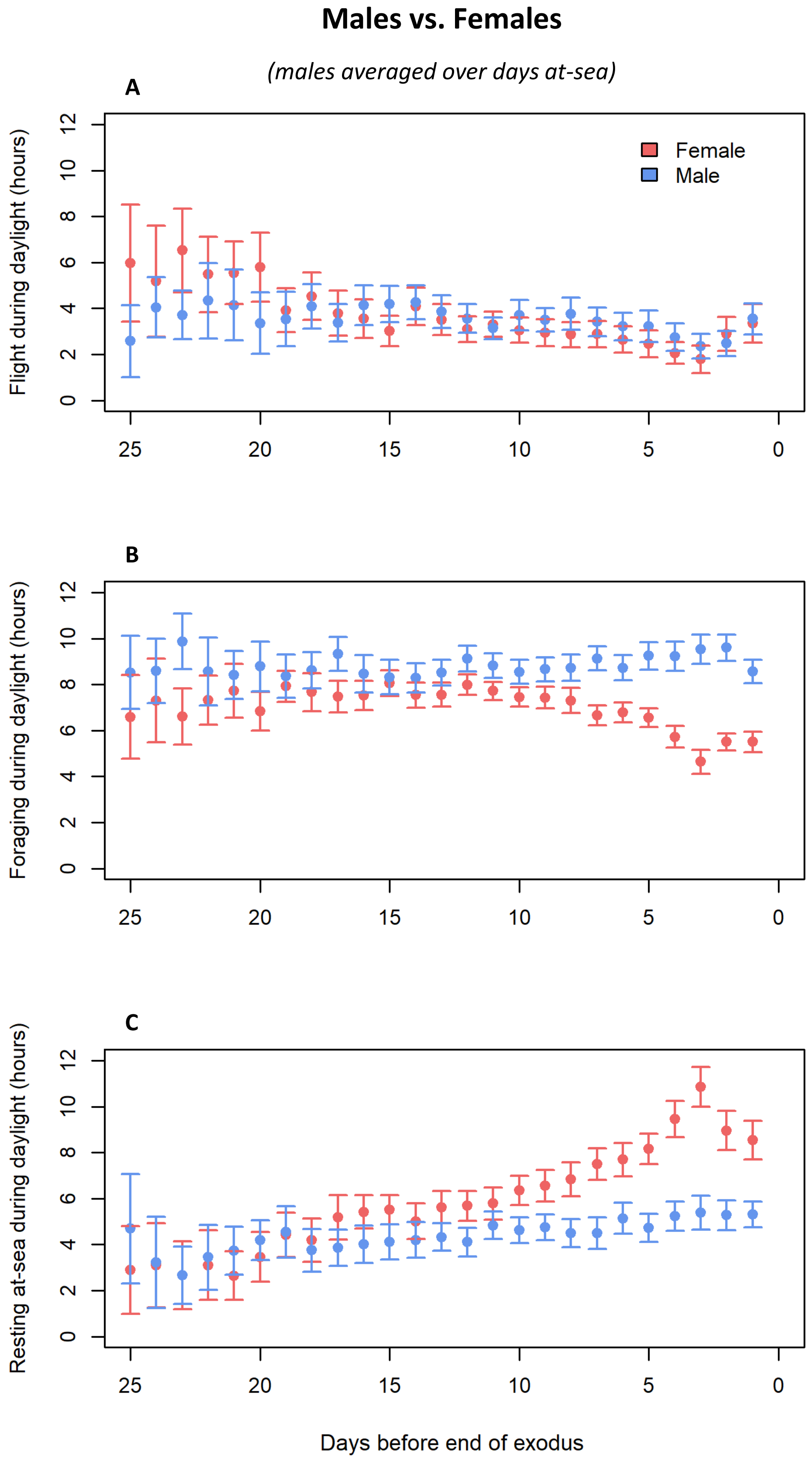


Figure 10. Daily means of duration (A) in flight, (B) foraging and (C) resting at-sea during daylight against the number of days before the end of exodus, for all females combined (in red) and all males combined (in blue). Error bars show 95% confidence limits.

In contrast, the allocation of daytime to foraging and resting at-sea among males changed relatively little over the course of the exodus. The allocation of daytime to foraging was between 8-10 hours a day throughout exodus, while the allocation of time to resting at-sea increased slightly from around 3-4 hours per day at the start to around 4-5 hours per day towards the end of exodus.

Temporal variation in behaviour was also compared between colonies for females (Figure 11) and males (Figure 12 & Figure 13) separately. Between colonies, females showed remarkably similar patterns of behaviour. The only notable difference was that over the last 2 days before the end-date, Copeland females allocated around 1.5 hours more per day flying and around 1.5 hours less per day foraging than Skomer females. In comparison, males showed greater differences between colonies. For males, daily means were calculated both including days on-land (i.e. means of all days at-sea and on-land combined) and excluding days on-land (i.e. means of days spent at sea). Firstly, the mean allocation of daytime to different behaviours for days at-sea were examined (Figure 12). Flight and foraging were both relatively constant during exodus for Skomer and Copeland males, although Copeland males tended to fly and forage marginally more per day than Skomer males on certain days. Skomer males spent more time resting than Copeland males, particularly towards the end of exodus (1-5 days before the end-date), as reflected by the significantly greater allocation of daytime to rest at-sea when averaged over the whole of exodus among Skomer males (Table 5). Secondly the allocation of daytime to different behaviours over all days was examined (Figure 13). Flight and foraging differences between Skomer and Copeland males were less apparent, while the difference in time spent resting at-sea became more distinct. These differences indicate that Copeland males may adjust their behaviour at-sea to compensate for the greater number of days spent on land compared to Skomer males.

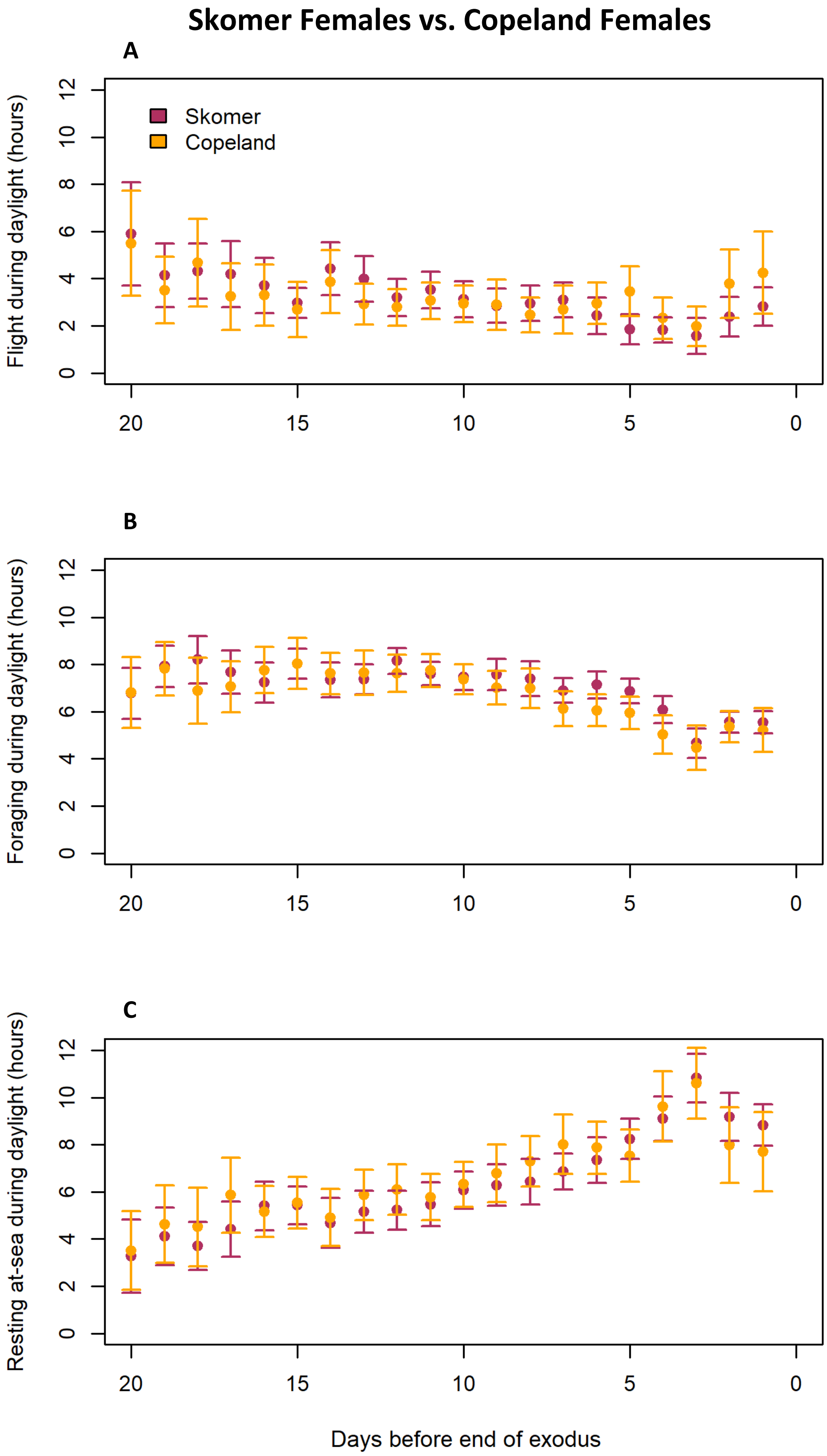


Figure 11. Daily means of duration (A) in flight, (B) foraging and (C) resting at-sea during daylight, plotted against the number of days before the end of exodus, for Skomer females (in maroon) and Copeland females (in orange). Error bars show 95% confidence limits.

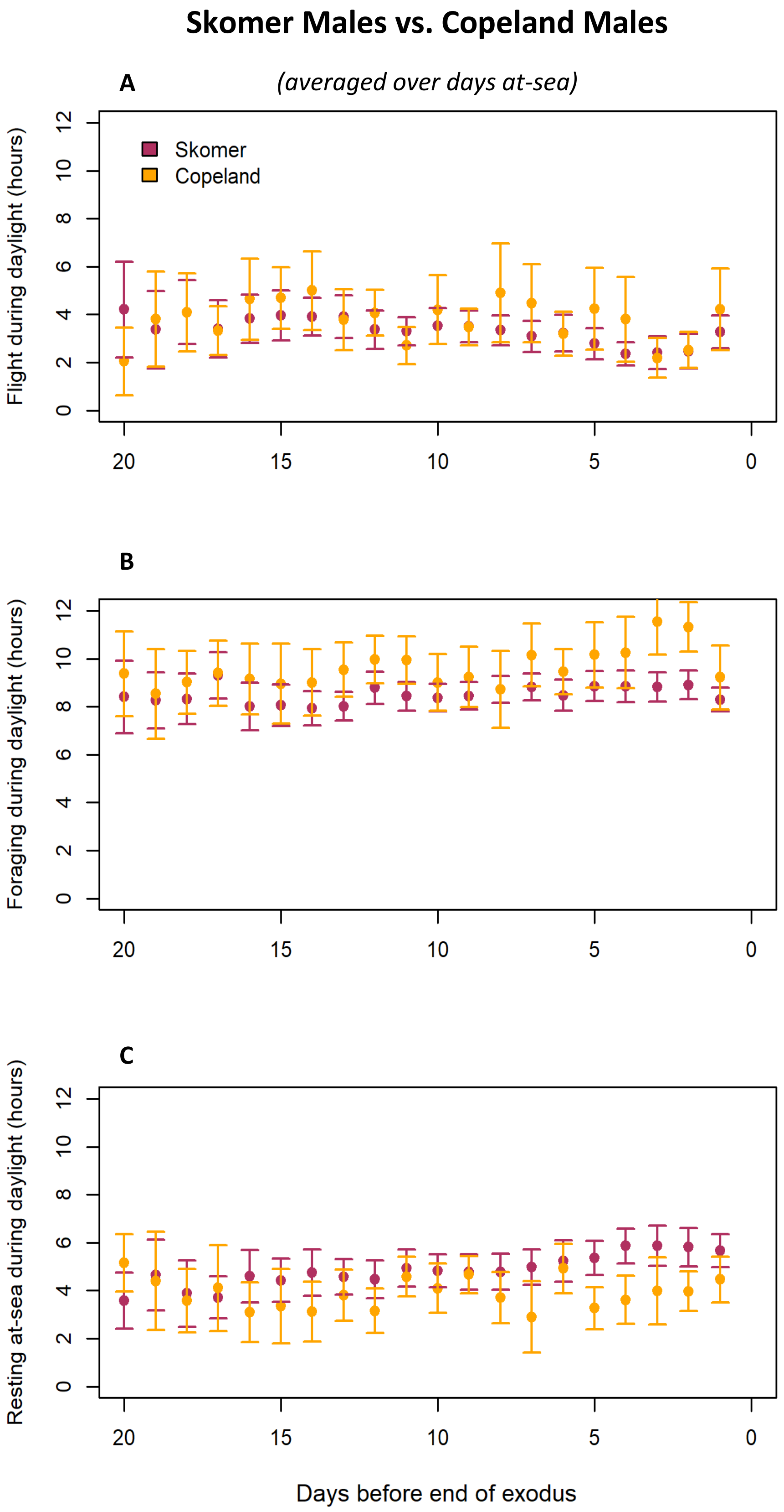


Figure 12. Daily means of duration (A) in flight, (B) foraging and (C) resting at-sea during daylight (averaged over days spent at-sea i.e. excluding days spent on-land over day), plotted against the number of days before the end of exodus, for Skomer males (in maroon) and Copeland males (in orange). Error bars show 95% confidence limits.

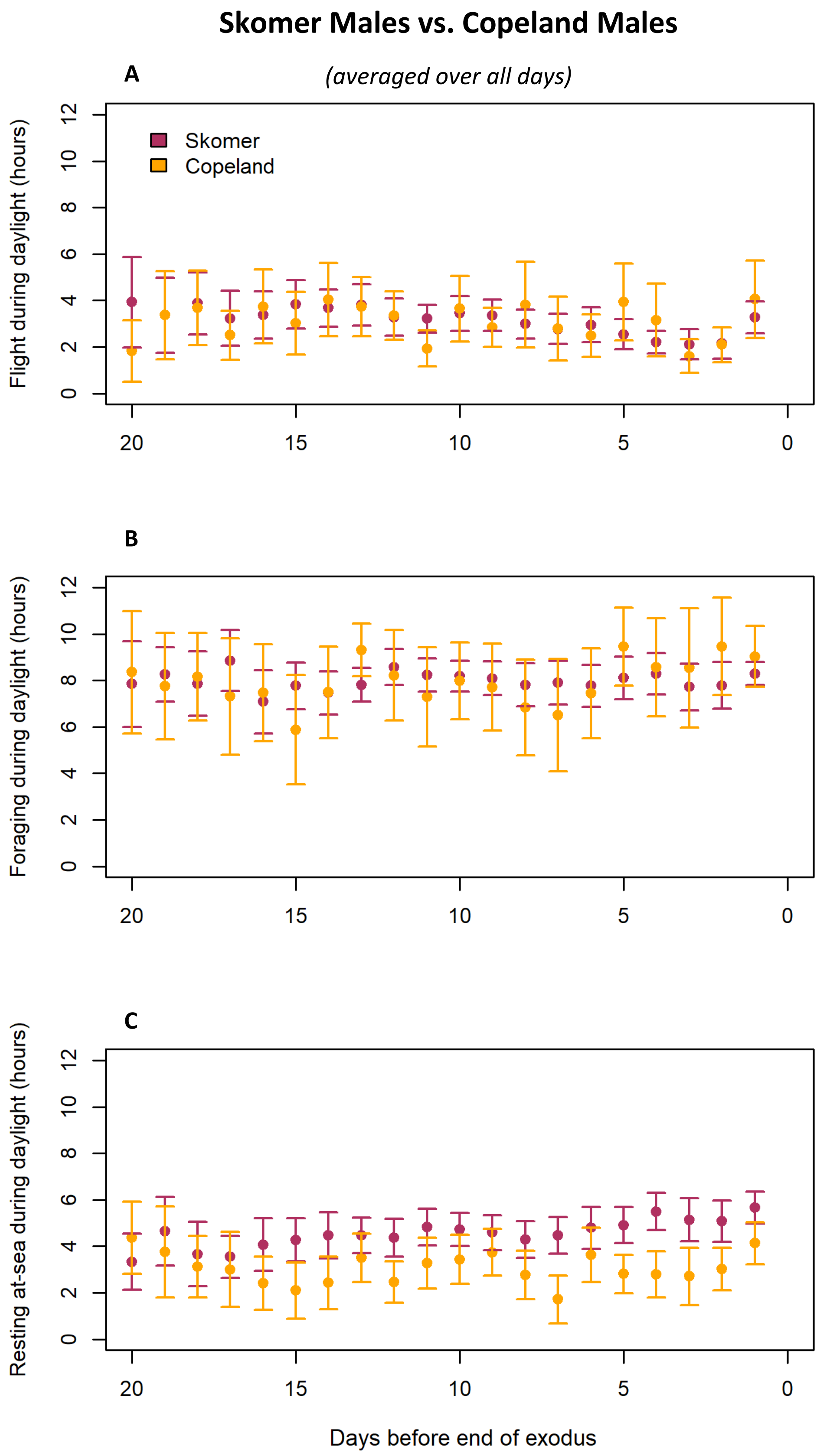


Figure 13. Daily means of duration (A) in flight, (B) foraging and (C) resting at-sea during daylight (averaged over all days i.e. including days spent on-land over day), plotted against the number of days before the end of exodus for Skomer males (in maroon) and Copeland males (in orange). Error bars show 95% confidence limits.

Spatial distributions of behaviour at-sea during exodus

In addition to temporal variation during exodus, spatial variation in the allocation of time to different behaviours at-sea was examined. For each sex within colony, 25% occupancy kernels for foraging, flight and rest at-sea were generated from the subsets of locations at which each behaviour was predominant, with each location weighted by the behavioural index score for that behaviour (see methods). Kernels were mapped and used to assess how time spent foraging, flying and resting at-sea varied within and between sexes and colonies (Figure 14).

Among males, there was a relatively high degree of overlap between the spatial distributions of behaviours within colonies, and each behavioural kernel was distributed similarly to overall male distribution within each colony (Figure 14, also refer to Figure 9). All three behavioural kernels overlapped in 56% and 52% of the total area covered by behavioural kernels among Skomer and Copeland males, respectively, which indicated that there was relatively little spatial segregation of behaviours among males within each colony, at least at the resolution of light-derived kernel estimates. Comparing Skomer males to Copeland males, there was only 1.7%, 4.3% and 0.4% overlap across foraging, resting and flying kernels, respectively, as the two populations showed abutting distributions in which Skomer males occupied the Celtic Sea while Copeland males were distributed further north in the Irish Sea.

