The foraging ecology of European shags (*Phalacrocorax aristotelis*): flexibility, consistency and constraint.

Elizabeth Alyson Morgan

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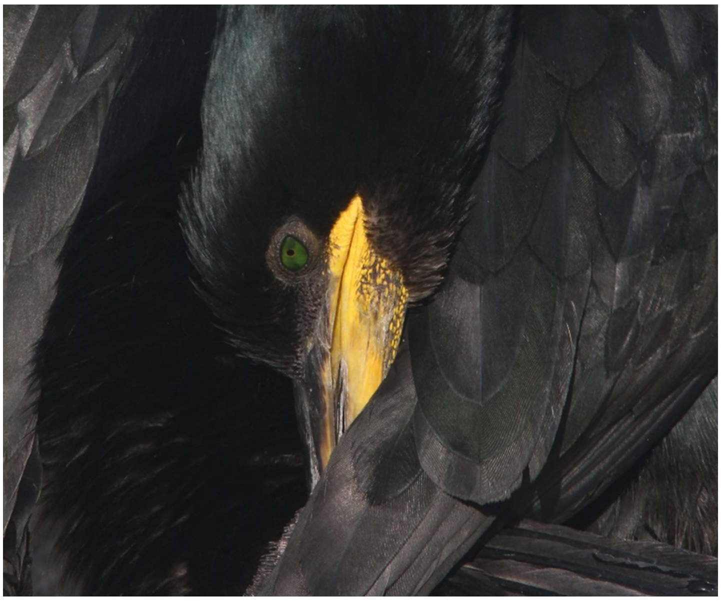

"The green cormorant or shag, Lays its eggs inside a paper bag.

The reason you will see no doubt, It is to keep the lightning out.

But what these unobservant birds, Have never noticed is that herds

Of wandering bears may come with buns, And steal the bags to hold the crumbs."

- Adapted from poem by Christopher Isherwood (1904-1986)

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Abstract

Consistency and flexibility in foraging behaviour play vital roles in organisms' responses to variable and changing environments. There is a need to understand the causes and consequences of this variation, and to establish how different intrinsic and extrinsic factors alter behaviour at individual, population and species levels. Here I examine individual and population-level variation in the three-dimensional foraging behaviour of a short-ranging benthic-feeding marine predator, the European shag *Phalacrocorax aristotelis*, focusing on birds breeding in the Farne Islands, UK. Across three years, I found that birds breeding on neighbouring islands were spatially segregated at sea but that this segregation was much stronger in years with higher productivity. I also found that birds displayed individual foraging site fidelity (IFSF), both within and across years, and that females with higher IFSF bred earlier and were in better condition than birds with low IFSF, although this effect was not seen in males. In addition to annual and spatial variation, the characteristics of birds' foraging trips were also affected by time of day, state of tide and wind speed and direction, with females tending to respond more strongly than males. At a larger spatial scale, the foraging ranges of birds at different colonies around the UK showed a positive relationship with distance to the nearest coastline. These findings highlight the importance of considering variation in foraging behaviour at an appropriate scale, and could help improve predictions of individual and population-level responses to future environmental changes.

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Abbreviations

GPS	Global positioning system
TDR	Time-depth recorder
IFSF	Individual foraging site fidelity
MPA	Marine protected area
PCA	Principal component analysis
GLMM	General linear mixed effects model
LMM	Linear mixed effects model
CV	Coefficient of variation
AON	Apparently occupied nest
SMP	Seabird monitoring programme
SPA	Special protection area
SSSI	Site of special scientific interest

Chapter 1 - General Introduction

'In search of sandeel' Illustration by Liz Morgan 2014 (created for the first world seabird twitter conference #WSTC1)

1.1 Flexibility, consistency and constraint

Behavioural plasticity enables individuals to deal with changes in their environment. However, information on the capacity of species to change their behaviour is lacking or restricted for many taxa (Pistorius et al. 2015). The level of behavioural flexibility within species, i.e. the capacity to alter behaviour in the face of change, may constrain or enhance their ability to adapt to climate change or other anthropogenic stressors. Traits that affect fitness are likely to have the greatest impact.

The acquisition of food is closely linked with population processes such as survival and reproduction (Furness & Birkhead 1984, Lewis et al. 2001, Ainley et al. 2003, Ballance et al. 2009, Elliott et al. 2009). Therefore, species with flexible behavioural traits—i.e. generalists—may be better equipped to adapt to new environments (Sol et al. 2002, Wright et al. 2010, Phillips 2012). However, generalist populations can be composed of specialised individuals or groups, where wide population-level niches mask a subset of restricted individual niches (Bolnick et al. 2003, Araujo et al. 2011). As such, the level of behavioural flexibility expressed may be dependent upon the scale over which it is examined. A species may appear to be flexible across its global distribution, but certain populations or even individuals may be more constrained in their behaviours than others.

Physiological limitations (e.g. intrinsic factors such as sex, age or 'personality'), habitat availability, density-dependent effects (e.g. competition) or dispersal capabilities could result in certain members of a population displaying more consistency in behaviours than others (e.g. Wakefield et al. 2013, Lewis et al. 2015, Patrick & Weimerskirch 2017, Spiegel et al. 2017). Consistency could also be driven by individual preferences or habits. For instance, individuals may be capable of changing their behaviour; however, it may be more advantageous to adopt consistent behaviours in order to increase fitness (Bradshaw et al. 2004, Patrick & Weimerskirch 2014a). Consistent individual differences in migratory behaviour have been well documented in avian species (Wilson et al. 1991, Bêty et al. 2004, Phillips et al. 2005, Grist et al. 2014, Lourenco et al. 2016). The benefits to survival in these cases is likely due to site familiarity (Piper 2011) and the refinement of migration tactics (Sergio et al. 2014).

1.2 Quantifying behavioural consistency

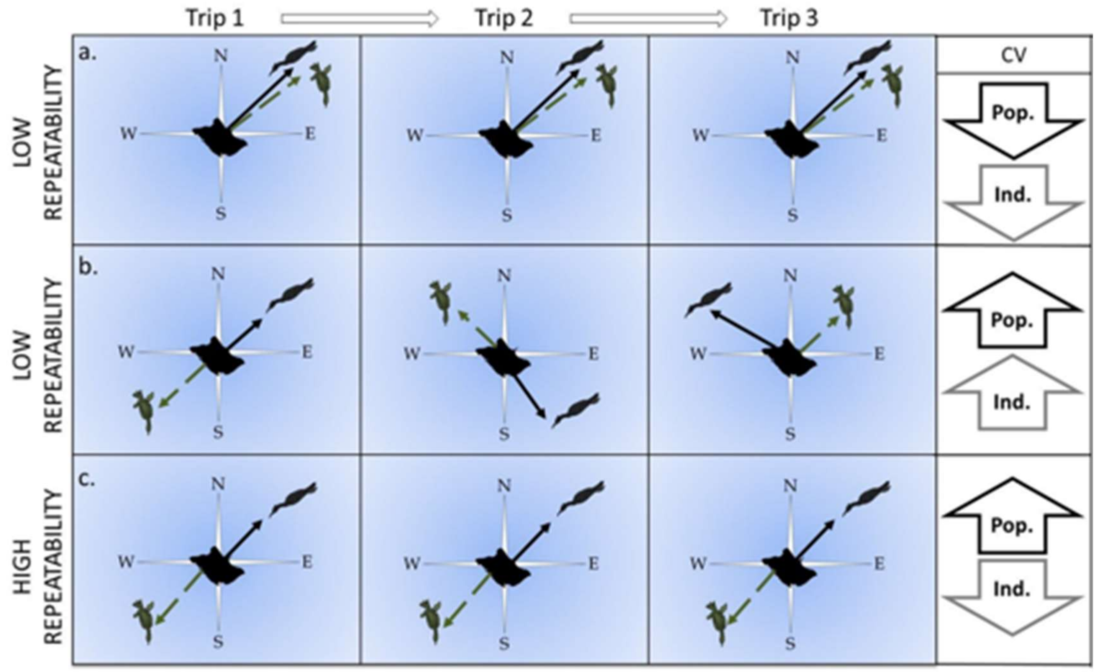

Figure 1-1. How levels of individual repeatability in a population may differ. The illustrated example shows two individuals (green dashed line and black solid line) foraging from the same colony. Populations with low individual repeatability could arise in scenarios a) and b). In scenario a), all individuals forage at the same destination, resulting in a low coefficient of variation (CV) within the population and within each individual, while in scenario b), individuals visit different locations every trip, which results in a high CV at both the population and individual levels. Cases of high repeatability may arise from scenario c), where individuals consistently use the same location but visit different locations from each other, resulting in high variation within the population but low variation within the individuals themselves.