Among females, there was relatively little overlap in the spatial distributions of different behaviours within colonies (Figure 14). All three behavioural kernels overlapped in only 1.7% and 1.6% of the total area covered by behaviour kernels for Skomer and Copeland females, respectively. Among Copeland females, the foraging kernel was located mainly along the continental shelf edge to the south and southwest of the Porcupine Bight, and exclusively in this area for Skomer females. The foraging kernel of Copeland females included an additional

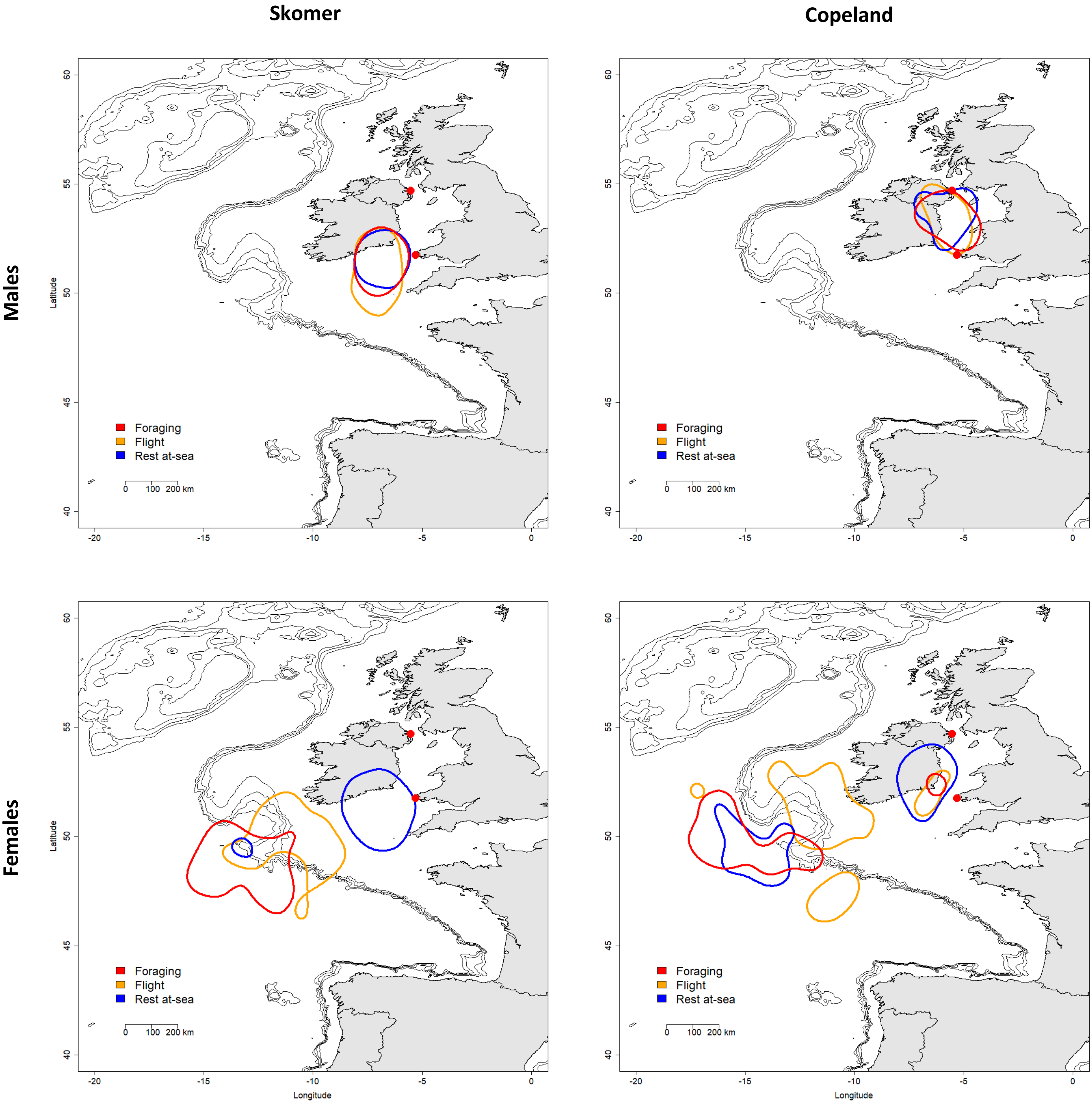


Figure 14. Maps show the spatial distribution of behaviours for each sex within colony during exodus. Coloured lines enclose 25% occupancy kernels for foraging (red), flight (orange) and rest at-sea (blue), generated from the subsets of locations at which each behaviour was predominant, with each location weighted by the behavioural index score for that behaviour. Skomer is shown by the southern red circle, Copeland by the northern red circle. Contours at sea represent ocean depths from 500 m to 2000 m at 500 m intervals.

region off the southeast coast of Ireland, although its area constituted only 5% of the total foraging kernel. Resting kernels for Skomer and Copeland females were distributed both along the continental shelf edge within or close to foraging areas (in regions that constituted 6% and 55% of the total area covered by resting kernels of Skomer and Copeland females, respectively) and to the southeast of Ireland (in regions that constituted 94% and 45% of the total area covered by resting kernels of Skomer and Copeland females, respectively). As expected given the need to travel between their colonies and distant foraging grounds, flying kernels of Skomer and Copeland females were distributed between their respective colonies and foraging areas along the continental shelf edge*.

Comparing Skomer females to Copeland females, resting kernels overlapped by 10% and flying kernels also overlapped by 10%, both less than half the 25% overlap observed between the foraging kernels. Even though females were distributed further from their respective colonies compared to males, there was a notably greater between-colony overlap of kernels for each behaviour among females compared to males, particularly for foraging where female kernels overlapped 14-fold more than male kernels.

---

*More detailed interpretation of flying kernels was omitted, since the precision and accuracy of light-derived locations during long-distance movements (which are suggested by the large allocations of time to flight) is limited.

Discussion

Overview of results

The results of this study demonstrate numerous sex- and colony-specific strategies during the pre-laying exodus, as well as some distinct similarities. Previous studies had shown that Manx Shearwaters from Skomer have sex-specific distributions, in which males generally remain close to the colony which they visit regularly, while females make distant, long-duration trips to the south-west of Ireland, concentrated in areas around the continental shelf edge and Porcupine Bight (Dean, 2012; Guilford et al., 2009). Similar conclusions were reached here from data spanning a 10-year period, suggesting that the drivers of these at-sea distributions have been maintained for at least this period.

In addition to the extended number of years over which exodus was examined, this study has provided new insights into the amount of time that is devoted to different behaviours, both over the entire exodus, and daily over the course of exodus. Overall during exodus, males foraged more and rested less than females, but both sexes spent similar amount of time in flight. In addition, the sexes were highly distinct in how their levels of different behaviours changed during exodus; males maintained relatively constant levels of each behaviour, while females decreased the time they spent foraging and flying and increased the time they spent resting as the lay date approached. The temporal shifts in female behaviour were also associated with location, with high foraging levels around the continental shelf edge, high resting levels near to the colony, and high flight levels between them.

Finally, this investigation has gone beyond previous work by additionally contrasting exodus across two colonies: Skomer, the subject of the previous exodus studies, and the Copeland Islands, from which Manx Shearwater exodus has hitherto never been described. Copeland is inhabited by around 3000 breeding pairs of Manx Shearwater, around 100-fold less than the breeding population on Skomer (CBO, 2018; Perrins et al., 2012), and is located approximately 300 km north of Skomer and about 250 km further from the continental shelf edge. Copeland is however much closer than Skomer to the Irish Sea Front, an important foraging area for Manx Shearwaters from both colonies and others during incubation and chick rearing (Dean et al., 2012, 2015). It was therefore unclear whether and to what extent space-use and behaviour during exodus would differ between Manx Shearwaters breeding on Copeland, which face both different demographic and ecological constraints compared to Skomer birds.

Comparisons between Skomer and Copeland exodus locations showed many similarities in female space use around the continental shelf edge, with the longer average duration of exodus probably resulting from the extra travel time between Copeland and the shelf edge. Copeland males occupied the Irish Sea south of Copeland, further north than the area of the Celtic Sea used by Skomer males with virtually no overlap between their distributions. However, males from both colonies were similar in that they remained near their respective colonies. In a similar vein, females from both colonies allocated almost identical amounts of time to different behaviours, both averaged over the entire exodus and daily over the course of exodus, while males showed subtle but significant differences between colonies in their levels of different behaviours. Generally, between-colony differences were much smaller than the between-sex differences.

Finally, comparisons of metrics describing night-time visits to land between Skomer and Copeland males highlighted further differences among males, notably: (i) Skomer males decreased the duration of their visits over exodus beyond the level predicted by shortening nights, while Copeland males only decreased theirs in proportion to shortening nights, (ii)

Skomer males increased their visit frequency over the course of exodus from infrequent to very frequent while Copeland males maintained a moderate visit frequency throughout, and (iii) Copeland males remained at the colony over-day significantly more than Skomer males.

Egg production underlies sex-specific exodus behaviour

In a species with negligible sexual dimorphism and biparental care, the pre-laying exodus of Manx Shearwaters is a unique period within the annual cycle in that males and females exhibit highly distinct behaviour (Brooke, 1990; Dean, 2012; Guilford et al., 2009). These differences are underpinned by an asymmetry between the sexes in their nutrient and energy demands, imposed by differing reproductive roles. Specifically, females must produce the egg, while males are clearly free from this constraint. Ultimately, the need to satisfy different energy and nutrient demands is likely to drive the sex-specific strategies during exodus in Manx Shearwater (Brooke, 1990; Dean, 2012; Guilford et al., 2009) and other Procellariforms such as the Fulmar and Balearic Shearwater (e.g. Guilford et al., 2012; Mallory et al., 2008).

All Procellariforms lay a single, large, energy-rich egg, which in the Manx Shearwater comprises about 15% of female body mass (Brooke, 1990; Warham, 1983). Producing such an egg carries significant energy and nutrient demands, and as such egg production incurs costs on other components of female fitness (Williams, 2005). Egg production requires the transfer of large quantities of macronutrient, namely lipids and proteins, from the female to her developing egg (Astheimer & Grau, 1990; Nager, 2006). Nutrients may be sourced from body reserves and current diet, the relative contributions of which vary between species (Drent & Daan, 1980; Meijer & Drent, 1999). As female Manx Shearwaters lose mass between migration and departure on exodus, they are unlikely to have the body reserves necessary to produce the egg, and therefore they must supply its production through increased dietary intake relative to energetic expenditure (Brooke, 1977). Females gain overall mass including the mass of the egg, showing that their dietary intake relative to energetic expenditure increases during exodus (Brooke, 1990; Dean, 2012). However, if the mass of the egg is discounted, females in fact lose body mass, suggesting that the level of dietary intake relative to normal expenditure plus expenditure on the egg is insufficient to maintain body condition (Brooke, 1990; Dean, 2012). In contrast, males also lose mass between migration and the start of exodus, but they are then able to gain mass during exodus (Brooke, 1990).

Although the energy and nutrient demands of egg production are likely to be highly influential in shaping sex-specific exodus strategies, other changes related to egg development may also have an influence. For example, the significant mass of the egg increases wing loading and reduces flight and foraging efficiency as it grows during the exodus, and it may also disturb the normal centre of gravity or alter buoyancy during foraging dives (Ropert-Coudert et al., 2007; Warham, 1977). The decrease in active behaviours (flight and foraging) and increase in resting in females over the course of exodus suggests that egg-induced costs to flight and diving may play a significant role, with females perhaps accumulating most resources towards the beginning of exodus when these costs are minimal.

At-sea distribution and behaviour

Male body weight increases over exodus while remaining near to their respective colonies, demonstrating that local waters are sufficient to supply males and their fitness is not food-limited during exodus (Brooke, 1990). However, females from both Skomer and Copeland make costly journeys to distant areas during exodus, which implies that the benefits of visiting these areas outweigh the costs of travelling there and improve fitness, since they would otherwise forage locally around the colony. Females foraged less and rested more than males during exodus, despite additional demands of producing the egg, suggesting that the foraging areas they visited were more productive for prey than those visited by males.

Previous analyses based on oceanic chlorophyll concentrations have suggested that the areas visited by females are in fact less productive than areas closer to the colony (Dean, 2012). However, the mass gain of females (egg mass included) during exodus relative to their mass loss prior to exodus (when they are located in waters near to the colony; Kirk, 2016) suggests that the areas visited by females are more productive than local waters, and that it is more likely that chlorophyll concentration was a poor indicator of relative prey abundance in the two areas (Grémillet et al., 2008). Greater prey abundance in the areas visited by females is supported by the fact that the sea floor topography of continental shelf edges likely interacts with ocean currents and tides to cause upwellings and mixing of the water column (Sharples et al., 2009), generating foraging conditions that attract Procellariforms, of which many species are known to favour foraging over shelf edges (Christensen-dalsgaard et al., 2018; Pollock et al., 2000; Studwell et al., 2017; Wynn & Krastel, 2012).

Dean (2012) found that individuals from Skomer, and particularly females, were flexible in their destination between years, with individuals foraging in the Celtic Sea in some years and along the continental shelf edge in others. Those birds that foraged along the shelf edge made direct commutes to and from Skomer, which suggests that the two occupancy kernel cores for Skomer females found here reflect separate birds that foraged either distantly or locally, rather than birds that foraged in both areas within the same exodus (Dean, 2012). Switching between distant or local foraging grounds was related to local foraging conditions, with females favouring local foraging when local productivity was high (Dean, 2012).

Drivers of male visits to land

Once pairs have established a nest, completed courtship and copulated, they are no longer tied to land by these activities and might be expected not to visit land before laying, given the travel costs of doing so. In several species including the Short-tailed Shearwater *Ardenna tenuirostris* (Serventy, 1967) and Great Shearwater *Ardenna gravis* (Brooke, 1990), both sexes follow this prediction and completely desert the breeding colony for several weeks prior to laying. However, the results of this study show that Manx Shearwater males continue to visit the colony on over 50% of nights during exodus, implying that there must be some benefit to doing so that outweighs the costs of travelling there. Comparisons across Procellariform species that with synchronous breeding at the colony level is associated with both males and females departing the colony for long periods, whilst asynchronous breeding at the colony level is associated with males that continue to visit the colony during exodus (Brooke, 1990). This suggests that the continued presence of other individuals at the colony during exodus is an important driver for males to continue to visit, which has led to several hypotheses attempting to explain why this is so (Brooke, 1990).

One hypothesis proposes that competition for nest sites at breeding colonies may favour males that defend their nest from pairs still prospecting for breeding burrows (Brooke, 1990). In Manx Shearwater, the existence of intraspecific competition for burrows is supported by frequent territorial fights during the pre-laying period, high population densities at many colonies, and the observation that birds that would not usually breed will occupy and breed in artificial burrows when they are made available (Brooke, 1990). There is clear observational evidence for burrow competition in other Procellariforms including Great Shearwater (Rowan, 1965), Sooty Shearwater (Richdale, 1963) and Short-tailed Shearwater (Serventy, 1967), in which breeding birds outnumber available burrows by such an extent that up to 300,000 eggs may be laid on the surface and fall victim to predation (Brooke, 1990). There is also experimental evidence that shows the presence of breeders is important for burrow retention in Cassin's Auklet *Ptychoramphus aleuticus*: burrows from which breeding pairs were removed were mostly reoccupied in the same season by new breeding pairs which had never bred previously (Manuwal, 1974). Similar results were obtained in Eurasian Oystercatcher *Haematopus ostralegus* (Harris, 1970). Interspecific competition for burrows could also favour burrow defence (Brodier et al., 2011; Sullivan & Wilson, 2000), and this may be pertinent to Manx Shearwaters breeding alongside Atlantic Puffins *Fratercula arctica* at some colonies (Ashcroft, 1976; Brooke, 1990).

A second hypothesis posits that males may benefit from visiting land by securing extra-pair copulations (EPC) potentially leading to extra-pair paternity (EPP). The occurrence of EPP is highly variable across species and populations of birds (Petrie & Kempenaers, 1998), but is less common in seabirds compared to terrestrial bird taxa but does occur in several species (Huyvaert & Parker, 2010; Jouventin et al., 2007; Quillfeldt et al., 2012; Sakao et al., 2018). To date, EPP has not been genetically tested in Manx Shearwater and EPC has not been knowingly observed, but this does not rule out its occurrence, especially given the difficulty of observing any copulations in nocturnal, burrow-nesting shearwaters. Indeed, EPP has been confirmed in the closely related Short-tailed Shearwater (Austin & Parkin, 1996).

These two hypotheses make opposite predictions about how the probability of visiting land on a night might change over the course of exodus. The EPC hypothesis predicts that males will have a greater probability of visiting land on a night at the start of exodus and that this will subsequently decrease, since later copulations are less likely to improve fitness and receptive females will become less numerous over time (Brooke, 1978; Perrins, 1966). The burrow-defence hypothesis predicts that males will have a lower probability of visiting land on a night at the start of exodus and that this will subsequently increase, as the increasing frequency of returning females carrying eggs increases the risk of burrow eviction over time. In this study, the probability of visiting land on a night among male Manx Shearwaters from Skomer was found to significantly increase over the course of exodus, supporting the burrow defence hypothesis as the primary driver of male visits refuting the EPC explanation, although not ruling it out. However, the probability of visiting land on a night among Copeland males did not change over the course of exodus, suggesting that one or several factors driving male colony visits are different on Copeland, perhaps due to the smaller size of the colony or the lack of interspecific competition for burrows from Atlantic Puffins (Ashcroft, 1976; Brooke, 1990). Alternatively, different spatial distribution of prey resources around Copeland and Skomer could shift the relative costs of visiting each colony, and thus also affect the differences in male visits (Dean et al., 2012). Genetic paternity testing in Manx Shearwaters from both colonies, as well correlative and experimental investigation of the risks of losing the breeding burrow to other pairs are needed to further clarify the factors driving male Manx Shearwaters to visit land.

In addition to normal night-time visits to land frequently made by males at both colonies, over-day visits to land occurred. These were ubiquitous among Copeland males during exodus, whereas significantly fewer Skomer males made over-day visits. The adaptive value of over-day visits during exodus has not been discussed previously in the literature and is likely different to that of night-time visits. Nest defence is an unlikely explanation, since burrow prospecting only occurs when shearwaters are active on the colony-surface at night. It could be the case that an individual’s condition and local foraging or weather conditions may favour remaining in the burrow over day (Schreiber, 2001). Alternatively, days spent at the colony could represent instances where males have found and are mating with an extra-pair female, since social pairs typically spent a full day on land before departing on exodus, presumably engaged in copulation (Brooke, 1990; Dean, 2012).

Conclusions and future directions

This study has corroborated previous work on the at-sea distribution of Manx Shearwaters from Skomer during exodus and demonstrated further differences between male and female exodus strategies, particularly with respect to their different allocations of time to different at-sea behaviours, which are relatively constant in males but change in females as they develop their egg. In addition, this work is the first to describe the pre-laying exodus of Manx Shearwaters breeding on the Copeland Islands, which show many remarkable parallels with Skomer birds as well as subtle differences. The shared use by females of the waters around the continental shelf edge and Porcupine Bight strongly suggest that this area is highly important for Manx Shearwaters during exodus. Further tracking studies are recommended to investigate the variation in behaviour between a greater diversity of different colonies, which would allow higher resolution contrasts to be made to help clarify the differing effects of location, resource availability and colony demographics on the costs of breeding, and the behavioural strategies that Manx Shearwaters use to deal with them.

References

Abbott, C. L., Double, M. C., Gales, R., & Cockburn, A. (2006). Copulation behaviour and paternity in shy albatrosses (Thalassarche cauta). *Journal of Zoology*, *270*(4), 628–635. https://doi.org/10.1111/j.1469-7998.2006.00185.x

Arizmendi-Mejía, R., Militão, T., Viscor, G., & González-Solís, J. (2013). Pre-breeding ecophysiology of a long-distance migratory seabird. *Journal of Experimental Marine Biology and Ecology*, *443*, 162–168. https://doi.org/10.1016/j.jembe.2013.02.047

Ashcroft, R. E. (1976). *Breeding biology and survival of puffins*. University of Oxford.

Astheimer, L. B., & Grau, C. R. (1990). A comparison of yolk growth rates in seabird eggs. *Ibis*, *132*(3), 380–394. https://doi.org/10.1111/j.1474-919X.1990.tb01057.x

Austin, J. J., & Parkin, D. T. (1996). Low frequency of extra-pair paternity in two colonies of the socially monogamous short-tailed shearwater Puffinus tenuirostris. *Molecular Ecology*, *5*(1), 145–150. https://doi.org/10.1111/j.1365-294X.1996.tb00300.x

Brodier, S., Pisanu, B., Villers, A., Pettex, E., Lioret, M., Chapuis, J. L., & Bretagnolle, V. (2011). Responses of seabirds to the rabbit eradication on Ile Verte, sub-Antarctic Kerguelen Archipelago. *Animal Conservation*, *14*(5), 459–465. https://doi.org/10.1111/j.1469-1795.2011.00455.x

Brooke, M. . D. L. . (1978). Some Factors Affecting the Laying Date, Incubation and Breeding Success of the Manx Shearwater, Puffinus puffinus. *Journal of Animal Ecology*, *47*(2), 477–495.

Brooke, M. D. L. (1977). THESIS: The Breeding Biology of the Manx Shearwater.

Brooke, M. D. L. (1990). *The Manx Shearwater*. London: T & A D Poyser.

Brooke, M. D. L. (2018). *Far From Land: The Mysterious Lives of Seabirds*. Princeton University Press.

CBO. (2018). Manx Shearwaters on Copeland. Retrieved October 4, 2018, from http://www.thecbo.org.uk/birds/manx-shearwaters/

Chastel, O., Weimerskirch, H., & Jouventin, P. (1995). Influence of Body Condition on Reproductive Decision and Reproductive Success in the Blue Petrel. *Auk*, *112*(4), 964–972.

Christensen-dalsgaard, S., May, R., & Lorentsen, S. (2018). Taking a trip to the shelf : Behavioral decisions are mediated by the proximity to foraging habitats in the black-legged kittiwake. *Ecology and Evolution*, *8*, 866–878. https://doi.org/10.1002/ece3.3700

Clay, T. A., Phillips, R. A., Manica, A., Jackson, H. A., & Brooke, M. D. L. (2017). Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's petrels. *Marine Ecology Progress Series*, *579*, 139–155. https://doi.org/10.3354/meps12244

Dean, B. (2012). The at-sea behaviour of the Manx shearwater. *PhD Thesis*.

Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R. A., Perrins, C. M., & Guilford, T. (2012). Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of the Royal Society, Interface / the Royal Society*, rsif.2012.0570-. https://doi.org/10.1098/rsif.2012.0570

Dean, B., Kirk, H., Fayet, A., Shoji, A., Freeman, R., Leonard, K., … Guilford, T. (2015). Simultaneous multi-colony tracking of a pelagic seabird reveals cross-colony utilization of a shared foraging area. *Marine Ecology Progress Series*, *538*, 239–248. https://doi.org/10.3354/meps11443

Drent, R. H., & Daan, S. (1980). The Prudent Parent: Energetic Adjustments in Avian Breeding. *Ardea*, *38–90*, 225–252. https://doi.org/10.5253/arde.v68.p225

Fayet, A. L., Freeman, R., Shoji, A., Kirk, H. L., Padget, O., Perrins, C. M., … Verhulst, S. (2016). Carry-over effects on the annual cycle of a migratory seabird: an experimental study. *Journal of Animal Ecology*, *85*(6), 1516–1527. https://doi.org/10.1111/1365-2656.12580

Fayet, A. L., Freeman, R., Shoji, A., Boyle, D., Kirk, H. L., Dean, B. J., … Guilford, T. (2016). Drivers and fitness consequences of dispersive migration in a pelagic seabird. *Behavioral Ecology*, *27*(4), 1061–1072. https://doi.org/10.1093/beheco/arw013

Freeman, R., Dean, B., Kirk, H., Leonard, K., Phillips, R. A., Perrins, C. M., & Guilford, T. (2013). Predictive ethoinformatics reveals the complex migratory behaviour of a pelagic seabird, the Manx Shearwater. *Journal of the Royal Society, Interface / the Royal Society*, *10*(84), 20130279. https://doi.org/10.1098/rsif.2013.0279

Green, J. A., Boyd, I. L., Woakes, A. J., Warren, N. L., & Butler, P. J. (2009). Evaluating the prudence of parents: Daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin Eudyptes chrysolophus. *Journal of Avian Biology*, *40*(5), 529–538. https://doi.org/10.1111/j.1600-048X.2009.04639.x

Grémillet, D., Lewis, S., Drapeau, L., Lingen, C. D. Van Der, Huggett, J. A., Coetzee, J. C., …

Ryan, P. G. (2008). Spatial match – mismatch in the Benguela upwelling zone : should we expect chlorophyll and sea-surface temperature to predict marine predator distributions ? *Journal of Applied Ecology*, *45*, 610–621. https://doi.org/10.1111/j.1365-2664.2007.01447.x

Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., … Perrins, C. M. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater Puffinus puffinus: insights from machine learning. *Proceedings of the Royal Society B*, *276*(1660), 1215–23. https://doi.org/10.1098/rspb.2008.1577

Guilford, T., Wynn, R., McMinn, M., Rodríguez, A., Fayet, A., Maurice, L., … Meier, R. (2012). Geolocators reveal migration and pre-breeding behaviour of the critically endangered balearic shearwater Puffinus mauretanicus. *PLoS ONE*, *7*(3), 1–8. https://doi.org/10.1371/journal.pone.0033753

Harris, M. P. (1970). Territory Limiting the Size of the Breeding Population of the Oystercatcher (Haematopus ostralegus). *Journal of Animal Ecology*, *39*(3), 707–713.

Hedd, A., & Gales, R. (2005). Breeding and overwintering ecology of Shy Albatrosses in southern Australia: year-round patterns of colony attendance and foraging-trip durations. *The Condor*, *107*(2), 375–387. https://doi.org/10.1650/7563

Hedd, A., Montevecchi, W. A., Phillips, R. A., & Fifield, D. A. (2014). Seasonal sexual segregation by monomorphic sooty shearwaters Puffinus griseus reflects different reproductive roles during the pre-laying period. *PLoS ONE*, *9*(1), 1–11. https://doi.org/10.1371/journal.pone.0085572

Hegemann, A., Matson, K. D., Versteegh, M. A., & Tieleman, B. I. (2012). Wild skylarks seasonally modulate energy budgets but maintain energetically costly inflammatory immune responses throughout the annual cycle. *PLoS ONE*, *7*(5). https://doi.org/10.1371/journal.pone.0036358

Huyvaert, K. P., & Parker, P. G. (2010). Extra-pair paternity in waved albatrosses: Genetic relationships among females, social mates and genetic sires. *Behaviour*, *147*(12), 1591–1613. https://doi.org/10.1163/000579510X512096

Imber, M. J. (1976). Breeding biology of the grey-faced petrel *Pterodroma macroptera gouldi*. *Ibis*, *118*(1), 51–64. https://doi.org/10.1111/j.1474-919X.1976.tb02010.x

Jouventin, P., Charmantier, A., Dubois, M. P., Jarne, P., & Bried, J. (2007). Extra-pair paternity in the strongly monogamous Wandering Albatross Diomedea exulans has no apparent benefits for females. *Ibis*, *149*(1), 67–78. https://doi.org/10.1111/j.1474-919X.2006.00597.x

Kirk, H. (2016). THESIS: Annual and individual patterns in the behavioural cycle of the Manx Shearwater.

Macdonald, M. A. (1977). The Pre-Laying Exodus of the Fulmar Fulmarus Glacialis. *Ornis Scandinavica*, *8*(1), 33–37.

Mallory, M. L., Forbes, M. R., Ankney, C. D., & Alisauskas, R. T. (2008). Nutrient dynamics and constraints on the pre-laying exodus of High Arctic northern fulmars. *Aquatic Biology*, *4*(3), 211–223. https://doi.org/10.3354/ab00113

Manuwal, D. A. (1974). The Natural History of Cassin’s Auklet (Ptychoramphus aleuticus). *American Ornithological Society*, *76*(4), 421–431.

Meijer, T., & Drent, R. (1999). Re-examination of the capital and income dichotomy in breeding birds. *Ibis*, *141*(3), 399–414. https://doi.org/10.1111/j.1474-919X.1999.tb04409.x

Mugaas, J., & King, J. (1981). Annual variation of Daily Energy Expenditure by the Black-billed Magpie: Study of thermal and behavioral energetics. *The Cooper Ornithological Society*, 87. Retrieved from http://onlinelibrary.wiley.com/doi/10.1002/cbdv.200490137/abstract

Nager, R. G. (2006). The challenges of making eggs. *Ardea*, *94*(3), 323–346.

Perrins, C. M. (1966). Survival of young Manx Shearwaters Puffinus puffinus in relation to their presumed date of hatching. *Ibis*, 132–135.

Perrins, C. M., Wood, M. J., Garroway, C. J., Boyle, D., Oakes, N., Revera, R., … Taylor, C. (2012). A whole-island census of the Manx Shearwaters Puffinus puffinus breeding on Skomer Island in 2011. *Seabird*, *25*(Brooke 1978), 1–13. Retrieved from http://eprints.glos.ac.uk/565/1/A whole-island census of the Manx Shearwaters.pdf

Petrie, M., & Kempenaers, B. (1998). Extra-pair paternity in birds: Explaining variation between species and populations. *Trends in Ecology and Evolution*, *13*(2), 52–57. https://doi.org/10.1016/S0169-5347(97)01232-9

Phillips, R. A., Xavier, J. C., & Croxall, J. P. (2003). Effects of Satellite Transmitters on Albatrosses and Petrels, *120*(4), 1082–1090.

Pinet, P., Jaquemet, S., Phillips, R. A., & Le Corre, M. (2012). Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Animal Behaviour*, *83*(4), 979–989. https://doi.org/10.1016/j.anbehav.2012.01.019

Pollock, C. M., Mavor, R., White, R. W., Tasker, M. L., Webb, A., & Reid, J. B. (2000). *The* *distribution of seabirds and marine mammals in the Atlantic Frontier, north and west of Scotland.*

Quillfeldt, P., Masello, J. F., & Segelbacher, G. (2012). Extra-pair paternity in seabirds: A review and case study of Thin-billed Prions Pachyptila belcheri. *Journal of Ornithology*, *153*(2), 367–373. https://doi.org/10.1007/s10336-011-0751-9

Rayner, M. J., Taylor, G. A., Gummer, H. D., Phillips, R. A., Sagar, P. M., Shaffer, S. A., & Thompson, D. R. (2012). The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (Pterodroma axillaris). *Emu*, *112*(2), 107–116. https://doi.org/10.1071/MU11066

Richdale, L. E. (1963). Biology of the Sooty Shearwater Puffinus griseus. *Proceedings of the Zoological Society of London*, *141*(1), 1–117. https://doi.org/10.1111/j.1469-7998.1963.tb01603.x

Ropert-Coudert, Y., Wilson, R. P., Yoda, K., & Kato, A. (2007). Assessing performance constraints in penguins with externally-attached devices. *Marine Ecology Progress Series*, *333*, 281–289. https://doi.org/10.3354/meps333281

Rowan, M. K. (1965). Regulation of sea-bird numbers. *Ibis*, *107*, 54–59.

Sakao, M., Takeshima, H., Inoue, K. (2018). Extra-pair paternity in socially monogamous Streaked Shearwaters: forced copulation or female solicitation? *Journal of Ornithology*.

Schreiber, E. A. (2001). Climate and weather effects on seabirds. In E. A. Schreiber & J. Burger (Eds.), *Biology of marine birds* (pp. 179–216). Boca Raton.

Serventy, D. (1967). Aspects of the population ecology of the Short-tailed Shearwater. *Proceedings of the International Ornithological Congress*, *XIV*, 165–190.

Sharples, J., Moore, C. M., Hickman, A. E., Holligan, P. M., Tweddle, J. F., Palmer, M. R., & Simpson, J. H. (2009). Internal tidal mixing as a control on continental margin ecosystems. *Geophysical Research Letters*, *36*(December), 1–5. https://doi.org/10.1029/2009GL040683

Shoji, A., Aris-Brosou, S., Culina, A., Fayet, A., Kirk, H., Padget, O., … Guilford, T. (2015). Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biology Letters*, *11*(10), 20150671. https://doi.org/10.1098/rsbl.2015.0671

Studwell, A. J., Hines, E., Elliott, M. L., Howar, J., Holzman, B., Nur, N., & Jahncke, J. (2017). Modeling Nonresident Seabird Foraging Distributions to Inform Ocean Zoning in Central California, 1–26. https://doi.org/10.1371/journal.pone.0169517

Sullivan, W., & Wilson, K. J. (2000). Differences in habitat selection between Chatham petrels (Pterodroma axillaris) and broad-billed prions (Pachyptila vittata): Implications for management of burrow competition. *Emu*, *100*(4), 329–333. https://doi.org/10.1071/MU00058

Tyson, C., Kirk, H., Fayet, A., Van Loon, E. E., Shoji, A., Dean, B., … Guilford, T. (2017). Coordinated provisioning in a dual-foraging pelagic seabird. *Animal Behaviour*, *132*, 73–79. https://doi.org/10.1016/j.anbehav.2017.07.022

Warham, J. (1977). Wing loadings, wing shapes, and flight capabilities of procellariiformes. *New Zealand Journal of Zoology*, *4*(1), 73–83. https://doi.org/10.1080/03014223.1977.9517938

Warham, J. (1983). The composition of petrel eggs. *The Condor*, *85*(2), 194–199.

https://doi.org/10.2307/1367254

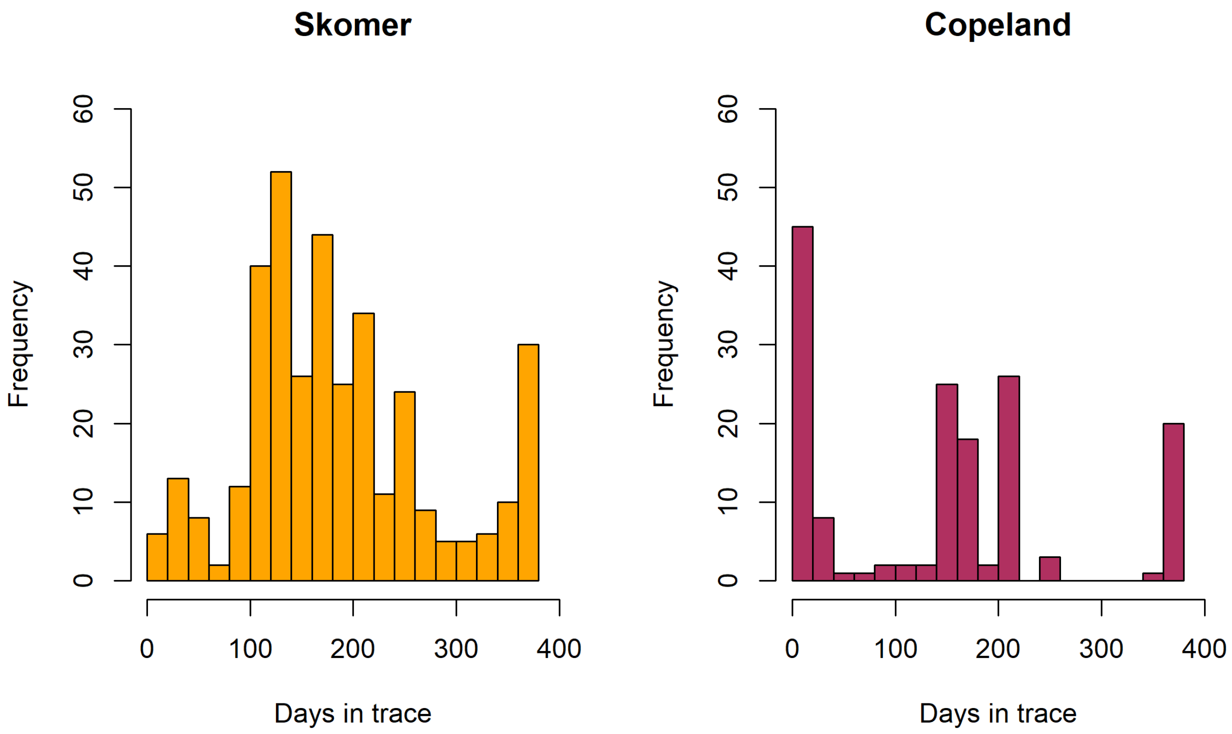
Warham, J. (1990). *The petrels: their ecology and breeding systems*. San Diego: Academic Press.

Williams, T. D. (2005). Mechanisms underlying the costs of egg production. *BioScience*, *55*(1), 39–48. https://doi.org/10.1641/0006-3568(2005)055[0039:MUTCOE]2.0.CO;2

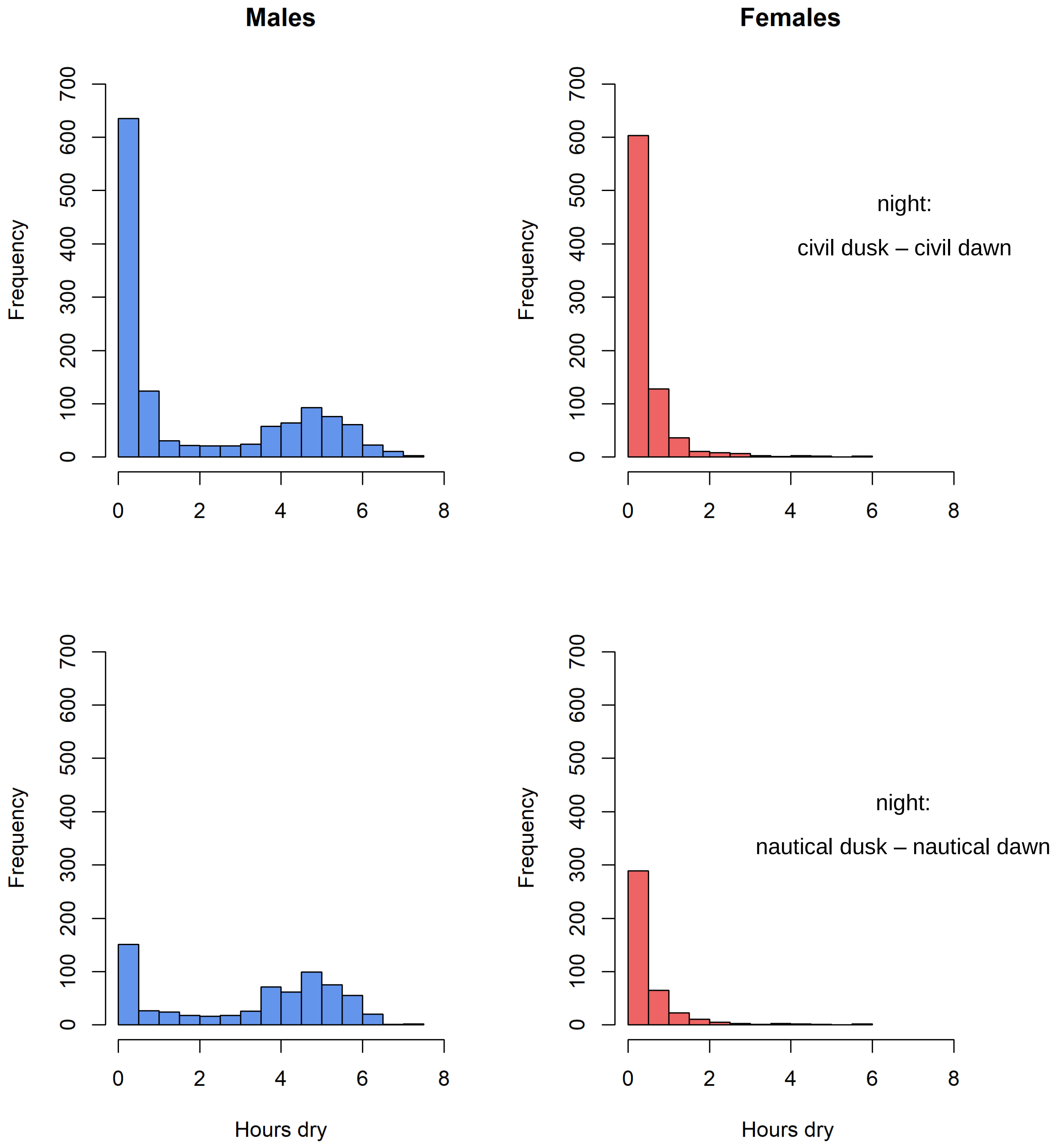
Witter, M. S., & Cuthill, I. C. (1993). The Ecological Costs of Avian Fat Storage. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *340*(1291), 73–92. https://doi.org/10.1098/rstb.1993.0050

Wynn, R. B., & Krastel, S. (2012). An unprecedented Western Palearctic concentration of Wilson's Storm-petrels Oceanites oceanicus at an oceanic upwelling front offshore Mauritania. *Seabird*, *25*, 47–53.