Behavioural consistency is most commonly measured by estimating repeatability, defined as the fraction of behavioural variation that is due to differences between individuals (Bell et al. 2009). The most widely used method to calculate this takes the ratio of between-subject variance to total variance (Lessells & Boag 1987, Nakagawa & Schielzeth 2010), giving an indication of repeatability within a population or sample. When repeatability is high, most individuals behave differently from each other in a consistent way (Figure 1-1). Low repeatability could indicate that all individuals are behaving in the same way as each other (i.e. highly consistent) or that individuals are acting differently each time they perform a behaviour (i.e. inconsistently) (Figure 1-1). However, these estimates do not provide information about how each individual differs in their level of behavioural consistency over time or in different situations (Réale & Dingemanse 2001). If the behaviour of individuals is highly repeatable on average, some individuals may nonetheless be more consistent than others.

Individual consistency has been documented in the behaviour of many species independently of factors such as age and sex (Bolnick et al. 2003, Sih et al. 2004, Bell et al. 2009). For example, individual meerkats (*Suricata suricatta*) show repeatability in their contribution to babysitting and provisioning behaviour (English et al. 2010); repeatable patterns in activity, boldness and exploration behaviours have been found in harvest mice (*Micromys minutus)* (Schuster et al. 2017); and pike (*Esox lucius*) show individual variation in migratory timing with some individuals consistently returning early or late to spawning grounds (Tibblin et al. 2016).

The advent of bio-telemetry devices has enhanced our ability to study animal movement and examine behaviour in greater detail than had previously been possible (Burger & Shaffer 2008, Tomkiewicz 2010). This kind of data has increased our understanding of how birds utilise their environments (Hamer et al. 2007, Watanuki et al. 2008, Votier et al. 2013, Wakefield et al. 2013, Scales et al. 2014). Spatial consistency seems to be widespread in avian taxa, and repeatability has been documented in migration routes (Schwemmer et al. 2016, Vardanis et al. 2016, Hasselquist et al. 2017), breeding and wintering sites (Wilson et al. 1991, Grist et al. 2014, Clark et al. 2016) and foraging areas (Weimerskirch 2007, Harris et al. 2014, Potier et al. 2015, Wakefield et al. 2015).

This information is pertinent to conservation management; for example, it can be used to determine the location of protected areas and to assess potential impacts of anthropogenic activities (Pichegru et al. 2009, BirdLife International. 2010, Yorio et al. 2010, Thaxter et al. 2012, Cleasby et al. 2015). Therefore, understanding individual consistency is highly relevant with respect to effectively managing populations: if certain members of a population are reliant on different areas, they may be more at risk than others.

1.3 **Factors that could influence consistency**

What drives and maintains the level of individual consistency in foraging behaviour is not well understood (Dall et al. 2004, Piper 2011, Wakefield et al. 2015). Consistent foraging behaviours should benefit fitness to be maintained within a population (Marra et al. 1998, Vander Zanden et al. 2014). There is some evidence that repeatable behaviours enhance individual fitness in both the long and short term (Bradshaw et al. 2004, Patrick & Weimerskirch 2014a, Patrick & Weimerskirch 2017), but there are also studies that report weak or no relationships between repeatability and fitness (Woo et al. 2008, Ceia et al. 2012, Patrick et al. 2014, Wakefield et al. 2015). However, variation in the level of behavioural consistency within a population could arise if the fitness benefits of a specific behavioural trait was context dependent; for example, bold individuals can have higher reproductive success but lower survival rates than shy individuals

(Smith and Blumstein 2008). Different consistent behavioural traits or 'personalities' could also be maintained in a population if the fitness pay-offs were dependent upon the frequency of that trait in a population (Dall et al. 2004) or if an individual's state altered the cost/benefit of performing specific behaviours e.g. energy reserves and risk-taking behaviour (Dall et al. 2004, Wolf et al. 2007). The persistence of these 'personalities' across time is unclear. The levels of consistency expressed by individuals can change depending upon the timescale examined (e.g. Woo et al. 2008, Harris et al. 2014). So far, most work has focused on short-term consistency, i.e. within days/months (see review by Ceia & Ramos 2015). The extent to which consistency is maintained across seasons/years is more difficult to establish, as it requires long-term datasets (e.g. Harris et al. 2014, Wakefield et al. 2015, Patrick & Weimerskirch 2017).

The level of consistency that animals express could also depend on extrinsic drivers, such as environmental heterogeneity (e.g. Laskowski & Bell 2013). With regard to foraging, individuals may show consistency only if their environment is stable, i.e. predictable prey patches exist. It has been shown that seabirds breeding in temperate and polar regions show more consistency in their foraging patterns than birds in less predictable tropical waters (Weimerskirch 2007). There could also be other context-dependent influences that could drive differences in behavioural consistency from site to site, such as habitat availability or density-dependent effects (Wakefield et al. 2013). Consequently, it is important not only to recognise intrinsic constraints on behaviour, but also to understand how they relate to environmental conditions. Strong or weak individual consistency in certain behaviours may be maladaptive in some contexts, which may explain why individual variation in behaviour is maintained within populations (Sih et al. 2004).

1.4 Consistency in seabird foraging behaviour

Seabirds provide a good model species for the study of consistency in foraging behaviours. Many are colonial central-place foragers that display high levels of philopatry to their breeding sites. As they are long-lived species, they will return to the same areas year on year. During the breeding season, birds are exposed to intense periods of inter- and intra-specific competition, as they are confined to foraging within reach of a central place—the nesting site—to provide for themselves and their offspring. They are also among the world's most threatened group of birds (Croxall et al. 2012). Understanding the factors that constrain their ability to adapt to change could potentially improve efforts to conserve these species.

Seabirds provide useful model systems upon which to base studies on the effect of demographics on competition and spatial distribution patterns (e.g. Ashmole 1963, Furness &

Birkhead 1984, Cairns 1989). Seabird studies have also led the way in the use of biotelemetry devices on birds and development of associated analysis methods (Bost et al. 2008, Burger & Shaffer 2008). These kinds of studies have enhanced our understanding of many aspects of seabird ecology at a population level, including state-dependent foraging behaviours, such as sex (Lewis et al. 2002, Quintana et al. 2011), age (Daunt et al. 1999, Cunningham et al. 2017) and condition (Hicks et al. 2016); associations with environmental variables (Hamer et al. 2009, Tremblay et al. 2009, Scheffer et al. 2012); interactions with anthropogenic activities (Votier et al. 2010, Cleasby et al. 2015); and foraging tactics (Weimerskirch et al. 1994, Zavalaga et al. 2011). Telemetry data has also been used to link foraging behaviour with reproductive success and/or survival (Daunt et al. 2014, Patrick & Weimerskirch 2014b).