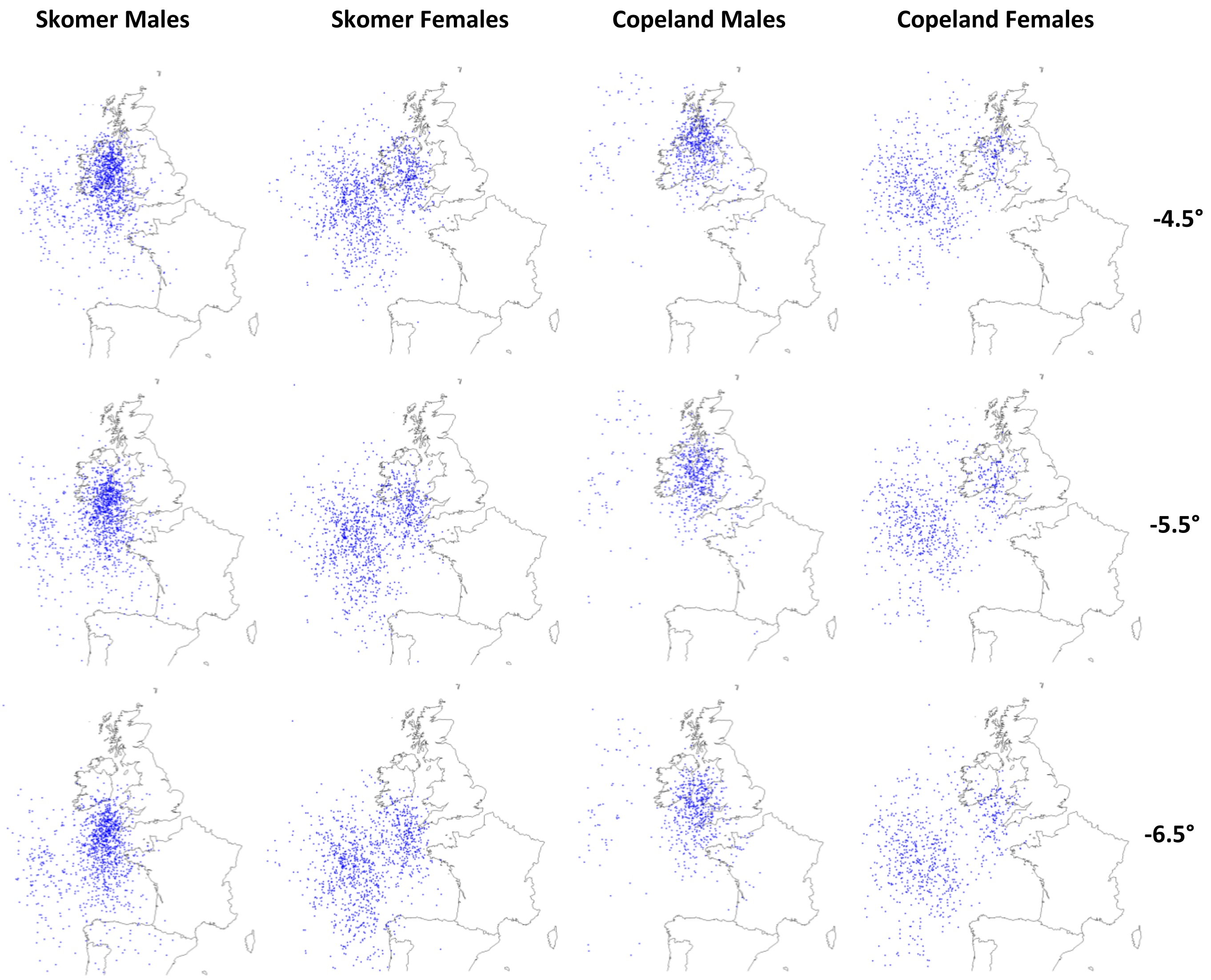
Supplementary Material



Supplementary Figure 1. Histograms showing the frequency of different lengths of immersion traces after pre-processing of the entire Manx Shearwater long-term geolocator dataset from Skomer (n = 364) and Copeland (n = 156).



Supplementary figure 2. Histograms showing the frequency of durations of continuous dry data for each sex within nights including and excluding nautical twilight. Top row: night bounded by civil dawn/dusk, sun elevation angle -6°. Bottom row: night bounded by nautical dawn/dusk, sun elevation angle -12°. Short (< 3 hour) and long (≥ 3 hour) dry periods are interpreted as periods of flight and periods on land, respectively. There is a 4-fold and 2-fold increase in the frequency flight for males and females, respectively, for night bounded by civil rather than nautical dawn/dusk, while there is minimal change in the frequency of periods on land. This shows that ≥50% of night-time flights occur during nautical twilight i.e. when the sun is between 6° and 12° below the horizon.



Supplementary figure 3. Maps showing light-derived locations of birds during exodus from each island and sex calculated using three sun elevation angles. These maps illustrate the effect of sun elevation angle on positions: more negative angles shift points south, while less negative angles shift points north. The sun elevation angle of -5.5° was selected as the most plausible value by visual examination of positions.

Chapter 3

Short-term parental response to offspring demand in seabirds: an experimental study

Abstract

The offspring of many species require substantial parental care before they develop to independence. Offspring that receive more care are generally more likely to survive and breed, and thus parents benefit from providing more care to offspring. However, parental care is often costly for parents and has been shown to reduce their body condition and survival. In iteroparous species, parents are expected to balance investment in current reproduction against future reproduction to maximise lifetime reproductive success. Parental care will therefore not always be delivered to meet the needs of the offspring if costs to future reproduction outweigh the benefits to the current breeding attempt. This trade-off between current and future reproduction is most acute in long-lived species in which each reproductive attempt represents only a small proportion of lifetime reproductive potential.

With long-lifespans and slow life-history strategies, procellariform seabirds are expected to prioritise their own survival over the success of a single breeding attempt. This led to a hypothesis that parents provide a fixed level of parental investment independent of chick need. However, evidence from long-term studies and experimental manipulations of chick need and parent condition suggest that procellariform parents adopt a flexible investment strategy in which they are responsive to their own condition and the needs of their chick. Parental care adjustment has been well documented over the course of a breeding attempt, but much less is known about whether parents respond to changes in chick need over a long period of time or immediately change their behaviour following an interaction with their offspring. Understanding the time frame within which parents respond to chick need will help identify the mechanisms behind the adjustment of parental care, and ultimately help understand the evolution of parental care strategies.

In this study I investigate whether parents immediately adjust their foraging and provisioning behaviour in the subsequent foraging trip and provisioning visit in response to chick need. To test this, I used field experiments to artificially increase the chick need perceived by a parent and bird-borne geolocators to measure and compare the behaviour of the parents before and after the exposure to their offspring. Results showed a direct effect of increased provisioning to the hungry chick treatment, but no detectable effect of the hungry chick treatment on either subsequent foraging behaviour or provisioning. Taken together with the results of previous studies, this suggests that parents use chick hunger mediated through begging to inform provisioning load during a feeding visit and chick body condition to inform subsequent foraging effort and provisioning.

Introduction

Parental care functions to increase the survival and fitness of offspring, and hence increase the fitness of the care-giving parent (Clutton-Brock, 1991). It is exhibited by many taxa across the animal kingdom, including fish, amphibians, reptiles, arthropods and other invertebrates, but it is most widespread among birds and mammals (Royle et al., 2012). Parental care may be delivered by one or both parents and encompasses a diverse array of parental behaviours, ranging from the building of elaborate nests to distraction displays to lure predators away from vulnerable young (Hansell, 2000; Weston & Elgar, 2005). Although parents benefit from increasing the fitness of their current offspring, parental care can be costly because the time, energy and other resources invested in care may be traded-off against parent survival and future reproduction (Owens & Bennett, 1994). In iteroparous species, parental care is thus optimised by natural selection to maximise lifetime reproductive success, balancing the benefits of investment in current offspring against the associated costs to future reproductive success (Trivers, 1972; Williams, 1966). Since the costs and benefits of providing care may vary as conditions change, parents must constantly make and update decisions between investing in current reproduction and ensuring their own survival.

In order to make appropriate decisions that ultimately improve lifetime reproductive success, animals use information from both intrinsic and extrinsic sources to update their behavioural strategies (McFarland, 1977). There are numerous relevant factors that parents may consider in deciding how to allocate investment between offspring care and self-maintenance. As an indicator of adult survival (Chastel et al., 1995), parent body condition can have a significant effect on parental care decisions in some species, and parents in good body condition have been shown to invest more in their offspring than parents in poor body condition (Erikstad et al., 1997; Johnsen et al., 1994; Tveraa et al., 1998). Parents may also regulate their parental investment according to the needs of their offspring. Nutritional status as a proxy for chick need may be assessed by parents as offspring body mass (Tveraa et al., 1998) or the amount of food already provisioned (Ricklefs, 1987). Alternatively, offspring may communicate their need to parents through signals such as begging calls (Quillfeldt et al, 2004; Rector et al., 2014). However, such systems are vulnerable to exploitation as offspring benefit from conveying exaggerated need due to parent-offspring conflict (Trivers, 1974). Although the effects of many factors on parental investment decisions have been well characterised, there is a paucity of information on the mechanisms by which parents assess these factors, the timescales over which these operate, and how parents integrate multiple sources of information (Riou et al., 2012).

Decisions between investing in current reproduction and own survival are particularly critical in long-lived animals that have slow life-history strategies (Roff, 2002). Each reproductive attempt represents only a small component of lifetime reproductive success, and since future reproductive potential is high, costs to adult survival will have large consequences for lifetime reproductive success and fitness. Long-lived animals must therefore strike a fine balance between providing sufficient care to their offspring while minimising negative impact on their own survival, and in general they are expected to prioritise their own survival over the success of a single reproductive attempt (Mauck & Grubb, 1995). Long-lived animals are also more likely to experience greater interannual fluctuations in conditions over the course of their lifetime which may alter the optimal parental care strategy, and their ability to adjust their current strategy appropriately can have significant impacts on fitness (Erikstad et al., 1998).

Seabirds are all long-lived species with slow life-history strategies, and over their lifetime they may produce many small or single-chick broods (Ricklefs, 1990). Long incubation times and the slow development of semi-altricial chicks mean that each reproductive attempt involves a long and demanding period of biparental care (Schreiber & Burger, 2001). Seabird offspring are totally reliant on parental food provisioning to reach fledging age and condition. Under a certain threshold of provisioning, chicks will not survive. Above this threshold, increasing food provisioning may increase offspring fitness as higher fledging mass leads to higher subsequent survival and recruitment in many species (Perrins et al., 1973; Maness & Anderson, 2013; Morrison et al., 2009; Perrins, 2014; Sagar & Horning, 1998). Seabird parents therefore benefit from provisioning lots of food to their young, however this can be challenging for seabirds. Food is generally unpredictable and patchily distributed at-sea (Weimerskirch, 2007) meaning that parents must make time and energy consuming journeys to find food, which may also be distant to the colony if local prey have been depleted (Ashmole, 1963). In addition, parents are constrained in the time they can spend at-sea before they must return to feed the chick, effectively limiting the distance that they can travel and the quantity and quality of resources they can access, while carrying heavy food loads back to the colony may add to travel times and energetic costs (Orians & Pearson, 1979; Wetterer, 1989).

Despite strategies to deal with these problems such as dual foraging (Shoji et al., 2015) and coordinated biparental provisioning (Tyson et al., 2017; Wojczulanis-Jakubas et al., 2018), increased foraging effort and provisioning for chicks may still be have substantial costs on parental nutritional status, which can result in reduced survival and reproductive success in subsequent breeding attempts (Catry et al., 2013; Fayet et al., 2016). Parents are therefore predicted to carefully control their investment in food provisioning to avoid costs to future reproduction. It has been suggested that some seabird parents provide a fixed level of parental investment to prioritise their own survival over the needs of their offspring, with evidence supporting this from several seabird species (Hamer & Hill, 1994; Navarro & González-Solís, 2007; Takahashi et al., 1999). However, more recent findings suggest that most seabirds utilise a conservative but flexible investment strategy, whereby parents are responsive to offspring but only when costs to themselves are minimal (Harding et al., 2009; Tveraa et al., 1998; Weimerskirch et al., 2001).

Studies investigating the relationship between chick need and parental investment through provisioning have typically focussed on long term natural trends (e.g. Gray et al., 2014; Weimerskirch et al., 2001) or the effects of experimental manipulations that alter the benefits and/or costs of provisioning for a significant portion of the breeding season (e.g. Cook & Hamer, 1997; Gjerdrum, 2004; Harding et al., 2009; Tveraa et al., 1998). These approaches show effects averaged over a breeding season but reveal little about the time-scales over which parents assess and respond to changes in chick need. Whether parents adjust their provisioning behaviour immediately after being exposed to a change in chick need is currently poorly known (Quillfeldt et al., 2004). Improved understanding of the time-scales over which parents respond to chick need would provide insights into the mechanisms behind these responses and ultimately the evolution of parental care strategies.

In this study, Manx Shearwaters are examined as a model seabird to test the hypothesis that increased chick need during a single feeding visit results in an immediate parental response of increased foraging effort and food provisioning to the chick. Parents were tagged with miniature geolocators to measure their at-sea foraging effort during chick-rearing. To manipulate apparent chick-need, tagged parents were exposed to a hungry chick after they had fed their own chick upon return from an at-sea foraging trip. Chicks were returned to their original burrows after the parent returned to sea, with the hungry chick treatment used only once for each tagged-parent. Chicks were weighed on the night of manipulation and the subsequent feeding visit to estimate food provisioning. The foraging effort of parents was measured both before and for two trips after the manipulation to detect potential changes in their foraging effort. I used these data to test (i) whether parents fed more to hungry chicks, (ii) whether they increased the amount of food brought to the chick on the post-treatment visit, (iii) whether they increased their foraging effort after exposure to the hungry chick and (iv) whether they shortened the duration of foraging trips after exposure to the hungry chick.

Materials and methods

Study population and geolocator deployment

The experiment was carried out on Skomer Island, Wales (51°440 N, 5°190 W), inhabited by 300,000 breeding pairs of Manx Shearwater (Perrins et al., 2012). Manx shearwaters breed in burrows and only return to the colony at night. They do not recognise their chick and will feed any chick they are presented with, including an additional chick present alongside their own (Harris, 1966). A study population of 90 breeding pairs in the North Haven sub-colony was monitored from early April 2017 to record parent identities, egg lay dates and egg hatch dates. 28 burrows in which the chick could be easily accessed were randomly selected for the experiment. Pairs of study and replacement chicks with the same or similar hatch dates were randomly chosen from hatch dates ranging between 28th June – 19th July (median 7th July).

To detect when parents returned to their burrow, knock-down sticks were set up in burrow entrances with visual checks of the sticks made every 15 minutes during the night. Birds were captured by hand inside the nest. Once captured, C65 geolocators from Migrate Technology were deployed on one chick-rearing Manx Shearwater in each of the 28 breeding burrows between 24th July – 17th August. Geolocators were attached using two lightweight Panduit cable ties fastened to a BTO metal leg ring fitted to adult tarsi earlier in the season or in previous years. 26 devices were retrieved between 15th August – 10th September. 2 devices were not retrieved as the individuals were only recaptured in the subsequent breeding season and geolocators had been lost in the intervening period.

Bird handling time during deployment and retrieval of geolocators was generally less than 3 minutes and always less than 10 minutes. Geolocators weighed 1 gram, less than 0.3% of typical adult body weight and well under the 3% maximum (Phillips et al., 2003). All work was carried out with permission from the British Trust for Ornithology Unconventional Methods Technical Panel and Oxford University's Local Ethical Review Process, and followed methods used in previous studies (Fayet et al., 2016; Guilford et al., 2009).

Experimental design

Following geolocator deployment, geolocator-tagged parents were left for 2-14 foraging trips (5-26 days) to allow the devices to record unmanipulated behaviour. Tagged parents were then subjected once to either the control or hungry chick treatment when they returned to their burrow (see experimental treatments section below). The last foraging trip before the treatment was termed trip 1 and the first trip after the treatment was termed trip 2. Geolocators were left on for another trip – trip 3 – after which tagged parents were captured to retrieve the devices. See figure 3 for a summary. The design aimed to test whether parents altered their foraging and provisioning behaviour immediately after the treatment and whether any response persisted after a subsequent visit to the burrow.

From the night of the treatment until the subsequent visit to the burrow, chicks in the experiment were weighed at 21:00 GMT every evening before adults returned to the colony. To quantify feeds, chicks were weighed 30 minutes and 60 minutes after either parent returned to the burrow. During this hour, the burrow entrance was blocked to prevent the other parent feeding the chick at the same time. If both parents returned in the same night, only the feeds of the first adult were recorded to minimise overall disturbance to the chick and parents. No weights were taken on the 16th August as heavy rain and wind made it unsafe to remove chicks from their burrows.

Of the 28 tagged parents in the experiment, 2 evaded capture after trip 3 and devices were not retrieved, while 5 evaded capture until near the end of the breeding season and were not exposed to the experimental treatments. Overall, data were gathered from 10 parents in the hungry chick group and 11 parents in the control group. Data from one control parent lacked trip 3 as the device was retrieved early as the field season was ending. In addition, data from one parent in the control group were discounted because the condition of its chick and burrow were highly unrepresentative of the population. Specifically, the burrow was flooded with water and mud, and the chick was always wet. The chick was severely underweight for its age (Figure 1), with a Grubbs test supporting the chick's mean weight as an outlier (G=3.12, p=0.006). The chick perished soon after the experiment and was the only one of 74 chicks in the study colony which did not fledge. The chick and burrow were in this condition before the GLS was deployed on the parent. Overall, we collected complete datasets (from trip 1 to 3) for 10 birds in the treatment group and 9 birds in the control group.

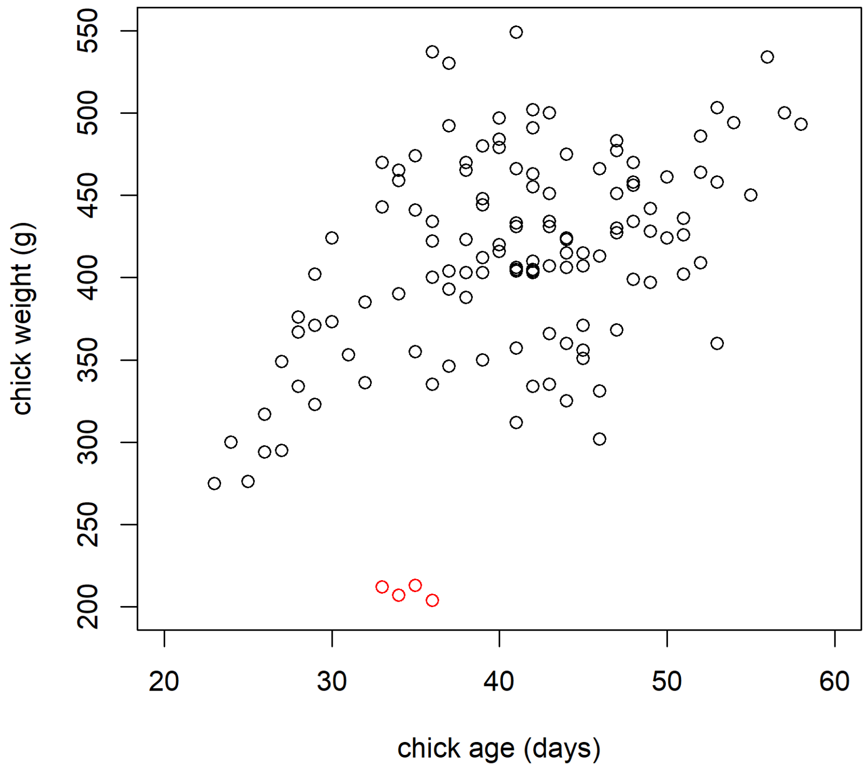


Figure 1. A scatterplot showing the relationship between chick age and weight for all measurements made during the experiment. Red circles show measurements of the control treatment chick in burrow 122, which was severely underweight for its age and excluded from the analysis.

Experimental treatments

Two treatments were used in this experiment – a hungry chick and a control treatment – one of which was applied once to each tagged parent. All chicks in the 28 study nests were paired with another chick of the same age outside of the study nests, which would act as hungry replacement during the chick-swap manipulation. The 28 tagged parents were not pre-allocated to either treatment group. Instead, treatments were assigned alternately to parents as they returned to their burrow after phase 1. This was done to account for possible effects of temporal changes in environmental variables (e.g. prey distribution, wind conditions, water turbidity) on foraging and provisioning over the study period, by having both treatments balanced across the duration of the study. There was no significant difference in the mean dates of treatment between the control and hungry chick groups (welch two-sample t-test; df=18, t=0.72, p=0.48), with a mean of 17th August and 15th August, respectively.

In both treatments, the tagged parent was blocked in its burrow within 15 minutes of arrival and left to feed its chick for 30 minutes. In the control treatment, the original chick was then removed from the burrow, weighed and placed back into its original position in the burrow. In the hungry chick treatment, the original chick was removed from the burrow, weighed and housed in a secure box indoors overnight, and its paired replacement chick, which had been kept unfed by blocking the entrance to its burrow, was weighed and swapped into the same position as the original chick in the study burrow. Both treatments took under one minute to complete, after which the study burrow was left blocked for a further 30 minutes to expose the tagged parent to a hungry chick. In both treatments, the chick in the study burrow was then removed, weighed and returned to the study burrow, which was unblocked and not disturbed again. At dawn, all chicks were returned to their original burrows.

To source hungry replacement chicks, each study burrow was assigned a group of potential replacement chicks from the North Haven sub-colony, chosen to match the hatch date of study chick as closely as possible. During trip 1 of each study burrow, the entrance of one potential replacement chick burrow was blocked before dusk to ensure that the replacement chick would not be fed that night. If the tagged parent of the paired study burrow returned and was assigned to the hungry chick group, then the unfed replacement chick was used for the swap. If the tagged parent of the partnered study burrow did not return or was assigned to the control group, then the burrow of the potential replacement chick was unblocked to allow parents to access their chick. Hatch dates of original and replacement chicks matched by ±2 days for 6 swaps, and by 4, 6, 8 and 12 days in the other 4 swaps. For the latter swaps in which precise matches were not possible, a replacement chick of similar weight to the original chick was selected. Burrows of potential replacement chicks were not blocked for more than one night during the study to minimise possible impacts on the parents and chicks. Replacement chicks all continued to be fed by their parents and fledged after the experiment.

Quantification of foraging behaviour from geolocator data

Geolocators were set to record maximum light intensity every 5 minutes and salt-water immersion (i.e. whether the device was immersed in saltwater or not) as a series of wet-dry transitions at 6 second resolution (mode 9 on the device). The number of wet/dry transitions has been used as an indicator of foraging activities in procellariforms as it corresponds to short bouts of flight searching for prey alternated with short wet bouts when birds land on the water or dive to catch prey (Dias et al., 2012). Wet/dry transitions were counted in 5-minute bins and a daily foraging score was calculated as the number of 5-minute bins that contained at least one transition in each day. Only transitions during daylight (light >2 lux) were counted as Manx Shearwaters are not known to forage at night (Shoji et al., 2016).

To validate daily foraging score as a good estimate of foraging effort, a separate geolocator dataset collected on breeding Manx shearwaters was compared against simultaneously recorded dive data from dive loggers, co-deployed with geolocators on 17 chick-rearing Manx Shearwaters in the same sub-colony and season (July and August 2017) as the current study. From the geolocator data, daily foraging score was calculated as described above. From dive data, an equivalent daily dive-bout score was calculated as the number of 5-minute bins that contained a dive (defined as changes in depth of >1m), and a daily dive-number score was calculated as the number of dives per day during daylight (Figure 2). To assess daily foraging score as a measure of foraging, linear mixed-effects models (LMMs) were performed with daily dive-bout score and daily dive-number as the response variables, daily foraging score as the fixed effect, and random intercepts for individual. Models confirmed that daily foraging score was a strong predictor of daily dive-bout score and daily dive-number, explaining a high proportion of variance in both dive scores (Figure 2; LMMs: daily dive-bouts, n=91 days, R^2=0.76, χ_1^2=94.4, p<0.001; daily dive-number, n=91, R^2=0.67, χ_1^2=43.7, p<0.001).

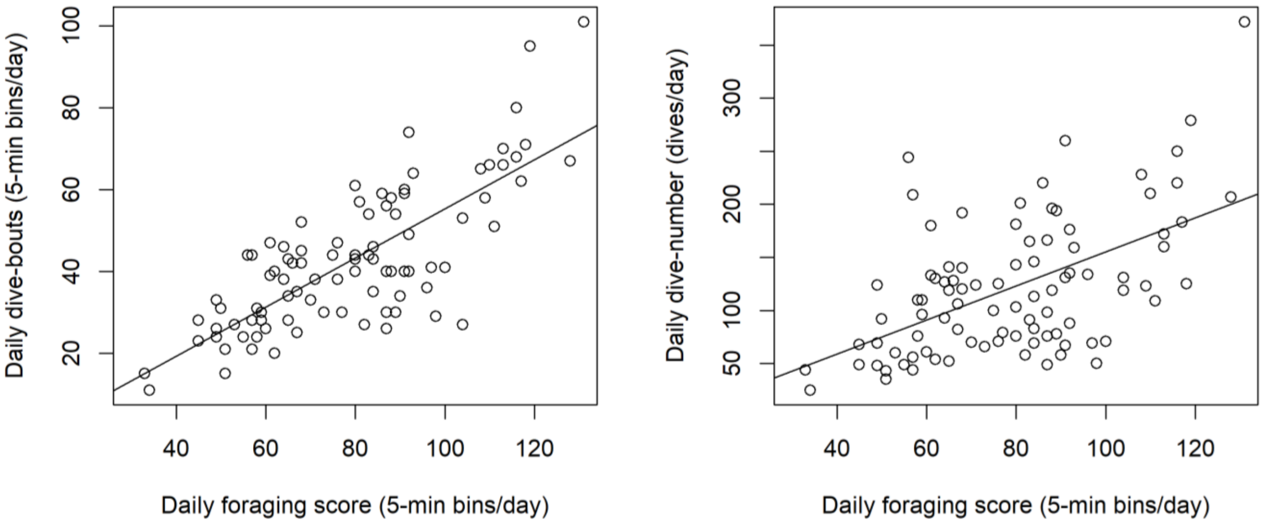


Figure 2. Graphs showing the relationship between daily foraging score, calculated from wet-dry transition data, and two different measures of daily foraging extracted from depth recorders. Lines show the linear regression model predictions for each relationship.

Foraging trip metrics

Foraging trip duration (i.e. the number of days at-sea between successive visits to the colony) was calculated from visits to land estimated from immersion and light data. Periods of at least 30 minutes of continuous dry starting at least 40 min after dusk and ending at least 30 min before dawn (where dusk and dawn were the start and end times of nights, defined where light intensity was below 2 lux) were classified as visits to land. These thresholds were chosen after examination of both the frequency distributions of different length dry periods at night in the geolocator data (supplementary figure 1) and of the lengths of burrow visits precisely recorded from RFID sensors placed at burrow entrances during the 2018 field season (Supplementary figure 2; see Tyson et al., 2017 for detials of RFID setup). RFID data showed that the mean burrow visit duration was 2.95 hours (SD=±1.3, n=1400) with only 3.6% of visits lasting fewer than 30 minutes. RFID data also showed that burrow visits were infrequent just after dusk and just before dawn. Specifically, only 1% of burrow visits started before 40 minutes after civil dusk*, and only 1% of burrow visits were ongoing within 30 minutes of civil dawn. These periods are also the most likely periods of the night to contain flight at-sea as birds may be flying to or from the colony or may engage in pre-rafting flights.

In addition to trip duration, other foraging trip metrics were calculated from daily foraging scores. Trip total foraging scores were calculated as the sum of daily foraging scores for each foraging trip, whilst trip daily foraging scores were calculated for each foraging trip as the average daily foraging score over that entire trip. These scores were used as proxies for foraging effort.

Provisioning was also quantified for trips 1 and 2 by weighing chicks 30 and 60 minutes after adults returned to the burrow during both the hungry chick and control treatments and on the subsequent visit to the burrow. Chicks were weighed in the field on a digital scale accurate to one decimal place, with weights rounded to the nearest gram. Since wind and uneven ground may have increased random measurement error, a 3-component Gaussian mixture model was fitted to the data using the ‘normalmixEM’ function from the Mixtools package (Benaglia et al., 2009) in R 3.4.4 (R Core Development Team 2018) to attempt to distinguish random errors from true weight changes. The model predicted distributions with means of -0.4g (SD=±3.6), 10.1g (SD=±3.0) and 52.0g (SD=±2.2), termed no feed, small feed and large feed, respectively. Data points were labelled as no feed, small feed or large feed, depending on to which distribution they had the highest probability of belonging.

*Night defined by civil twilight, with a sun elevation angle of -6°. This corresponds closely to that defined by the 2-lux light threshold used in this study.

Statistics

Statistical analyses were performed in R 3.4.4. All means have associated standard error, unless otherwise stated. The normality assumptions of statistical tests were checked by visual inspection of histograms in R, and non-parametric statistical tests were used if data normality assumptions were not met. For control vs. treatment group comparisons of foraging score, Welch two-sample t-tests or Wilcoxon rank sum tests were used, while paired t-tests or Wilcoxon signed rank tests were used for between-trip comparisons to account for between-individual variation. Chi-squared tests and Fishers exact tests were used to compare frequency data. The lm function in R was used to run ordinary least squares regressions.

Results

Chick weight and age

Mean chick weight and age on the night of the treatment were compared between the control and hungry chick groups. Mean chick weight on the night of treatment was 434g (±14g, n=10) for control chicks and 397g (±23g, n=10) for study chicks in the hungry chick treatment group; there was no significant difference between the groups (welch two sample t-test; df=14, t=1.37, p=0.191). There was also no significant difference between the age of the control and treatment group chicks at the time of the treatment (welch two-sample t-test; df=17, t=1.34, p=0.198), with a mean of 42 days (±2.7 days, n=10) and 37 days (±2.5 days, n=10), respectively. Chick age had no effect on: chick total weight gain in the hour after the adult returned (OLS regression; $F_{1,23}$=1.04, p=0.319), trip daily foraging score ($F_{1,57}$=1.18, p=0.283), trip total foraging score ($F_{1,57}$=0.29, p=0.595) or trip duration ($F_{1,57}$=0.39, p=0.533). Chick age was therefore not included in the analyses that follow.

Chick provisioning

Direct effect of exposure to increased chick need during treatment

To assess whether the treatment caused parents to feed more food to the hungry replacement chick than they would to their own partially satiated chick, weight gain (a proxy for feed size) of replacement chicks over minutes 30-60 of the hungry chick treatment was compared against weight gain of original chicks over minutes 30-60 on nights of the control treatment. Mean weight gain of replacement chicks was marginally larger than that of original chicks over minutes 30-60, at 7.4g (±4.9g) and 1.5g (±1.4g), respectively (wilcoxon rank sum test; n_1=10, n_2=58, W=397, p=0.063). Mean weight gain of original chicks over minutes 0-30

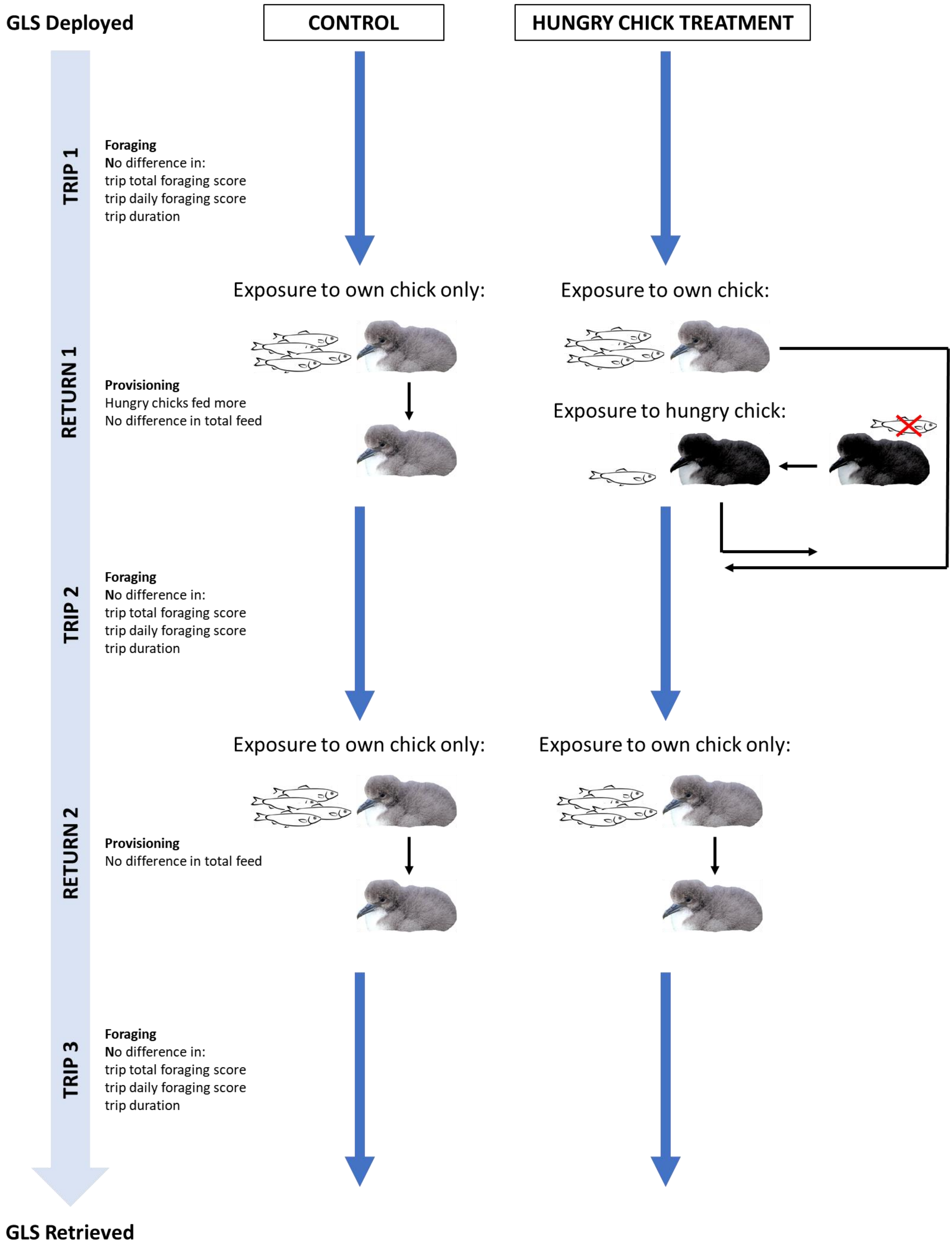


Figure 3. A summary figure to show the design of the experiment and the observed effects of the treatment on parent foraging and provisioning behaviour. Vertical arrows represent the passage of time while horizontal arrows show the translocation of chicks in and out of nests.

did not differ significantly between the nights of the hungry chick treatment and nights of the control treatment, with feeds of 60.7g (±6.4g, n=10) and 71.5g (±3.5g, n=61), respectively (welch two-sample t-test; df=15, t=1.48, p=0.159). Mean total weight gain of chicks over minutes 0-60 was similar between both groups, at 68.1g (±7.4g, n=10) on nights of the hungry chick treatment and 73.8g (±3.5g, n=58) on nights of the control treatment (welch two-sample t-test; df=13, t=0.69, p=0.500).

Weight changes over minutes 30-60 were typically small, and it was possible that some weight changes were due to random measurement error in chick weights taken in the field. To attempt to distinguish measurement errors from true weight changes, a 3-component normal mixture model was fitted to the data. The model predicted groups with means of -0.4g (SD=±3.6g), 10.1g (SD=±3.0g) and 52g (SD=±2.2g), and weight changes were labelled as no feed, small feed or large feed based on which distribution they had the highest probability of belonging. The relative frequencies of feeds over minutes 30-60 between the control and hungry chick treatments differed significantly, with 30% (3/10) of replacement chicks receiving food compared to 5% (3/58) of original chicks (Table 1; chi-squared test; df=2, χ^2=7.86, p=0.02; fisher's exact test; p=0.037). This suggested that the hungry chick treatment made parents more likely to feed over minutes 30-60 compared to the control treatment.

Table 1. The number of different feed types between 30-60 minutes after adult return, with feeds classified using the 3-component normal mixture model.

	Original chick	**Replacement chick**
No feed	55	7
Small feed	1	2
Large feed	2	1

Chi-squared test; df=2, χ^2=7.86, p=0.02; fisher's exact test; p=0.037.

Subsequent visits to the nest

To test whether the hungry chick treatment influenced food provisioning during the tagged-parent's first visit to the burrow after the treatment, chick weight changes were compared within treatment groups between the night of the treatment and the subsequent visit to the burrow (trip 1 and trip 2). Paired tests were used to account for between-individual differences. Although burrows were monitored at 10-minute intervals every night, visits to land identified from GLS data showed that 6/10 parents in the hungry chick group and 6/10 parents in the control group evaded detection during their first visit to land after the hungry chick treatment, so sample sizes for paired tests were limited to 4 for each group.

In the control group, mean chick weight gain over minutes 0-30 did not differ significantly, at 79.3g (±9.6g) on the night of the treatment and 72.5g (±9.8g) on the subsequent visit to the burrow (paired t-test; df=3, t=0.38, p=0.729). Mean chick weight gain over minutes 30-60 also did not differ significantly, at 3g (±1.3g) on the night of the treatment and -2g (±2g) on the parent's subsequent visit to the burrow (Wilcoxon signed rank test; n=4, W=6, Z=1.67, p=0.25). Finally, mean chick weight gain over minutes 0-60 did not differ significantly, at 82.3g

(±10.1g) on the night of treatment and 70.5g (±10.6g) on the parent's subsequent visit to the burrow (paired t-test; df=3, t=0.60, p=0.589).