Recent studies are beginning to focus on behaviours at an inter-individual level and have found spatial and behavioural consistency in birds' foraging patterns (see review by Ceia & Ramos 2015). For example, Wandering albatrosses, *Diomedea exulans,* show consistency in both their dietary niches and habitat preferences (Ceia et al. 2012). Northern gannets, *Morus bassanus*, have also been found to display high levels of repeatability in their foraging routes and show individual variation in environmental cues associated with feeding behaviours (Patrick et al. 2014). One common form of consistency in foraging behaviour is individual foraging-site fidelity (IFSF), where an individual repeatedly uses the same foraging location. Site familiarity can increase an individual's fitness as a result of previous experience of the location of resources and threats (Piper 2011). IFSF has been frequently recorded in marine birds (Hamer et al. 2001, Weimerskirch 2007, Woo et al. 2008, Montevecchi et al. 2009, Schwemmer & Garthe 2011, Baylis et al. 2015) and other colonial central-place foragers such as pinnipeds (Bradshaw et al. 2004, Call et al. 2008, Baylis et al. 2012, Arthur et al. 2015), bats (Kerth et al. 2001, Hillen et al. 2009) and ants (Beverly et al. 2009).

1.5 Factors constraining seabird foraging patterns

Knowledge of the interactions between individual consistency and intrinsic and extrinsic factors is crucial for the assessment of population dynamics in a changing environment (Lewis et al. 2009). Individuals could be constrained in their foraging capabilities due to intrinsic factors, such as sex (Phillips et al. 2004, Page et al. 2005, Quintana et al. 2011, Wilson et al. 2015, Beerman et al. 2016, Rosciano et al. 2016), age (Pelletier et al. 2014, Weimerskirch et al. 2014, Fayet et al. 2015), breeding stage (Gonzalez-Solis et al. 2007, Campioni et al. 2016), social status (Pelletier & Festa-Bianchet 2004), health status (Pelletier & Festa-Bianchet 2004, Patrick & Weimerskirch 2014a, Hicks et al. 2016) or even 'personality' traits such as boldness (Patrick & Weimerskirch 2014a).

Extrinsic factors, such as prey availability and weather conditions, can also affect seabird foraging behaviour (Daunt et al. 2006, Hamer et al. 2007, Burke & Montevecchi 2009, Hennicke & Weimerskirch 2014, Lewis et al. 2015). Conspecifics can vary in their responses to these extrinsic factors depending on the size of their breeding colony and/or the nature of their immediate physical environment (Davies et al. 2013, Angel et al. 2016, Warwick-Evans et al. 2016).

In colonial-breeding central-place foragers, such as seabirds, intra-specific competition for food resources can play an important role in determining colony size and can influence foraging distribution patterns (Furness & Birkhead 1984, Wakefield et al. 2009). The 'Hinterland' model (Cairns 1989) predicts that foraging ranges of colonies in close proximity should segregate along equidistant boundaries, driven by the need to balance the energetic costs of travelling to more distant foraging areas (Cairns 1989). Evidence to support this model has been found in some seabird species (Wanless & Harris 1993, Grémillet et al. 2004). However, density-dependent effects also play a role in limiting population growth between neighbouring colonies (Furness & Birkhead 1984, Davies et al. 2013). Individuals from larger colonies have to travel further to find food (Lewis et al. 2001, Ainley et al. 2004, Ballance et al. 2009, Jovani et al. 2016) due to density-dependent depletion or disturbance of prey around breeding sites (Ashmole 1963, Lewis et al. 2001). These processes can lead to the development of colony-specific home ranges (Wakefield et al. 2013, Corman et al. 2016). However, variations in environmental conditions can alter the nature of the relationship between density-dependent competition and foraging effort (Davies et al. 2013, Bogdanova et al. 2014). For example, in northern gannets, stronger relationships were observed in years with low prey availability and these were particularly marked at larger colonies (Davies et al. 2013).

Despite this, few studies have examined how these colony-specific segregation patterns persist across contrasting environmental conditions. Colony-specific foraging patterns could also arise indirectly due to individual-based memory processes (Riotte-Lambert et al. 2015). For instance, if individuals experience foraging success at a particular location, they may remember the location and return to it; i.e. they may show high foraging site fidelity. If other individuals arrive at the same location after the prey have been disturbed or depleted, they may perceive the area as unproductive and, consequently, seek out alternative 'successful' locations, which they then remember and return to (Riotte-Lambert et al. 2015).

Regardless of whether colonies are segregated due to physical or biological processes, segregation has the potential to restrict certain members of a population to a given area where they could be exposed to different environmental conditions. Seabird foraging behaviours have been found to vary between geographic regions and between close colonies (e.g. Hamer et al.

2001, Angel et al. 2016, Mott et al. 2016). Spatial variation in diet composition has also been widely documented in seabirds and is generally linked to prey availability (Hamer et al. 1997, Phillips et al. 1997, Velando & Freire 1999). Comparisons between and within populations of conspecifics can provide insights into the adaptive capabilities of species (Tremblay & Cherel 2003) and enable relationships between density-dependent effects and differences in local habitats or environmental conditions to be explored. Despite this, comparatively few studies have examined these foraging constraints across multiple colonies within metapopulations (Wakefield et al. 2013, Dean et al. 2015, and most recently Wakefield et al. 2017).

1.6 Comparing short- and long-range foraging species

The majority of avian bio-telemetry research was initially carried out on large species such as albatrosses, which often spend days away from their breeding sites and travel hundreds to thousands of kilometres in a single foraging trip. With the reduction in size and cost of telemetry devices, seabird tracking studies are proliferating and now encompass a wide range of species (Burger & Shaffer 2008). The resultant data is accessible through online databases, e.g. Movebank (www.movebank.org) and BirdLife International's Seabird Tracking Database (www.seabirdtracking.org). Still, much of what we know about consistencies in foraging behaviour, IFSF and mechanisms driving segregation between colonies is based on data from mid-to long-ranging species. For the purpose of this thesis, a mid to long-ranging species is defined as having a foraging range of > 50 km. In these species, having knowledge of where profitable foraging patches occur is likely to reduce energy costs associated with searching for prey and may increase foraging success.

Recent research is beginning to reveal that short-range foragers—i.e. those with a foraging range of < 50 km, such as *Phalacrocorax* spp.—also show consistency in their foraging behaviours (e.g. Harris et al. 2014, Potier et al. 2015). As they are not travelling as far, we might expect it to be less costly for short-ranging species to change foraging locations even within a single trip (e.g. Watanuki et al. 2008). However, species restricted to narrower foraging ranges, particularly those that exploit largely sessile benthic prey, may be more strongly affected by competition and could potentially deplete prey resources (e.g. Birt et al. 1987). Therefore, birds that are constrained to take specific prey items from particular patches (e.g. a suitable substrate within their maximum foraging range) may be limited in their ability to respond to changing conditions.

An advantage of studying a short-ranging species is that the conditions they experience during foraging trips are generally closer to the shore or visible from the colony, providing an opportunity to look at how birds respond to extrinsic influences on a much finer scale than can be achieved for longer-ranging species.

1.7 Study species

European shags, *Phalacrocorax aristotelis* (hereinafter referred to as “shags”) are short-ranging seabird species that have a wide geographical range. They inhabit coastal regions from Northern Europe (c. 70^{o}N) to the North African coast (c. 27^{o}N) (Birdlife International 2017). Shags are piscivorous, foot-propelled, pursuit-diving predators that rely on visual cues to catch prey on or close to the seabed (Wanless & Harris 2004). As a result, they only forage diurnally (Wanless et al. 1999). Their principal prey are sandeels—particularly *Ammodytes marinus,* especially during chick rearing—but they also take a range of other benthic prey items (Harris & Wanless 1991, 1993, Velando & Freire 1999, Swann et al. 2008). Sandeels are strongly associated with areas of coarse sandy substrates (Wright et al. 2000, Holland et al. 2005); hence, shag foraging behaviour is closely linked with similar benthic substrates (Wanless et al. 1998).

The average lifespan for the species is 12 to 14 years. Immature birds (1-3 years old) begin to recruit into the breeding population between 3-4 years of age, and are largely site faithful to their breeding colony once they begin breeding. The breeding season usually spans from early March to mid-August). Birds lay between 1-4 eggs (mean clutch size = 3) per year which are incubated for approximately 30 days. Both members of a pair share incubation, brooding and chick feeding duties. During the chick-rearing period, birds generally make 3-4 foraging trips per day (Bogdanova et al. 2014) and spend between 2-7 hours a day at sea (Daunt et al. 2006). Shags are partially migratory, some birds will remain around their breeding colonies overwinter while others can move up to 500 km. Birds are highly consistent in their overwintering strategy and locations (Grist et al. 2014).

Unlike most other water birds, they have a partially wettable plumage (Grémillet et al. 2005), which restricts the length of time they are able to spend in water and constrains them to coastal habitats year-round. As a result, their maximum foraging range is shorter than many other seabirds: generally, less than 25 km (Thaxter et al. 2012). They are sexually dimorphic and can be easily sexed in the field by their voice (Baker 1993). Their foraging behaviours have previously been linked to state-dependent variation in breeding phenology and reproductive success (Daunt et al. 2006, Daunt et al. 2014). Older/ more experienced birds generally have higher breeding success and are more efficient foragers (Daunt et al. 2007a, Daunt et al. 2007b). In addition, there is the potential to identify these older/higher quality individuals as they tend to breed earlier than younger/inexperienced birds (Potts et al. 1980, Aebischer 1993, Harris et al. 1994, Daunt et al. 1999).

The aforementioned behavioural traits make shags an ideal subject on which to examine repeatability in foraging behaviour, as multiple trips from an individual can be recorded in just a few days. In addition, data collected on the timing of breeding and productivity could be used to link bird quality and age to consistent behavioural traits. As a short-ranging species that exploits relatively immobile benthic prey, shags may experience more intense density dependence due to greater prey depletion around larger colonies (e.g. Birt et al. 1987). Also, their ability to respond to reduced prey availability may be limited by their behavioural and energetic constraints. The distances they travel at sea may be more affected by the locations of suitable foraging substrate than prey availability; therefore, they provide an interesting opportunity for a comparative study with wide-ranging pelagic species.

Conversely, their behavioural and physiological limitations also make them vulnerable to climatic changes (Grémillet et al. 1998). Populations have declined in recent years due to an increase in the frequency of winter storms and climate-mediated shifts in prey abundance (Frederiksen et al. 2008, Huebeck 2015, Gunn et al. 2016). Shags have potential as ecological indicators for the health of local marine environments (Fortin et al. 2013), and have been identified as a species that could be impacted by the development of offshore marine renewable technologies (Bradbury et al. 2014). They are a species of conservation concern in the UK (Eaton et al. 2015) and their global population is decreasing (Birdlife-International 2017). Currently, 13 SPAs have been designated to protect the species at breeding colonies; however, many of the marine areas on which they rely remain largely unprotected (Daunt et al. 2015).

1.8 **Study site**

The data presented in this thesis were primarily gathered from a population of shags breeding on the Farne Islands, UK (55°36'57.30"N, 1°39'20.19"W). This study site is an special protection area (SPA) and site of special scientific interest (SSSI) consisting of 15 to 28 islands (depending on tidal state) in the North Sea stretching between 2 km and 7 km from the north-east coast of the UK (Figure 1-2). Two main shag sub-colonies within the archipelago were selected as the main study populations (Figure 1-2): birds breeding at one site on the inner group of islands (Inner Farne, c. 2 km from the shore) and two sites within the outer group of islands (Brownsman and Staple Island, c. 5 km from the shore).

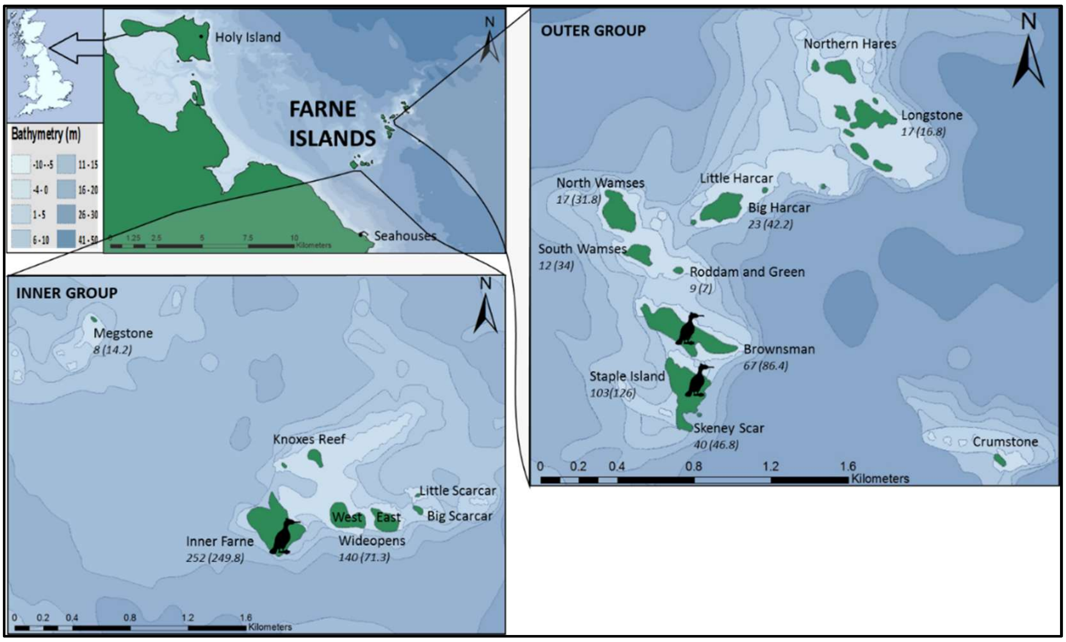

Figure 1-2: Location of the study site and the surrounding bathymetry. The number of breeding pairs of shags are indicated below each island. Data shown are the most recent estimates (2016) from National Trust breeding survey. Five-year mean values are shown in parentheses (errors were not available) . Islands with no breeding shags are shown without numbers. Study colonies are marked with a shag.

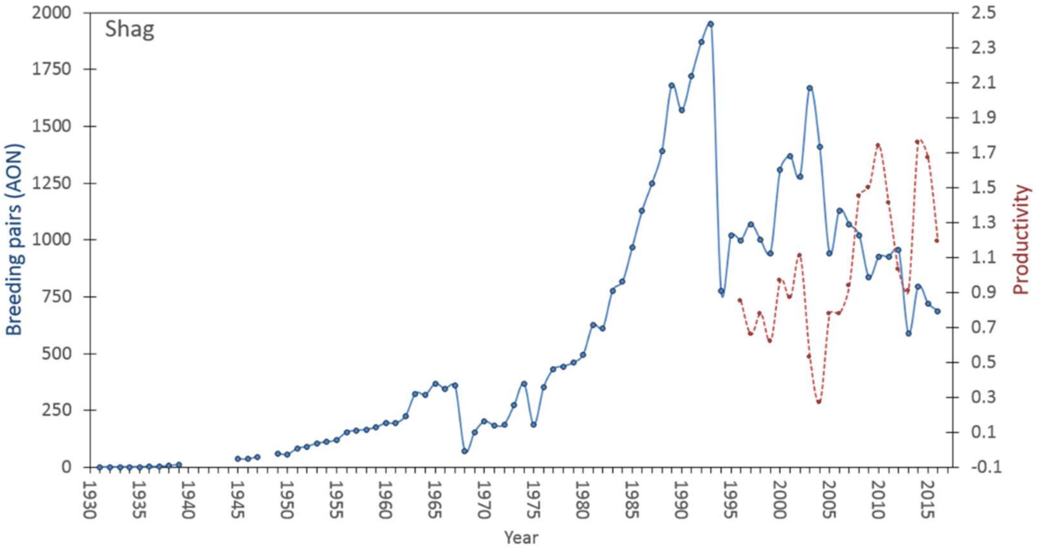

Figure 1-3. Breeding pairs of shags on the Farne Islands from 1931-2016 and trends in their productivity from 1996-2016. Figure updated from (Wilson & Noble-Rollin 2008). Breeding pairs represent apparently occupied nests (AON) and productivity is shown as the average number of chicks successfully fledged per nest. Data obtained from annual Farne Island reports (Tooth et al. 2016).