In the hungry chick group, mean chick weight gain over minutes 0-30 did not differ significantly, at 58g (±7.7g) on the night of the treatment and 66.5g (±12.3g) on the subsequent visit to the burrow (paired t-test; df=3, t=0.76, p=0.501). Mean chick weight gain over minutes 30-60 also did not differ significantly, at 15.8g (±11.7g) on the night of the treatment and -0.5g (±2.5g) on the parent's subsequent visit to the burrow (wilcoxon signed rank test; n=4, W=8.5, Z=1.29, p=0.375). Finally, mean chick weight gain over minutes 0-60 did not differ significantly, at 73.8g (±10.8g) on the night of treatment and 66g (±11.5g) on the parent's subsequent visit to the burrow (paired t-test; df=3, t=2.53, p=0.086).

Parent foraging behaviour

Trip total foraging scores derived from light/immersion data were compared between the hungry chick and control groups for each numbered trip (Figure 4A). There was no difference between the trip total foraging scores of the two groups for any of the trips (Table 2). There was also no difference between the trip daily foraging scores (trip total foraging/trip duration) of the two groups (Figure 4B; Table 3).

In addition to comparing foraging scores of each trip between groups, trips were also compared within groups to test for any change in foraging behaviour between trips in response to the treatment (Figure 4A). Between trips, there were no significant differences in trip total foraging score within the hungry chick or the control groups (Table 2). There were also no significant differences in trip daily foraging scores between trips within the hungry chick and control groups (Figure 4B; Table 3).

Table 2. Mean trip total foraging scores for each experimental trip within treatment groups. Trip total foraging scores represent the total foraging effort for each foraging trip (unit = number of 5 min bins with at least one wet/dry transition). Numbered arrows relate to statistical comparisons, below.

	Trip 1		**Trip 2**		**Trip 3**
Control	103.6 (±31.1, n=10)	↔ 4	85.0 (±13.4, n=10)	↔ 5	158.7 (±61.7, n=9)
	↕ 1		↕ 2		↕ 3
Hungry chick	153.1 (±35.7, n=10)	6 ↔	161.3 (±58.9, n=10)	7 ↔	236.4 (±59.3, n=10)

Wilcoxon rank sum tests: $^{1}n_1$=10, n_2=10, W=26, p=0.076; $^{2}n_1$=10, n_2=10, W=51.5, p=0.940; $^{3}n_1$=9, n_2=10, W=39, p=0.661. Wilcoxon signed rank tests: ^{4}n=10, W=33, Z=0.56, p=0.625; ^{5}n=9, W=12, Z=1.25, p=0.238; ^{6}n=10, W=29, Z=0.15, p=0.922; ^{7}n=10, W=20, Z=0.76, p=0.492.

Table 3. Mean trip daily foraging scores for each experimental trip within treatment groups. Trip daily foraging scores represent the average daily foraging effort for each trip (unit = number of 5 min bins with at least one wet/dry transition). Numbered arrows relate to statistical comparisons, below.

	Trip 1		**Trip 2**		**Trip 3**
Control	71.8 (±3.6, n=10)	↔ 4	70.1 (±5.0, n=10)	↔ 5	80.4 (±7.5, n=9)
	↕ 1		↕ 2		↕ 3
Hungry chick	72.6 (±3.3, n=10)	6 ↔	62.6 (±8.0, n=10)	7 ↔	77.4 (±7.0, n=10)

Welch two-sample t-tests: ^{1}df=17, t=0.17, p=0.870; ^{2}df=15, t=0.80, p=0.435; ^{3}df=16, t=0.29, p=0.774. Paired t-tests: ^{4}df=9, t=0.38, p=0.710; ^{5}df=8, t=1.14, p=0.286; ^{6}df=9, t=1.60, p=0.145; ^{7}df=9, t=2.15, p=0.060.

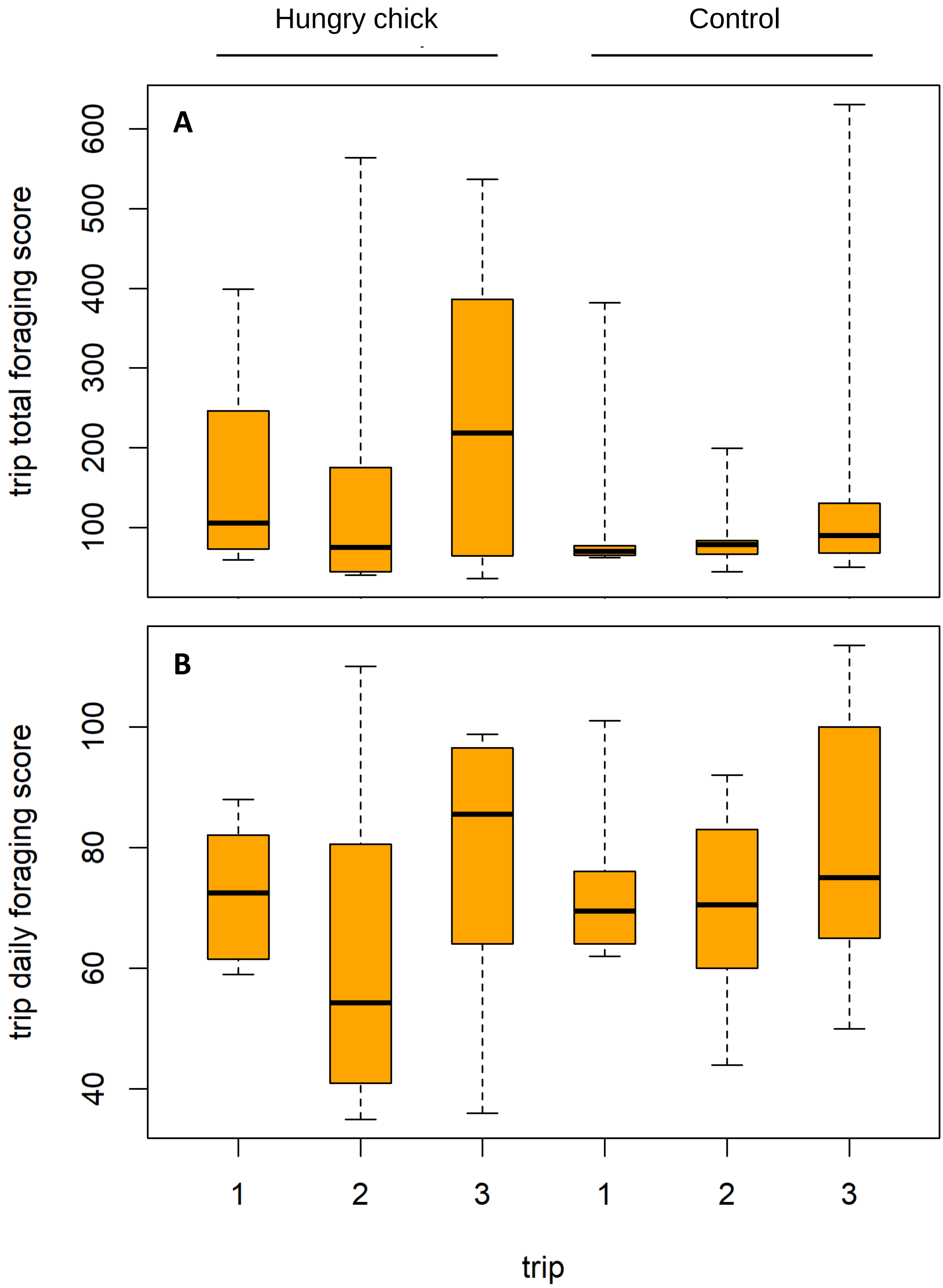


Figure 4. Box plots showing the distributions of the trip total foraging scores (A) and trip daily foraging scores (B) for hungry chick and control groups, separated into experimental trips. Thick horizontal black lines show medians, orange boxes show interquartile range, whiskers show range.

Foraging trip duration

Foraging trip duration during trips 1-3 of the experiment ranged from 1-7 days, with 66% of trips lasting 1 day (Figure 5). Foraging trip duration in the Manx Shearwater has previously been shown to be bimodally distributed (Shoji et al., 2015). Following Shoji et al. (2015), foraging trips were classified as either short trips of 1-3 days or long trips of 4 or more days (Table 4), which are functionally distinct and prioritise chick provisioning and adult self-maintenance, respectively (Shoji et al., 2015; Tyson et al., 2017). Between the hungry chick and control groups for each trip, there were no significant differences in the proportions of short and long trips (fisher's exact test; phase 1: OR=2.16, p=1; phase 2: OR=2.16, p=1; phase 3: OR=7.15, p=0.141).

In addition to comparing trip duration between hungry chick and control groups for each trip, trip duration was also compared between trips within groups to test whether the treatment had any effect on trip duration. Wilcoxon signed rank tests showed no significant change in trip duration between trips in either group (wilcoxon signed rank test; hungry chick: trip 1-2, W=19, Z=0.10, p=1; trip 2-3, W=10, Z=0.57, p=0.594; control: trip 1-2, W=1, Z=1, p=1, trip 2-3, W=0, Z=1.73, p=0.25).

Table 4. Counts of long (>3 days) and short foraging trips (≤3 days) during each experimental trip for the hungry chick group and the control group.

Trip duration (days)		**Short**	**Long**	**Total**
Trip 1	**Hungry chick**	8	2	10
	Control	9	1	10
Trip 2	**Hungry chick**	8	2	10
	Control	9	1	10
Trip 3	**Hungry chick**	5	5	10
	Control	8	1	9

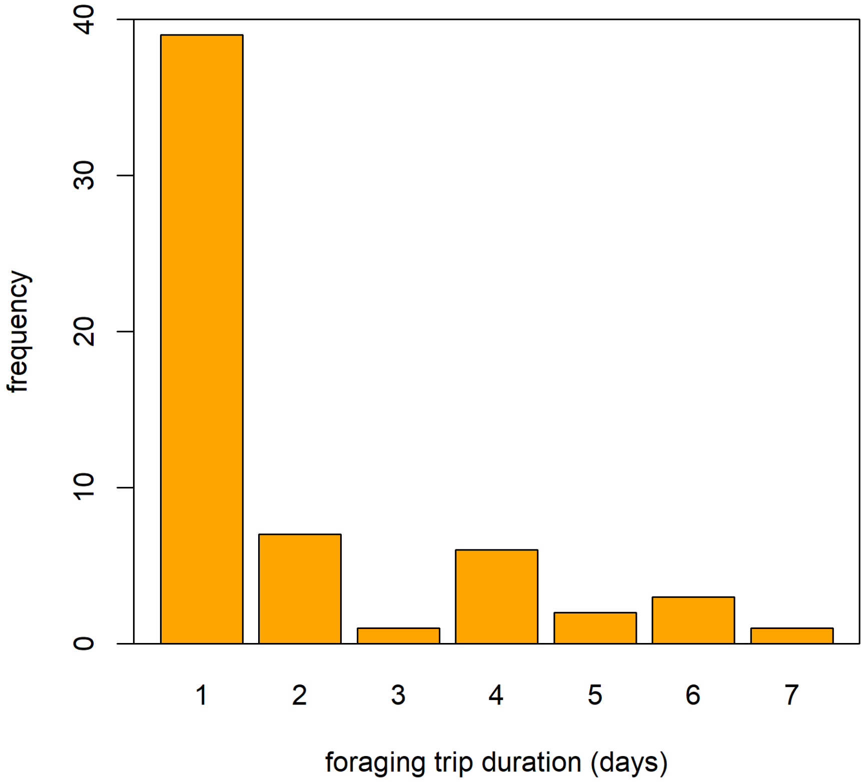


Figure 5. A bar chart showing the frequencies of different duration foraging trips during trips 1-3 of the experiment for the hungry chick and control groups pooled together.

Discussion

Direct provisioning response to hungry chicks

At least 3 and possibly up to 7 of the 10 replacement chicks were fed by tagged parents, which was significantly greater than the proportion of original chicks that were fed in the same interval during the control treatment. Replacement chicks also received larger food loads on average than control chicks during this interval, although this difference was not statistically significant. Together, these results show that the hungry chick treatment was an effective manipulation of chick demand, while they also demonstrate that parents were able to respond to the changes in chick demand within a chick-feeding visit by providing food to hungry replacement chicks after they would normally have stopped provisioning.

Since the treatment manipulated short-term chick hunger rather than chick mass or body condition, hungry replacement chicks were believed to have elicited the direct provisioning response through begging vocalisations. Manx Shearwater chicks have been shown to beg equally in response to parent and non-parent vocalisations played back over a speaker (Brooke, 1978), and indeed replacement chick begging to foster parents was observed during the experiment. Begging is known to indicate offspring hunger in many species (Mock et al., 2011). Variables of chick begging intensity have been shown to change after food deprivation of just four hours in three auk species (Klenova, 2015), while in the Manx Shearwater, begging variables are positively correlated with the number of days since the chick was last fed and represent honest signals of need in the species (Quillfeldt et al., 2004).

Given that unfed original and replacement chicks would likely have been equally hungry and begged at equal intensity when first provisioned, one might simplistically predict that they would be fed equally if begging was the sole determinant of provisioning load. However, parents provided far smaller food loads to replacement chicks after feeding their own chick. To a large extent, this is probably due to parents having little food left after the first 30 minutes of a chick-feeding visit when most provisioning occurred. Indeed, provisioning has been estimated to take only 20 minutes in Manx Shearwaters (Brooke, 1990), and the closely related Short-tailed Shearwater is known to entirely empty its stomach contents during provisioning (Brooke, 1990; Fitzherbert, 1985). However, the results here show that parents were able to feed more to replacement chicks after they would normally have ceased provisioning, from which we can infer that unlike in the Short-tailed Shearwater, adult Manx Shearwaters may retain some food after provisioning (Fitzherbert, 1985).

It is unlikely that adult food retention results from chicks becoming fully satiated, since Manx Shearwater chicks have been shown to take on larger quantities of food than observed here (Brooke, 1990; Gray & Hamer, 2001; Hamer et al., 1998). Alternatively, it is possible that the retention of modest amounts of food by adults is an example of parents strategically allocating their resources between their chick and maintenance of their own body condition, mediated by chick need signalled honestly through begging (Quillfeldt et al., 2004), as is seen in the Grey-headed Albatross *Thalassarche chrysostoma* (Phillips & Croxall, 2003).

The fact that parents provisioned replacement chicks also shows that parents were unable to specifically recognise their own chick. This contrasts with certain auks, gulls and penguins in which parent-offspring recognition has been identified (Beer, 1969; Evans, 1970; Jones et al., 1987; Lefevre et al., 1998; Seddon & van Heezik, 1993; Tschanz & Hirsbrunner-Scharf, 1975), but is in agreement with previous chick-swap studies in the Manx Shearwater and several other seabird species in which parents were apparently unable to recognise their offspring (Erikstad et al., 1997; Fayet et al., 2016; Tveraa et al., 1997). Alongside ‘twinning’ experiments

(Harris, 1966) this study provides one of the most direct examples of this inability, as parents did not discriminate against replacement chicks despite being swapped during a provisioning visit. The lack of parent-offspring recognition in the Manx Shearwaters and some other seabirds is probably a consequence of their burrow-nesting habit, since recognising their own offspring is of little fitness value for a parent if foreign chicks are rarely, if ever, encountered (Brooke, 1978, 1990). Conversely, the seabird species in which parent-offspring recognition has been demonstrated are all surface-nesters that breed in close proximity to each other, where parents must correctly locate their chick among many others (Lefevre et al., 1998).

Hungry chicks have no immediate effect on subsequent foraging effort and provisioning

By the end of the chick-feeding visit during the hungry chick treatment, replacement chicks had received far less food overall compared to control chicks. Thus, before leaving for their next foraging trip, parents in the treatment group would be exposed to a much hungrier chick that probably signalled its greater demand through begging. Despite this, there were no significant differences in trip daily foraging score, trip total foraging score and trip duration between groups and between trips within each group, nor any significant differences in provisioning between groups or before and after treatment. Hence, there was no detectable immediate effect of exposure to higher chick need on parent foraging effort or provisioning after the treatment. These findings contrast with previous studies which found that Manx Shearwater parents responded to experimentally decreased chick need by reducing their provisioning (Hamer et al., 1998; Hamer et al., 2005), while responses to chick need have also been shown under natural conditions (Quillfeldt et al., 2004).

It is noted that the lack of immediate effects on subsequent foraging effort and provisioning may be a result of the small sample sizes, which, along with high levels of residual variation, may have meant that possible effects fell below the detection threshold of the statistical tests. Particularly with respect to provisioning, conclusions were limited by small sample sizes since some parents returned to the colony undetected after trip 2 and hence their provisioning was not recorded. It is unclear how these parents evaded detection, as burrow checks were carried out every 15 minutes and RFID data showed most burrow visits last at least 30 minutes. It is possible that parents had arrived through alternative entrances as burrow systems are known to be complex (Brooke, 1990). For the purposes of this discussion the statistical findings are treated as accurate reflections a lack of parental response, however, a further repeat study expanding the number of study birds in both treatment groups would be necessary to confirm this.

Previous studies that found Manx Shearwater parents adjusted their provisioning in response to chick demand used long-term manipulations of chick need through supplemental chick feeding (Hamer et al., 1998; Hamer et al., 2005). This method simultaneously manipulated chick demand both in terms of hunger mediated by begging and other indicators of chick need such as chick body condition. In contrast, the short-term chick-swap method used here systematically manipulated only chick hunger, with no effect on subsequent provisioning. This shows that chick body condition, not hunger, was the cause of parental response in the supplemental chick feeding experiments (Hamer et al., 1998; Hamer et al., 2005). Unlike in many passerines which adjust subsequent provisioning is in response to chick begging (Hussell, 1991), chick begging in seabirds like the Manx Shearwater may be a poor indicator of chick need since chick hunger may change rapidly between provisioning visits depending on the length of foraging trips and in relation to feeds provided by the partner (Ricklefs, 1987).

Concurring with the finding in this study showing that hungry chicks were fed more, Quillfeldt et al. (2004) found that, under natural conditions, Manx Shearwater chick begging intensity was positively correlated with feed size during a provisioning visit. They did not test whether chick demand mediated by begging influenced subsequent provisioning by parents, as has effectively been done in the present study. They did, however, find that female parents whose chicks were in higher body condition (i.e. had lower demand) at the end of each provisioning subsequently carried out longer duration foraging trips (i.e. reduced parental effort; Shoji et al., 2015). When the results of the present and aforementioned studies (Hamer et al., 1998; Hamer et al., 2005; Quillfeldt et al., 2004) are taken together, a system emerges in which adults use chick begging intensity and chick body condition as functionally distinct indicators of current and future chick need, respectively. Specifically, it seems that adults may use information on current chick body condition to predict future chick demand, and adjust subsequent foraging effort accordingly (Hamer et al., 1998; Hamer et al., 2005; Quillfeldt et al., 2004), but then integrate this with new information obtained during the current visit to update provisioning decisions (Quillfeldt et al., 2004).

Conclusions and future directions

In summary, this study found that increased chick demand through exposure of parents to a hungry chick during a single provisioning visit led only to increased provisioning to the hungry chick during that visit, with no effect on subsequent foraging effort or provisioning. Alongside parental responses to chick demand found previously in the Manx Shearwater (Hamer et al., 1998; Hamer et al., 2005; Quillfeldt et al., 2004), two distinct but interacting indicators appear to be employed by parents to control their provisioning: (i) chick begging vocalisations reflecting chick hunger, to which parents only make provisioning responses within visits, and

(ii) chick body condition reflecting long-term chick need, to which parents respond by adjusting subsequent foraging effort and provisioning at the next visit. Several previous experimental studies in various species have, often inadvertently, manipulated both of these indicators of chick demand simultaneously, which has led to unclear and to seemingly inconsistent interpretations of parental responsiveness to chick demand (Bertram et al., 1996; Harding et al., 2002).