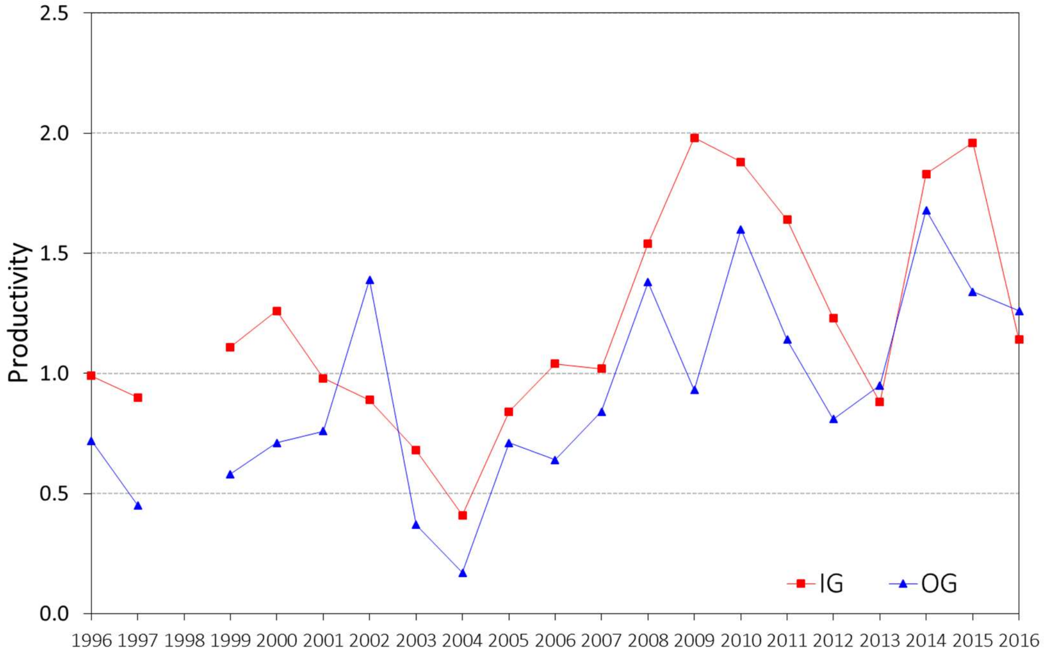

Figure 1-4. Differences in the productivity (the average number of chicks successfully fledged per nest) of shags nesting on the inner group of Farne Islands (IG) and the outer group of islands (OG) over the last 20 years. Data courtesy of Anne Wilson/National Trust archives.

The islands hold a population of over 140,000 seabirds during the summer months, with 14 different species regularly breeding on the islands. Historically, sandeels were the most important prey item for most of these species during the breeding season (Pearson 1968). However, little is known about sandeel population dynamics around the Farne islands. More recent dietary data from the islands are scarce and no studies on the diets of shags have been conducted since the early 1960s.

The shag population across all of the Farne islands during this study (2014-2016) averaged 734 apparently occupied nests (AON). Historically, populations have been much greater, reaching a peak of almost 2,000 pairs in 1993 (Figure 1-3); however, breeding success in this year was apparently very poor (Walton 1994). Periodic crashes in the population have been caused by red-tides (e.g. 1968 and 1975 (Potts et al. 1980)) and mass mortality due to severe winter weather conditions i.e. ‘winter wrecks’ (e.g. 1994, 2004 and 2013 (Harris & Wanless 1996, Gunn et al. 2016)). Shags experience high mortality during prolonged onshore winds (Frederiksen et al. 2008). Climate models predict extreme weather events will become more common across the North Sea region in the future (McInnes et al. 2011), therefore the frequency of these winter wrecks is also likely to increase.

Similar to the rest of the UK population (Eaton et al. 2015), there has been an ongoing decline in numbers in recent years (Wilson & Noble-Rollin 2008, Tooth et al. 2016). Since 1998, the number of shags breeding on the islands has decreased by approximately 33% (Tooth et al.

2016). Average productivity on the islands is around 1.04 (SD = 0.41) chicks per nest (20-year average) but fluctuates widely (Figure 1-3). In most years, the reproductive success of birds breeding on the inner islands seems to be higher than that on the outer islands (Figure 1-4); however, the statistical significance of this trend could not be established due to the lack of raw data.

The benthic environment around the islands consists of a mix of sandy and rocky sediments interspersed with patches of sandy sediments (see Figure 2-4 in Chapter 2). Benthic habitat surveys were carried out in the region between 1993-1997 as part of the BioMar project at the University of Newcastle-upon-Tyne (Davies et al. 1997). These surveys used acoustic data in conjunction with biological information to produce biological resource maps. This gave habitat maps for the area at a higher resolution (c. 50 × 50 m) than data available from the UK/European broad-scale habitat mapping projects, e.g. EMODnet Seabed Habitats (www.emodnet-seabedhabitats.eu) or British Geological Society maps (www.bgs.ac.uk/products/offshore.html). This fine-scale habitat data was used throughout this thesis.

Telemetry data (GPS and TDR) were collected from shags at this site on an ad-hoc basis between 2001 and 2013 (R. Bevan Pers. Comm.). However, this study represents the first comprehensive effort to examine the foraging ecology of the species at this site in detail using these devices. The islands have been open to the public for almost 60 years, which means the birds are somewhat habituated to human presence. This was advantageous for this study, as birds were able to be caught and re-caught with relatively little impact to the surrounding colony or to the birds themselves.

1.9 Aims and structure of thesis

There is a need to better understand the causes and consequences of variation in foraging behaviour at species, population and individual level, yet few studies have comprehensively assessed variation in foraging behaviour across multiple scales within a single species (e.g. Potier et al. 2015, Wakefield et al. 2015). The overarching aim of this thesis is to increase our understanding of the levels of flexibility, consistency and constraint in the foraging ecology of the European shag. To do this, I investigate factors that could impose constraints on the species' behaviour and assess spatial distribution patterns and individual consistency across various spatial and temporal scales. Due to their benthic feeding habits and the restrictions imposed on their behaviour because of their partially wettable plumage, shags could respond differently to the foraging constraints seen in mid- to long-ranging pelagic predators. As such, they provide an interesting opportunity for the comparison and contrast of relationships between extrinsic variables, demographics and foraging behaviour between species. I initially focus on broad-scale comparisons of foraging ecology between shag colonies across Europe, then go on to focus on fine-scale behaviour of individuals within a single study site. The data I present were largely collected specifically to address the questions posed within this thesis. However, to address issues on a wider scale, I also compile information on shag foraging ecology from existing sources.

Chapter 2 contains a broad overview of how shag foraging ecology differs between colonies and begins to explore factors that may be driving differences in foraging behaviour between sites. More specifically, this chapter looks at the effect that colony size and proximity to suitable habitats have on the foraging ranges of shags.

Chapter 3 focuses solely on data collected from a single study site: the Farne Islands. Here, I explore whether processes similar to those documented in chapter 2 are driving colony differences over a much smaller spatial scale and examine the extent to which these are context dependent. To do this, I investigate segregation patterns and differences in foraging behaviours between birds breeding on different islands within close proximity (sub-colonies) across three years with varying environmental conditions.

Chapter 4 concentrates on foraging behaviour at an inter-individual level, exploring individual variations in foraging-site fidelity and consistency both within and between breeding seasons. I also aim to see if consistent foraging behaviour has short-term fitness benefits.

In **Chapter 5,** I focus on how individual foraging behaviour is shaped by intrinsic and extrinsic factors. Rather than focusing on single facets of trips in isolation, I explore the relationships between trip parameters and condense correlated variables into independent factors. I then use these methods as a more integrative approach to investigate how foraging-trip characteristics change in relation to both static and dynamic environmental variables. I go on to explore how these variables interact with individual traits to see how individuality can affect responses to environmental factors.

Finally, in **Chapter 6**, I draw together the key findings from this thesis and discuss these in light of their relevance to seabird conservation and beyond. I also consider some of the limitations of this research project and suggest directions for future studies.

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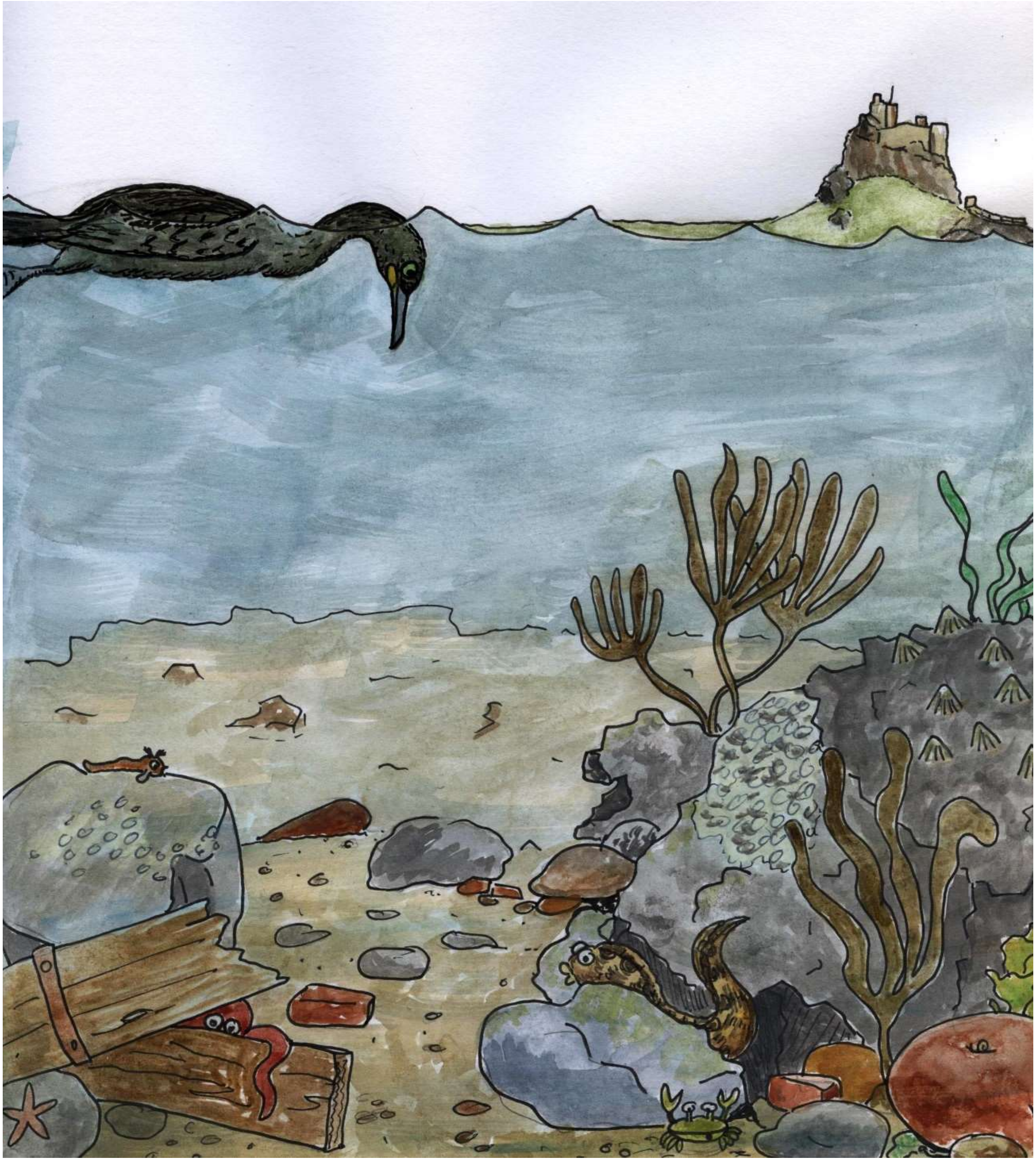
Chapter 2 - Colony size and foraging habitat influences shag behaviour.



'Foraging along the Northumbrian coast' Illustration by Liz Morgan 2014 (created for the first world seabird twitter conference)

Abstract

Marine prey resources have a patchy distribution and to understand how marine predators are able to exploit such prey, it is crucial to determine the patterns of variation in the foraging behaviour of species utilising different marine habitats. Short-ranging species, particularly those that exploit relatively immobile benthic prey, may experience high levels of intra-specific competition for food and may also be strongly affected by the locations of suitable foraging substrate. Here, I use telemetry data from European shags, *Phalacrocorax aristotelis*, breeding at six separate colonies, to examine the relationships between population size, colony location, diet and foraging range in a short-ranging benthic predator. I also present, for the first time, tracking (GPS (Global positioning systems) and TDR (time-depth recorders)), habitat preference and dietary data for shags breeding on the Farne Islands, UK. On a multi-colony scale, foraging ranges varied between geographic locations, as did the primary components of birds' diets. There was a strong positive relationship between foraging range and distance of the colony to the mainland coast, presumably reflecting the proximity of suitable shallow foraging habitats. This relationship could potentially be used to provide as simple cost-effective tool to improve predictions of site-specific foraging patterns in shags. Data from Farne Islands enabled a more detailed examination of individual responses to environmental conditions than multi-colony analyses permitted. Birds increased their foraging range in a year when breeding success was lower, but also increased foraging intensity within trips. This data also showed the relationship between trip duration and foraging range in shags was much weaker than has been reported in other seabird species.

2.1 Introduction

Foraging behaviour is a large part of the daily routines of many species and forms a vital link between prey availability and predator reproductive success. A key issue in this context is the variability in foraging behaviour across heterogenous landscapes used by predators. Marine prey resources have a patchy distribution, reflecting interactions between bathymetry, ocean currents and other physical and biological processes that enhance productivity (Weimerskirch 2007, Scales et al. 2014). To understand how marine predators are able to exploit such patchily distributed prey, it is thus crucial to determine the patterns of variation in the foraging behaviour of species utilising different marine habitats.

Foraging trip ranges and durations of many species of seabird are longer under poorer conditions (Ainley et al. 2004, Hamer et al. 2007, Bogdanova et al. 2014, Hennicke & Weimerskirch 2014, Robertson et al. 2014, Warwick-Evans et al. 2016) and also increase as a function of colony size, providing strong evidence of intra-specific competition for prey resources at sea (Lewis et al. 2001, Ainley et al. 2003, Ballance et al. 2009, Elliott et al. 2009, Davies et al. 2013, Gaston et al. 2013). This competition can also have a limiting effect on conspecifics breeding in adjacent colonies and may result in the formation of colony-specific foraging areas (Furness & Birkhead 1984, Grémillet et al. 2004a, Wakefield et al. 2013, Corman et al. 2016, Wakefield et al. 2017). Consequently, fine-scale foraging behaviours have been found to vary not only between oceanographic regions but also between adjacent colonies, for example; Hamer et al. (2001) found northern gannets breeding at a colony in the North Sea were more consistent in their foraging routes and travelled further than birds from a colony in the Celtic Sea, whereas Mott et al. (2016) found that frigatebirds nesting in the same oceanic region differed in their dietary composition and foraging behaviours, largely based on the proximity of their colonies to neritic or pelagic food sources. Spatial variation in diet composition and habitat usage has been widely documented in many other seabirds and is generally linked to prey availability (Hamer et al. 1997, Phillips et al. 1997, Velando & Freire 1999, Chivers et al. 2012, Paredes et al. 2012). In addition, variation in environmental conditions can alter the nature of relationships between population size, foraging effort and reproductive success (Ashbrook et al. 2010). For instance, in northern gannets, density-dependence was stronger in years with low prey availability and this increase was particularly marked at larger colonies (Davies et al. 2013).