This system may provide fitness benefits to parents in several ways. For one, it may provide a safeguard against dishonest signalling of need from chicks that results from parent-offspring conflict (Riou et al., 2012), since increased provisioning during visits due to chicks exaggerating their need with increased begging would lead to eventual increase in chick body condition and resulting parent response of decreased foraging effort and provisioning. More generally, feedback loops associated with this system may have important implications for the control their parental investment in the face of changing conditions (Erikstad et al., 1998), for example, negative feedback loops may act as dampers preventing parent over-response to changing conditions. Modelling this system to explore its potential properties may be an exciting avenue of future research.

References

Ashmole, N. P. (1963). the Regulation of Numbers of Tropical Oceanic Birds. *Ibis*, *103 b*(3), 458–473. https://doi.org/10.1111/j.1474-919X.1963.tb06766.x

Beer, C. G. (1969). Laughing gull chicks: Recognition of their parents' voices. *Science*, *166*(3908), 1030–1032. https://doi.org/10.1126/science.166.3908.1030

Benaglia, T., Chauveau, D., Hunter, D. R., & Young, D. S. (2009). mixtools: An R package for analyzing mixture models. *Journal of Statistical Software*, *32*(1), 1–29. https://doi.org/10.18637/jss.v032.i06

Bertram, D. F., Welham, C. V. J., & Ydenberg, R. C. (1996). provisioning according to nestling age and mass, (August 2015).

Brooke, M. D. L. (1978). Sexual differences in the voice and individual vocal recognition in the Manx shearwater (Puffinus puffinus). *Animal Behaviour*, *26*(PART 2), 622–629. https://doi.org/10.1016/0003-3472(78)90074-X

Brooke, M. D. L. (1990). *The Manx Shearwater*. London: T & A D Poyser.

Catry, P., Dias, M. P., Phillips, R. A., & Granadeiro, J. P. (2013). Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: An experimental demonstration. *Ecology*, *94*(6), 1230–1235. https://doi.org/10.1890/12-2177.1

Chastel, O., Weimerskirch, H., & Jouventin, P. (1995). Influence of Body Condition on Reproductive Decision and Reproductive Success in the Blue Petrel Author (s): Olivier Chastel , Henri Weimerskirch and Pierre Jouventin Source : The Auk , Vol . 112 , No . 4 (Oct ., 1995), pp . 964-972 Published by : Ame, *112*(4), 964–972.

Clutton-Brock, T. H. (1991). *The Evolution of Parental Care*. Princeton: Princeton University Press.

Cook, M. I., & Hamer, K. C. (1997). Effects of Supplementary Feeding on Provisioning and Growth Rates of Nestling Puffins Fratercula arctica : Evidence for Regulation of Growth. *Oikos*, *28*(1), 56–62.

Dias, M. P., Granadeiro, J. P., & Catry, P. (2012). Do Seabirds Differ from Other Migrants in Their Travel Arrangements? On Route Strategies of Cory's Shearwater during Its Trans-Equatorial Journey. *PLoS ONE*, *7*(11). https://doi.org/10.1371/journal.pone.0049376

Erikstad, K. E., Asheim, M., Fauchald, P., Dahlhaug, L., & Tveraa, T. (1997). Adjustment of parental effort in the puffin; the roles of adult body condition and chick size. *Behavioral Ecology and Sociobiology*, *40*(2), 95–100. https://doi.org/10.1007/s002650050320

Erikstad, K. E., Fauchald, P., Tveraa, T., & Steen, H. (1998). On the Cost of Reproduction in Long-Lived Birds : The Influence of Environmental Variability. *Ecology*, *79*(5), 1781–1788.

Evans, R. M. (1970). Parental Recognition and the "Mew Call" in Black-Billed Gulls (Larus bulleri). *American Ornithological Society*, *87*(3), 503–513.

Fayet, A. L., Freeman, R., Shoji, A., Kirk, H. L., Padget, O., Perrins, C. M., … Verhulst, S. (2016). Carry-over effects on the annual cycle of a migratory seabird: an experimental study. *Journal of Animal Ecology*, *85*(6), 1516–1527. https://doi.org/10.1111/1365-2656.12580

Fitzherbert, K. (1985). *The role of energetic factors in the evolution of the breeding biology of the short-tailed shearwater (Puffinus tenuirostris, Temminck)*. Monash University, Australia.

Gjerdrum, C. (2004). Parental provisioning and nestling departure decisions: a supplementary feeding experiment in Tufted Puffins (Fratercula cirrhata) on Triangle Island, British Columbia. *The Auk*. https://doi.org/10.1642/0004-8038(2004)121

Gray, C. M., Brooke, M. D. L., & Hamer, K. C. (2014). Repeatability of Chick Growth and Food Provisioning in Manx Shearwaters Puffinus puffinus of chick growth in Manx and food provisioning Repeatability shearwaters Puffinus puffinus, *36*(5), 374–379.

Gray, C. M., & Hamer, K. C. (2001). Food-provisioning behaviour of male and female Manx shearwaters, Puffinus puffinus. *Animal Behaviour*, *62*(1), 117–121. https://doi.org/10.1006/anbe.2001.1717

Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., … Perrins, C. M. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater Puffinus puffinus: insights from machine learning. *Proceedings of the Royal Society B*, *276*(1660), 1215–23. https://doi.org/10.1098/rspb.2008.1577

Hamer, K. C., & Hill, J. K. (1994). The Regulation of Food Delivery to Nestling Cory ’s Shearwaters Calonectris diomedea : The Roles of Parents and Offspring. *Oikos*, *25*(3), 198–204.

Hamer, K. C., Lynnes, A. S., & Hill, J. K. (1998). Regulation of chick provisioning rate in Manx Shearwaters: Experimental evidence and implications for nestling obesity. *Functional Ecology*, *12*(4), 625–630. https://doi.org/10.1046/j.1365-2435.1998.00223.x

Hamer, K. C., Quillfeldt, P., Masello, J. F., & Fletcher, K. L. (2005). Sex differences in provisioning rules: Responses of Manx shearwaters to supplementary chick feeding.

Behavioral Ecology, *17*(1), 132–137. https://doi.org/10.1093/beheco/arj008

Hansell, M. (2000). *Bird nests and construction behaviour*. Cambridge: Cambridge University Press.

Harding, A. M. A., Kitaysky, A. S., Hall, M. E., Welcker, J., Karnovsky, N. J., Talbot, S. L., … Grémillet, D. (2009). Flexibility in the parental effort of an Arctic-breeding seabird, 348–358. https://doi.org/10.1111/j.1365-2435.2008.01488.x

Harding, A. M. A., van Pelt, T. I., Piatt, J. F., & Kitaysky, A. S. (2002). Reduction of provisioning effort in response to experimental manipulation of chick nutritional status in the Horned Puffin. *The Condor*, *104*(September 2001), 842–847.

Harris, M. P. (1966). Breeding Biology of the Manx Shearwater Puffinus puffinus. *Ibis*, *108*(1), 17–33. https://doi.org/10.1111/j.1474-919X.1966.tb07249.x

Hussell, D. J. . (1991). Regulation of food provisioning in broods of altricial birds. *Acta. Int. Ornithol. Congr.*, *20*, 946–960.

Johnsen, I., Erikstad, K. E., & Stether, B. (1994). Regulation of Parental Investment in a Long-Lived Seabird , the Puffin Fratercula arctica : An Experiment. *Oikos*, *71*(2), 273–278.

Jones, I. L., Falls, B. J., & Gaston, A. J. (1987). Vocal recognition between parents and young of Ancient Murrelets, Synthliboramphus antiquus (Aves: Alcidae). *Animal Behaviour*, *35*(5), 1405–1415. https://doi.org/10.1016/S0003-3472(87)80013-1

Klenova, A. V. (2015). Chick begging calls reflect degree of hunger in three auk species (Charadriiformes: Alcidae). *PLoS ONE*, *10*(11), 4–6. https://doi.org/10.1371/journal.pone.0140151

Lefevre, K., Montgomerie, R., & Gaston, A. J. (1998). Parent-offspring recognition in thick-billed murres (Aves: Alcidae). *Animal Behaviour*, *55*(4), 925–938. https://doi.org/10.1006/anbe.1997.0626

Maness, T. J., & Anderson, D. J. (2013). Predictors of Juvenile Survival in Birds. *Ornithological Monographs*, *78*(1), 1–55. https://doi.org/10.1525/om.2013.78.1.1.1

Mauck, R. A., & Grubb, T. C. (1995). Petrel parents shunt all experimentally increased reproductive costs to their offspring. *Animal Behaviour*, *49*(4), 999–1008. https://doi.org/10.1006/anbe.1995.0129

McFarland, D. J. (1977). Decision making in animals. *Nature*, *269*(5623), 15–21. https://doi.org/10.1038/269015a0

Mock, D. W., Dugas, M. B., & Strickler, S. A. (2011). Honest begging: Expanding from Signal of Need. *Behavioral Ecology*, *22*(5), 909–917. https://doi.org/10.1093/beheco/arr091

Morrison, K. W., Hipfner, J. M., Gjerdrum, C., & Green, D. J. (2009). Wing Length and Mass at Fledging Predict Local Juvenile Survival and Age at First Return in Tufted Puffins. *The Condor*, *111*(3), 433–441. https://doi.org/10.1525/cond.2009.080099

Navarro, J., & González-Solís, J. (2007). Experimental increase of flying costs in a pelagic seabird: Effects on foraging strategies, nutritional state and chick condition. *Oecologia*, *151*(1), 150–160. https://doi.org/10.1007/s00442-006-0559-0

Nick J. Royle, Per T. Smiseth, M. K. (2012). *The Evolution of Parental Care*. Oxford: Oxford University Press.

Orians, G. H., & Pearson, N. E. (1979). On the theory of central place foraging. In D. H. Horn, R. D. Mitchell, & G. R. Stairs, (Eds.), *Analyses of ecological systems* (pp. 155–177).

Owens, I. P. F., & Bennett, P. M. (1994). Mortality costs of parental care and sexual dimorphism in birds. *Proceedings of the Royal Society B: Biological Sciences*, *257*(1348), 1–8. https://doi.org/10.1098/rspb.1994.0086

Perrins, C. M. (2014). Factors affecting survival of fledgling Manx Shearwaters Puffinus puffinus, *27*, 62–71.

Perrins, C. M., Harris, M. P., & Britton, C. K. (1973). Survival of Manx Shearwaters Puffinus puffinus. *Ibis*, *115*(5), 535–548.

Perrins, C. M., Wood, M. J., Garroway, C. J., Boyle, D., Oakes, N., Revera, R., … Taylor, C. (2012). A whole-island census of the Manx Shearwaters Puffinus puffinus breeding on Skomer Island in 2011. *Seabird*, *25*(Brooke 1978), 1–13. Retrieved from http://eprints.glos.ac.uk/565/1/A whole-island census of the Manx Shearwaters.pdf

Phillips, R. A., & Croxall, J. P. (2003). Control of provisioning in grey-headed albatrosses (Thalassarche chrysostoma): do adults respond to chick condition? *Canadian Journal of Zoology*, *81*(1), 111–116. https://doi.org/10.1139/z02-234

Phillips, R. A., Xavier, J. C., & Croxall, J. P. (2003). Effects of Satellite Transmitters on Albatrosses and Petrels, *120*(4), 1082–1090.

Quillfeldt, P., Masello, J. F., & Hamer, K. C. (2004). Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, Puffinus puffinus. *Animal Behaviour*, *68*(3), 613–620. https://doi.org/10.1016/j.anbehav.2003.12.002

Rector, M. E., Walsh, C. J., Kouwenberg, A. L., Fitzsimmons, M. G., & Storey, A. E. (2014). Signals of need and quality: Atlantic puffin chicks can beg and boast. *Behavioral Ecology*, *25*(3), 496–503. https://doi.org/10.1093/beheco/aru009

Ricklefs, R. E. (1984). Meal Sizes and Feeding Rates of Christmas Shearwaters and Phoenix Petrels on Christmas Island , Central Pacific Ocean. *Ornis Scandinavica*, *15*(1), 16–22.

Ricklefs, R. E. (1987). Response of adult Leach's Storm-Petrels to increased food demand at the nest. *The Auk*, (October), 750–756.

Ricklefs, R. E. (1990). Seabird Life Histories and the Marine Environment: Some Speculations. *Colonial Waterbirds*, *13*(1), 1–6.

Ricklefs, R. E., Day, C. H., Huntington, C. E., & Williams, J. B. (1985). Variability in Feeding Rate and Meal Size of Leach's Storm-Petrel at Kent Island, New Brunswick. *Journal of Animal Ecology*, *54*(3), 883–898.

Riou, S., Chastel, O., & Hamer, K. C. (2012). Parent-offspring conflict during the transition to independence in a pelagic seabird. *Behavioral Ecology*, *23*(5), 1102–1107. https://doi.org/10.1093/beheco/ars079

Roff, D. A. (2002). *Life History Evolution*. Sunderland: Sinauer Associates.

Royle, N. J., Smiseth, P. T., Kolliker, M. (2012). *The Evolution of Parental Care*. Oxford: Oxford University Press.

Sagar, P. M., & Horning, D. S. (1998). Mass-related survival of fledgling Sooty shearwaters Puffinus griseus at The Snares, New Zealand. *Ibis*, *140*(2), 329–331. https://doi.org/10.1111/j.1474-919X.1998.tb04397.x

Schreiber, E. A., & Burger, J. (Eds.). (2001). *Biology of Marine Birds*. Boca Raton: Taylor & Francis.

Seddon, P. J., & van Heezik, Y. (1993). Parent-Offspring Recognition in the Jackass Penguin.

Journal of Field Ornithology, *64*(1), 27–31.

Shoji, A., Aris-Brosou, S., Fayet, A., Padget, O., Perrins, C., & Guilford, T. (2015). Dual foraging and pair coordination during chick provisioning by Manx shearwaters: empirical evidence supported by a simple model. *Journal of Experimental Biology*, *218*, 2116–2123. https://doi.org/10.1242/jeb.120626

Shoji, A., Dean, B., Kirk, H., Freeman, R., Perrins, C. M., Guilford, T., & Phillips, R. (2016). The diving behaviour of the Manx Shearwater Puffinus puffinus. *Ibis*, *158*(3), 598–606. https://doi.org/10.1111/ibi.12381

Takahashi, A., Kuroki, M., Niizuma, Y., & Watanuki, Y. (1999). Parental Food Provisioning Is Unrelated to Manipulated Offspring Food Demand in a Nocturnal Single-Provisioning Alcid , the Rhinoceros Auklet. *Oikos*, *30*(4), 486–490.

Trivers, R. L. (1972). *Parental investment and sexual selection. Sexual selection and the descent of man.* New York: Aldine de Gruyter.

Trivers, R. L. (1974). Parent-Offspring Conflict. *American Zoologist*, *14*(1), 249–264. https://doi.org/10.1093/icb/14.1.249

Tschanz, B., & Hirsbrunner-Scharf, M. (1975). Adaptations to colony life on cliff ledges: a comparative study of guillemot and razorbill chicks. In *Function and Evolution in Behaviour: Essays in Honour of Professor Niko Tinbergen, F.R.R.* (pp. 358–380). Oxford: Oxford University Press.

Tveraa, T., Lorentsen, S. H., & Sæther, B. E. (1997). Regulation of foraging trips and costs of incubation shifts in the Antarctic petrel (Thalassoica antarctica). *Behavioral Ecology*, *8*(5), 465–469. https://doi.org/10.1093/beheco/8.5.465

Tveraa, T., Sæther, B. E., Aanes, R., & Erikstad, K. E. (1998). Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. *Journal of Animal Ecology*, *67*(5), 699–704. https://doi.org/10.1046/j.1365-2656.1998.00234.x

Tyson, C., Kirk, H., Fayet, A., Van Loon, E. E., Shoji, A., Dean, B., … Guilford, T. (2017). Coordinated provisioning in a dual-foraging pelagic seabird. *Animal Behaviour*, *132*, 73–79. https://doi.org/10.1016/j.anbehav.2017.07.022

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part II: Topical Studies in Oceanography*, *54*(3–4), 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Weimerskirch, H., Zimmermann, L., & Prince, P. A. (2001). Influence of environmental variabilityon breeding effort in long-lived seabirds, the yellow-nosed albatross. *Behavioral Ecology*, *12*(1), 22–30.

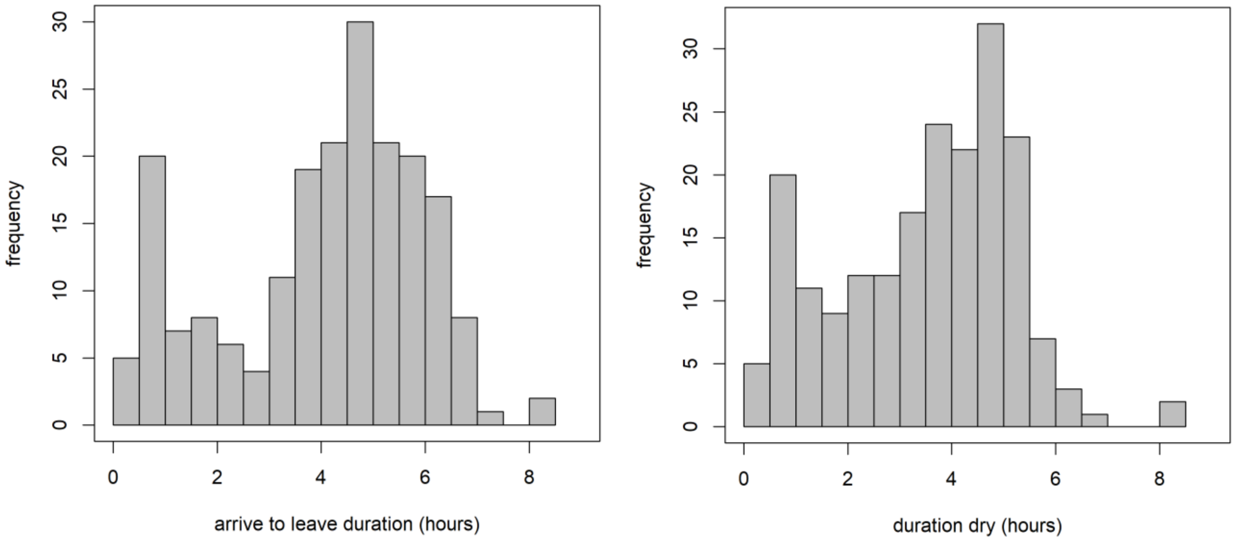
Weston, M. A., & Elgar, M. A. (2005). Parental care in Hooded Plovers (Thinornis rubricollis). *Emu*, *105*(4), 283–292. https://doi.org/10.1071/MU04004

Wetterer, J. K. (1989). Central Place Foraging Theory: When Load Size Affects Travel Time. *Theoretical Population Biology*, *36*, 267–280.