Maximum colony sizes of different species are strongly related to their foraging ranges (Jovani et al. 2016), suggesting that short-ranging species may have to compete more intensively for food resources around the colony. In particular, short-ranging species that exploit relatively immobile benthic prey may experience more intense density dependence due to greater prey depletion around larger colonies (Birt et al. 1987), resulting in longer search times within prey patches and hence longer trip durations. However, the extent to which such species could increase their foraging ranges and/or switch their diets in response to prey depletion is unclear. For instance, in such cases, distances travelled at sea might be more affected by the locations of suitable foraging substrate than by prey availability. A knowledge of how and why behavioural responses vary between sites could improve predictions of species-level responses to environmental change and enhance our ability to identify and protect important marine areas.

European shags *Phalacrocorax aristotelis* (hereafter shags), are a short-ranging coastal species (median foraging range 3.4km, IQR 1.6-7.5; (Wakefield et al. 2017)) that feeds primarily at or near the seabed (Grémillet et al. 1998a, Watanuki et al. 2008). Within the North Sea, birds forage mainly in coarse sandy sediments containing their main prey, lesser sandeels *Ammodytes marinus* (Wright & Bailey 1993 , Wanless et al. 1997a), which they capture by probing into the sand with their beak (Watanuki et al. 2008). Sandeels have a patchy distribution (Wright et al.

2000, Freeman et al. 2004, Holland et al. 2005), which could constrain birds' foraging locations, particularly if some patches are below the depths at which birds are capable of foraging. However, birds are also able to capture prey within the water column (Grémillet et al. 1998a) and, elsewhere, they have a more flexible and varied diet (Velando & Freire 1999). Long-term biotelemetry and population data from a single colony (Bogdanova et al. 2014) revealed a positive relationship between population size and foraging range, but only in years when breeding success was low. There are indications that foraging ranges and behaviour may differ between colonies of this species (Fortin et al. 2013, Soanes et al. 2014, Rijcke 2015, Evans et al. 2016), offering an opportunity to examine relationships between colony size, location and foraging range in a short-ranging benthic species.

The aim of this chapter is to investigate differences in shag foraging behaviour between different colonies and explore factors driving this variation. The following hypotheses were tested; (i) that colonies mean foraging ranges have a positive relationship with population size and distance to suitable foraging habitat, (ii) that diet composition will influence foraging range. In addition, tracking and dietary data from chick-rearing shags at the Farne Islands was examined to aid in the interpretation of among-colony variation in range and diet; specifically looking at the effect of environmental conditions and testing the strength of the relationship between foraging-trip duration and distance.

2.2 Methods

2.2.1 Among-colony analyses

2.2.1.1 Factors influencing differences in foraging behaviour between locations

Data on foraging ranges of shags calculated from biotelemetry devices were collated (n= 7) these studies ranged in latitude from the Norwegian coast (65°12'N, 11°00'E) and West coast to Northern France (47°33'N, 2°30'W). Primary data were obtained from published sources; however, information from accessible online literature (JNCC reports and MSc dissertations) was used if published data were not available.

To examine the influence of colony size, prey availability and habitat availability on foraging range the following information was attained for each colony;

Population data were obtained from the JNCC's seabird monitoring program database (www.jncc.defra.gov.uk/smp) for each colony. Where tracking data covering multiple years had been collected at a site, populations were averaged across the duration of the study.

Dietary information from colonies across the species range were collated, studies included both European subspecies, *P. a. aristotelis* and *P. a. desmarestii*. The proportion of sandeel in the diet was then calculated for each site and used to represent the key component of birds' diets in subsequent analyses.

In the absence of fine-scale benthic substrate maps for all colonies, proximity to the mainland was used to represent distances from each colony to potential shallow coastal foraging areas (i.e. habitat availability). The distance from the central point of each colony to the mainland coast or to the nearest substantial landmass (> 1 km^2) was estimated using straight-line distances calculated from Google Earth (Google Earth 7.0 2016). For colonies located on the mainland coast (n = 1), the distance was set as 0.01 m.

A general linear model (GLM) was used to test whether foraging ranges were significantly affected by colony size or by proximity to the mainland coast. Model simplification and selection were performed using a multi-model inference approach based on the methods and recommendations of Grueber et al. (2011) using the 'MuMIn' package v.1.13.4 (Barton 2015). Where there was no clear best model (i.e. ΔAICc <7) in the candidate model set, the top models (ΔAICc <7) were selected and parameter estimates and the relative importance (RI) of each parameter were averaged (Burnham & Anderson 2002). Predicted values for each factor were extracted for each individual trip from averaged coefficients from unstandardized models and back-transformed where necessary. As the principle aim of this paper was to explore the effect of each fixed factor on foraging range and to ensure the model would pick up any weak effects of this factor compared to other covariates, the natural average method was used to avoid shrinkage towards zero (Grueber et al. 2011).

Due to the fact that colony size affects foraging area, i.e. it is proportional to range squared, colony size was square root transformed (see Lewis et al. 2001 for details). Foraging range and was log transformed to improve model fit and remove skew in the data. As there were only a limited number colonies where both foraging range and dietary data were available (n=3), the proportion of sandeel in the diet could not be included in the GLM, therefore the relationship between foraging range and diet was tested separately using a linear model.

2.2.2 Within colony analyses

Additional fieldwork was carried out for this study; Bio-telemetry work, dietary and habitat preference analyses were carried out on breeding shags from the Farne Islands, UK (55°36'57.30"N, 1°39'20.19"W). For details please see supplementary material.

2.3 Results

2.3.1 Variation in foraging behaviour among colonies

Using data from existing telemetry studies on shags, foraging ranges were found to vary between geographic locations (Table 2-1). The mean foraging range of the species was 6.6km (SD ±6.8) and varied between 1.7km and 19.4km. The mean maximum foraging range displayed by individuals across the seven colonies was 13.2km (SD ±8.8) and varied between 4.4km and 25.4km. This variation equates to a >11-fold difference in mean foraging range and >5-fold difference in maximum foraging range between colonies (Table 2-1).

Table 2-1. Comparisons of shag foraging ranges from telemetry based studies. n = total number of birds instrumented during the study. Population sizes, where not indicated in the study itself, were obtained from the SMP database. For studies across multiple years, values represent the mean for that time period. Where annual data did not exist, the closest colony count to the study dates is shown.