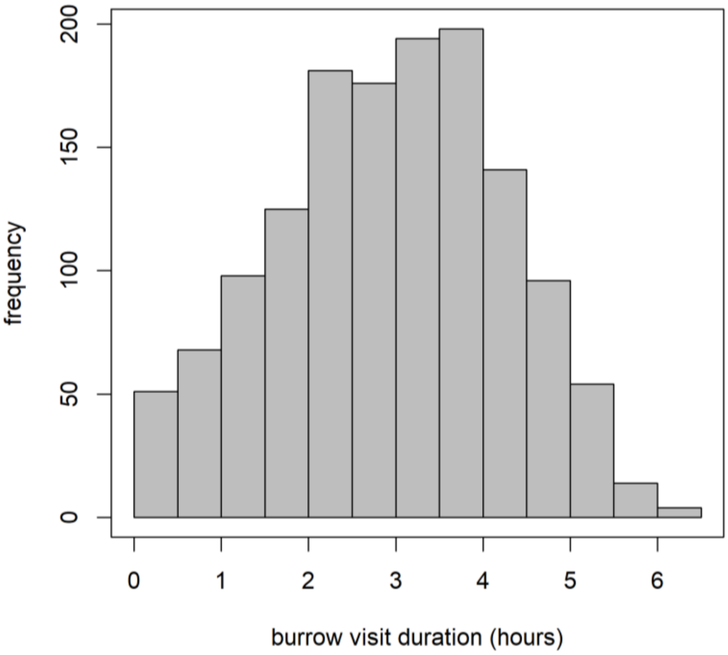
Williams, G. C. (1966). The Costs of Reproduction , and a Refinement of Lack's Principle. *The American Naturalist*, *100*(916), 687–690.

Wojczulanis-Jakubas, K., Araya-Salas, M., & Jakubas, D. (2018). Seabird parents provision their chick in a coordinated manner. *PLoS ONE*, *13*(1), 1–13. https://doi.org/10.1371/journal.pone.0189969

Supplementary Material



Supplementary figure 1. Histograms showing the frequency of visits to land estimated from GLS data. The histogram to the left shows duration of time from the first 30-minute period of dry to the last 30-minute period of dry in a night, while the histogram to the right shows the duration of each dry period of 30 minutes or more during the night. Night was determined from light data and shortened by 40 minutes after dusk and by 30 minutes before dawn.



Supplementary figure 2. A histogram showing the frequency of different durations of visits to the burrow measured by RFID sensors, with durations measured from the first entrance to last exit of the burrow each night.

Chapter 4

General discussion

Introduction

This thesis identifies previously unknown behaviours and helps to better understand others in relation to how a long-lived pelagic seabird deals with the demands of breeding. In the first chapter, I introduced two ways in which animals are constrained in their reproductive output during a breeding attempt. Firstly, an animal will be constrained by the physical and ecological conditions and the finite resources within the accessible radius of its breeding site, to which different species may be tied to different extents. Secondly, an animal will be constrained in its current reproductive effort by the costs to future reproductive success that result from life-history trade-offs. I investigated behavioural adaptations to these constraints in a long-lived pelagic seabird, the Manx Shearwater, a species in which both types of constraint play a major role in shaping life-history traits. In this final chapter, I summarise my main findings before ending with a brief discussion of how my results, and seabird research generally, are important to the conservation seabirds and the marine environment.

Summary of main results

Sex- and colony-specific strategies during pre-laying exodus

Making inferences on movement and behaviours from light and salt-water immersion data collected on geolocators over a 10-year period, I examined the pre-laying exodus of Manx Shearwaters from two breeding colonies 300 km apart in the Irish and Celtic Seas. In line with previous studies carried out on Skomer Island, Manx Shearwaters from Skomer showed highly distinct sex-specific strategies, in which males generally remained close to the colony which they visited regularly, while females made distant, long-duration trips to the south-west of Ireland, concentrated in areas around the continental shelf edge (Dean, 2012; Guilford et al., 2009). The daily allocations of time to different at-sea activities were described for the first time across the duration of exodus, which revealed novel changes in behaviour as the egg lay date approached, with females showing much greater shifts in behaviour than males over the course of exodus. Different daily allocations of time to different at-sea behaviours were also associated with different locations in females, but not in males.

The pre-laying exodus of Manx Shearwaters had never previously been investigated beyond birds breeding on Skomer, thus it was unclear to what extent exodus would differ for birds breeding on the Copeland Islands, which lie substantially further away from the continental shelf edge. Comparisons between Skomer and Copeland exodus locations showed many similarities between female space use, whilst males occupied distinct areas near to their respective breeding colonies. In a similar vein, females showed almost identical patterns of daily allocation of time to different behaviours over the course of exodus. While males showed some between-colony differences in their daily allocation of time to different behaviours, these were much smaller than differences between males and females. Finally, comparisons of metrics describing night-time visits to land between Skomer and Copeland males highlighted further differences among males, notably: (i) Skomer males decreased the duration of their visits over exodus beyond the level predicted by shortening nights, while Copeland males only decreased theirs in proportion to shortening nights, (ii) Skomer males increased their visit frequency over the course of exodus from infrequent to very frequent while Copeland males maintained a moderate visit frequency throughout, and (iii) Copeland males remained at the colony over-day significantly more than Skomer males.

Overall, this study demonstrated how Manx Shearwaters have adapted their behaviour in response to the demands of breeding, highlighted by the contrasts between the behavioural strategies of males and females - both need to improve their body reserves to sustain them through later stages of breeding (Chastel et al., 1995), but are separately constrained by the need to supply and carry the developing egg, and the need to defend the breeding burrow, respectively (Arizmendi-Mejía et al., 2013; Dean, 2012; Perrins, 1996). This study also shows that the effects of different breeding locations on pre-laying exodus strategies are complex, with behavioural similarities and differences between the two colonies probably emerging because of their different proximities to food resources. Males appear to remain near to their respective colonies because the benefits of defending their burrows (and potentially gaining extra-pair copulations) outweigh the benefits of travelling to richer feeding grounds such as the continental shelf edge. Evidence that males gain mass during the pre-laying exodus (Brooke, 1990) also suggests that local feeding grounds are sufficient for males to improve their body condition (Arizmendi-Mejía et al., 2013). In contrast, females lose mass during exodus (Brooke, 1990), which suggests that even the richer foraging grounds along the continental shelf edge may be insufficient to improve body condition during egg building.

Further work to investigate the variation in behaviour between a greater diversity of different colonies is suggested, which would allow higher resolution contrasts to be made to help clarify the differing effects of location, resource availability and colony demographics on the costs of breeding, and the behavioural strategies that Manx Shearwaters use to deal with them.

Short-term parental response to offspring demand

This experimental study used behavioural inference from geolocator data alongside measurements of chick food loads to test whether Manx Shearwater parents immediately adjust their foraging effort or provisioning in response to an increase in chick demand, manipulated by exposing each study parent to a hungry chick after they had fed their own chick. Results showed that parents respond to chick hunger, mediated by chick begging vocalisations (Quillfeldt et al., 2004), by adjusting the proportion of their current stomach content allocated to the chick, but make no adjustments of subsequent foraging effort or provisioning in response to the chicks current hunger. Previous studies had shown chick demand predicted subsequent provisioning and foraging effort (Hamer et al., 1998; Hamer et al., 2005) but were unable to distinguish whether this was a response to chick hunger or longer-term body condition (Bertram et al., 1996). By showing that hunger does not predict subsequent foraging effort or provisioning, the hungry chick experiment shows that longer-term body condition alone influences future behaviour.

Emerging from this study is a potential system that may function to optimally regulate Manx Shearwater forging and provisioning effort by using two distinct but interacting signals of chick demand. Firstly, chick begging vocalisations reflecting chick hunger, to which parents only make provisioning responses within visits, and secondly, chick body condition reflecting long-term chick need, to which parents respond by adjusting subsequent foraging effort and provisioning at the next visit. Since chick hunger and body condition are not independent, this provisioning regulation system is likely to have feedback properties, of which one function may be to safeguard parents from the dishonest signalling of need by chicks that might result from parent-offspring conflict (Riou et al., 2012). More generally, the potential feedback loops and emergent properties of this system may have important implications for the control of parental investment in the face of changing conditions (Erikstad et al., 1998), for instance, negative feedback may prevent a parent from over-responding to rapidly changing environmental conditions. Modelling this system to explore its potential properties is suggested as potentially rewarding area of future research.

Implications for conservation

As apex predators in marine food webs, seabirds can be vulnerable to perturbations at lower trophic levels and environmental change, and as such they may act as effective indicators of marine ecosystem health (Einoder, 2009; Gremillet & Charmantier, 2010; Lyday et al., 2015; Parsons et al., 2008; Walsh, 2017). Many seabirds are also threatened with extinction, and as a group they are among the world's most threatened birds (Croxall et al., 2012; Phillips et al., 2016). The anthropogenic threats faced by seabirds at-sea are diverse, and they include depleted fish stocks (Cury et al., 2011), plastic pollution (Wilcox et al., 2015), climate change (Grémillet & Boulinier, 2009; Sydeman et al., 2012) and light pollution (Davies et al., 2014; Syposz et al., 2018), among many others (Anderson et al., 2011; Masden et al., 2010). Threats on land can be severe, particularly invasive species such as mice, rats and cats, which have decimated some seabird colonies (Russell & Holmes, 2015; Spatz et al., 2017). Although the problem of invasive species persists at numerous seabird islands, progress is being made in eradication (Jones & Kress, 2012). Minimising threats to seabirds at-sea, however, faces many more challenges, in part because the at-sea movements of seabirds are not always well-known and can span entire oceans, and in part because applying and enforcing conservation policy can be logistically and politically difficult in both international waters as well as within many national jurisdictions (Aswani et al., 2018; Lewison et al., 2012; Yorio, 2009).

Given the high conservation priority status of seabirds, the numerous threats they face and the difficulties overcoming these threats with limited resources for marine conservation, it is essential that seabird conservation is targeted effectively (Gill et al., 2017). Seabird research plays an important role in ensuring that this can happen, helping to prioritise threats and identify particular areas or times at which conservation measures need to be applied (Croxall et al., 2012). As a case study, research into the at-sea movements and behaviour in the Manx Shearwater has already helped inform UK conservation policy, with the assignment of the Irish Sea Front as a marine Spatial Protection Area as a result of at-sea surveys and tracking studies showing the area as an important foraging area for large number of Manx Shearwaters from multiple breeding colonies (Dean et al., 2012; Kober et al., 2012). Although the research presented in this thesis was not motivated by conservation, it may bear some influence in future conservation decisions. In particular, the findings in my second chapter corroborate previous studies showing that continental shelf edge and Porcupine Bight (areas with no special protection measures) to the southwest of Ireland are hotspots of activity for female Manx Shearwaters on their pre-laying exodus, a critical period influencing later reproductive success (Chastel et al., 1995; Dean, 2012; Guilford et al., 2009). Additionally, the results here show that this area has been utilised by at least two major breeding colonies over a 10-year period, further advocating the potential special importance of this area for globally important numbers of Manx Shearwater. Further tracking of pre-laying exodus from other major colonies is advised, using both low-impact geolocators to test for broad patterns of shared space use, and later using high-resolution GPS tracking to pinpoint more precisely the areas of importance. This broader understanding will help to refine our knowledge of Manx Shearwater resource requirements during exodus and the risks associated with deterioration of their foraging areas, which can then be used to inform whether and how conservation measures should be applied.

Final remarks

The findings in this thesis have added to our knowledge about the at-sea behaviour of the Manx Shearwater. It is thanks to this already extensive knowledge that more refined and effective scientific study is possible, and with each new finding comes many more questions. I hope that some of the ambiguities and new questions raised from the findings in this thesis will aid others in formulating their research, to both broaden our scientific understanding and further enrich our appreciation for the myriad species with which we share the planet.

References

Anderson, O. R. J., Small, C. J., Croxall, J. P., Dunn, E. K., Sullivan, B. J., Yates, O., & Black, A. (2011). Global seabird bycatch in longline fisheries. *Endangered Species Research*, *14*(2), 91–106. https://doi.org/10.3354/esr00347

Arizmendi-Mejía, R., Militão, T., Viscor, G., & González-Solís, J. (2013). Pre-breeding ecophysiology of a long-distance migratory seabird. *Journal of Experimental Marine Biology and Ecology*, *443*, 162–168. https://doi.org/10.1016/j.jembe.2013.02.047

Aswani, S., Basurto, X., Ferse, S., Glaser, M., Campbell, L., Cinner, J. E., … Christie, P. (2018). Marine resource management and conservation in the Anthropocene. *Environmental Conservation*, *45*(2), 192–202. https://doi.org/10.1017/S0376892917000431

Bertram, D. F., Welham, C. V. J., & Ydenberg, R. C. (1996). provisioning according to nestling age and mass, *1881*, 1876–1881.

Brooke, M. D. L. (1990). *The Manx Shearwater*. London: T & A D Poyser.

Chastel, O., Weimerskirch, H., & Jouventin, P. (1995). Influence of Body Condition on Reproductive Decision and Reproductive Success in the Blue Petrel. *Auk*, *112*(4), 964–972.

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, *22*(01), 1–34. https://doi.org/10.1017/S0959270912000020

Cury, P. M., Boyd, I. L., Bonhommeau, S., & Anker-nilssen, T. (2011). Global Seabird

Response to Forage Fish Depletion—One-Third for the Birds. *Science*, *334*(6063), 1703–1707.

Davies, T. W., Duffy, J. P., Bennie, J., & Gaston, K. J. (2014). The nature, extent, and ecological implications of marine light pollution. *Frontiers in Ecology and the Environment*, *12*(6), 347–355. https://doi.org/10.1890/130281

Dean, B. (2012). The at-sea behaviour of the Manx shearwater. *PhD Thesis*.

Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R. A., Perrins, C. M., & Guilford, T. (2012). Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of the Royal Society, Interface / the Royal Society*, rsif.2012.0570-. https://doi.org/10.1098/rsif.2012.0570

Einoder, L. D. (2009). A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research*, *95*(1), 6–13. https://doi.org/10.1016/j.fishres.2008.09.024

Erikstad, K. E., Fauchald, P., Tveraa, T., & Steen, H. (1998). On the Cost of Reproduction in Long-Lived Birds : The Influence of Environmental Variability. *Ecology*, *79*(5), 1781–1788.

Gill, D. A., Mascia, M. B., Ahmadia, G. N., Glew, L., Lester, S. E., Barnes, M., … Fox, H. E. (2017). Capacity shortfalls hinder the performance of marine protected areas globally. *Nature*, *543*(7647), 665–669. https://doi.org/10.1038/nature21708

Grémillet, D., & Boulinier, T. (2009). Spatial ecology and conservation of seabirds facing global climate change: A review. *Marine Ecology Progress Series*, *391*(2), 121–137.

https://doi.org/10.3354/meps08212

Gremillet, D., & Charmantier, A. (2010). Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of ocean health. *Ecological Applications*, *20*(6), 1498–1503.

Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., … Perrins, C. M. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater Puffinus puffinus: insights from machine learning. *Proceedings of the Royal Society B*, *276*(1660), 1215–23. https://doi.org/10.1098/rspb.2008.1577

Hamer, K. C., Lynnes, A. S., & Hill, J. K. (1998). Regulation of chick provisioning rate in Manx Shearwaters: Experimental evidence and implications for nestling obesity. *Functional Ecology*, *12*(4), 625–630. https://doi.org/10.1046/j.1365-2435.1998.00223.x

Hamer, K. C., Quillfeldt, P., Masello, J. F., & Fletcher, K. L. (2005). Sex differences in provisioning rules: Responses of Manx shearwaters to supplementary chick feeding. *Behavioral Ecology*, *17*(1), 132–137. https://doi.org/10.1093/beheco/arj008

Jones, H. P., & Kress, S. W. (2012). A review of the world’s active seabird restoration projects. *Journal of Wildlife Management*, *76*(1), 2–9. https://doi.org/10.1002/jwmg.240

Kober Wilson, L.J., Black, J., O’Brien, S., Allen, S., Win, I., K., & Bingham J.B., C. & R. (2012). *The identification of possible marine SPAs for seabirds in the UK: The application of Stage 1.1 – 1.4 of the SPA selection guidelines*. *JNCC Report No. 461*. https://doi.org/ISSN 0963 8901

Lewison, R., Oro, D., Godley, B. J., Underhill, L., Bearhop, S., Wilson, R. P., … Yorio, P. (2012).

Research priorities for seabirds: Improving conservation and management in the 21st century. *Endangered Species Research*, *17*(2), 93–121. https://doi.org/10.3354/esr00419

Lyday, S. E., Ballance, L. T., Field, D. B., & David Hyrenbach, K. (2015). Shearwaters as ecosystem indicators: Towards fishery-independent metrics of fish abundance in the California Current. *Journal of Marine Systems*, *146*, 109–120. https://doi.org/10.1016/j.jmarsys.2014.08.010

Masden, E. A., Haydon, D. T., Fox, A. D., & Furness, R. W. (2010). Barriers to movement: Modelling energetic costs of avoiding marine wind farms amongst breeding seabirds. *Marine Pollution Bulletin*, *60*(7), 1085–1091. https://doi.org/10.1016/j.marpolbul.2010.01.016

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S., & Reid, J. B. (2008). Seabirds as indicators of the marine environment. *ICES Journal of Marine Science*, *65*(8), 1520–1526. https://doi.org/10.1093/icesjms/fsn155

Perrins, C. M. (1996). Eggs, egg formation and the timing of breeding. *Ibis*, *138*, 2–15. https://doi.org/10.1111/j.1474-919X.1996.tb04308.x

Phillips, R. A., Gales, R., Baker, G. B., Double, M. C., Favero, M., Quintana, F., Wolfaardt, A. (2016). The conservation status and priorities for albatrosses and large petrels. *Biological Conservation*, *201*, 169–183. https://doi.org/10.1016/j.biocon.2016.06.017

Quillfeldt, P., Masello, J. F., & Hamer, K. C. (2004). Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, Puffinus puffinus. *Animal Behaviour*, *68*(3), 613–620. https://doi.org/10.1016/j.anbehav.2003.12.002

Riou, S., Chastel, O., & Hamer, K. C. (2012). Parent-offspring conflict during the transition to independence in a pelagic seabird. *Behavioral Ecology*, *23*(5), 1102–1107. https://doi.org/10.1093/beheco/ars079

Russell, J. C., & Holmes, N. D. (2015). Tropical island conservation: Rat eradication for species recovery. *Biological Conservation*, *185*, 1–7. https://doi.org/10.1016/j.biocon.2015.01.009

Spatz, D. R., Holmes, N. D., Reguero, B. G., Butchart, S. H. M., Tershy, B. R., & Croll, D. A. (2017). Managing Invasive Mammals to Conserve Globally Threatened Seabirds in a Changing Climate. *Conservation Letters*, *10*(6), 736–747. https://doi.org/10.1111/conl.12373

Sydeman, W. J., Thompson, S. A., & Kitaysky, A. (2012). Seabirds and climate change: Roadmap for the future. *Marine Ecology Progress Series*, *454*, 107–117. https://doi.org/10.3354/meps09806

Syposz, M., Gonçalves, F., Carty, M., Hoppitt, W., & Manco, F. (2018). Factors influencing Manx Shearwater grounding on the west coast of Scotland. *Ibis*, 846–854. https://doi.org/10.1111/ibi.12594

Walsh, P. M. (2017). The Use of Seabirds as Monitors of Heavy Metals in the Marine Environment. In *Heavy Metals in the Marine Environment*. CRC Press.

Wilcox, C., Van Sebille, E., & Hardesty, B. D. (2015). Threat of plastic pollution to seabirds is global, pervasive, and increasing. *Proceedings of the National Academy of Sciences*, *112*(38), 11899–11904. https://doi.org/10.1073/pnas.1502108112

Yorio, P. (2009). Marine protected areas, spatial scales, and governance: implications for the conservation of breeding seabirds. *Conservation Letters*, *2*(4), 171–178. https://doi.org/10.1111/j.1755-263X.2009.00062.x