Colony	**Time period (n years data)**	**n**	**Av. Pop size**	**Dist. to nearest shoreline (km)**	**Av. Foraging range (Km)**	**Max foraging range (Km)**	**study**
Sklinna, Norway	2013 (1)	32	2200	20km	19.4	25	(Rijcke 2015)
North Suter, Scotland	1994 (1)	-	210 (1995)	0km	1.5	6.4	Lynnes 1994 (unpub. BSc thesis (Cited in Daunt et al. 2015))
Isle of May, Scotland	1987-2010 (15)	320	795	8km	9(± 3.8)	25.4 (11.9 excluding 1992)	(Bogdanova et al. 2014)
Farne Is., England	2014-2016 (3)	56	734.3	2km	3.17(±0.08)	14.1	This study
Puffin Is., Wales	2010-2012 (3)	67	494	1.25km	5(± 0.9)	10	(Soanes et al. 2014, Soanes et al. 2016)
Isles of Scilly, UK	2010-2012 (3)	13	1010 (2015)	1.5km (to larger islands)	1.74(±1.6)	4.4	(Evans et al. 2016)
Mor Braz, France	2011 (1)	4	565	6km	Not reported	7	(Fortin et al. 2013)

2.3.1.1 Effect of population size, diet and distance to shore on foraging range

For colonies where mean population sizes and foraging ranges were available, there was a strong positive relationship between foraging ranges and the distance from the colony to the nearest shoreline (model averaged coefficient= 0.11 (C.I=0.03 to 0.20), z = 2.74, p < 0.01) (Figure 2-1a). There was a positive trend between square-root population size and mean foraging range (Figure 2-1b), this trend was not significant (model averaged coefficient=0.07 (C.I= -0.02 to 0.15), z = 1.49, p = 0.14) but it was retained in the top model set. The Isles of Scilly had smaller foraging ranges than their population size would predict (Figure 2-1b/Table 2-1). However, population size and distance to shore were positively correlated (r = 0.89, t = 4.44, p = 0.006), i.e. larger colonies also tended to be further offshore, so these results should be interpreted with caution. There were few locations where dietary information was available and mean foraging range was known (n=3), using this dataset, no relationship was found between proportion of sandeel in the diet and foraging range (linear regression: $F_{1,1} = 0.66$ $p = 0.57$, $R_2 = -0.20$; figure 2-1c).

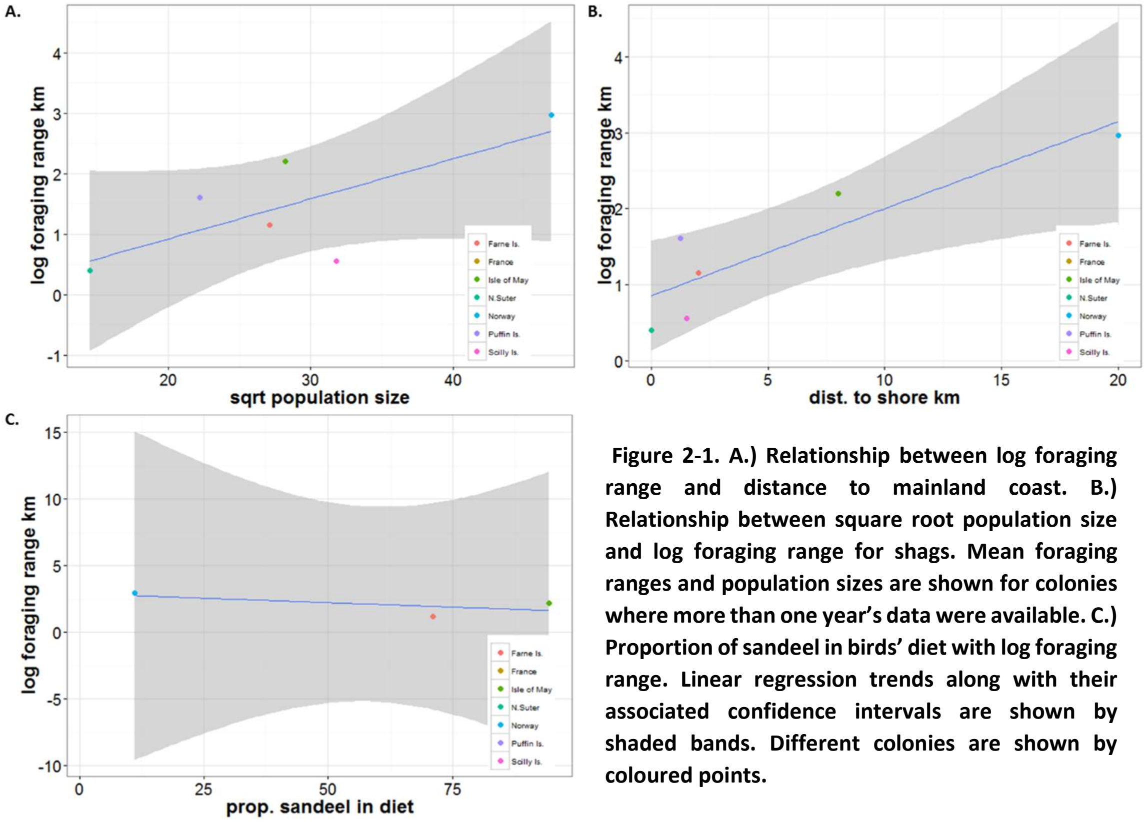


Figure 2-1. A.) Relationship between log foraging range and distance to mainland coast. B.) Relationship between square root population size and log foraging range for shags. Mean foraging ranges and population sizes are shown for colonies where more than one year's data were available. C.) Proportion of sandeel in birds' diet with log foraging range. Linear regression trends along with their associated confidence intervals are shown by shaded bands. Different colonies are shown by coloured points.

2.3.1.2 Variation in diet among colonies

The main prey species varied between locations. Sandeel numerically dominated diets from the North Sea and north-west Atlantic Ocean (Table 2-2 and Figure 2-2) but were not a major component of diets elsewhere. Along the Norwegian coast, young gadids were the most prevalent prey, whereas diet was more varied in the Mediterranean region, with species of *Antheridae, Gobidae* and *Labridae* being the main prey (Table 2-2).

Table 2-2. Main constituents of European shag diet across the latitudinal gradient of their range. Data represent numerical frequency unless otherwise stated (indicate data that show frequency of occurrence) from both European sub species *P. a. aristotelis* and *P. a. desmarestii*. The most common ≥ 75% prey species documented are shown in order of occurrence, based on taxonomic family level.**

Country	**Colony**	**Method**	**Season**	**Year(s)**	**Primary prey spp. (≥ 75% diet)**	**Study**
Norway	Hornoy	Pellets	Breeding	1989	*Ammodytes (56%), Gadidae (40%)*	(Barrett et al. 1990)
	Bleiksoy	Pellets	Breeding	1985-1986	*Gadidae (69%), Ammodytes (15%)*	(Barrett et al. 1990)
	Sklinna	Pellets	Breeding	2007-2010	*Gadidae (>90%)*	(Hillersoy & Lorentsen 2012)
	Rogaland	Pellets	Breeding	1988	*Gadidae (50%), Labridae (20%), Ammodytes (15%)*	(Barrett et al. 1990)
Iceland	West Coast	Stomach contents (chicks)	Breeding (annual)	1996-2000	*Ammodytes (97%)*	(Lilliendahl & Solmundsson 2006)
		Stomach contents (adults)	Breeding (annual)	1996-2000	*Ammodytes (96%)*	(Lilliendahl & Solmundsson 2006)
Scotland	Shetland	Regurgitates**	Breeding	1986-1988	*Ammodytes (100%)*	(Harris & Riddiford 1989)
	Loch Ewe	Stomach contents	Annual	1964-1966	*Gadidae (59%), Ammodytes (41%)*	(Mills 1969)
	Canna	Regurgitates**	Breeding	1981-2007	*Ammodytes (67%), Gadidae (36%)*	(Swann et al. 2008)
		Pellets**	Breeding	1981-2008	*Gadidae (88%)*	(Swann et al. 2008)
	Argyll	Stomach contents**	Non-breeding	1985-1987	*Gadidae (27%), Crustacea (19%), Pholidae (15%), Gobidae (15%)*	(Carss 1993)
	Isle of May	Pellets**	Breeding	1985-1990	*Ammodytes (97%)*	(Harris & Wanless 1991)
		Pellets**	Breeding	1991	*Ammodytes (83%),*	(Harris & Wanless 1993)
		Stomach contents**	Breeding	1991	*Ammodytes (98%)*	(Harris & Wanless 1993)
		Regurgitates**	Breeding	1991	*Ammodytes (100%)*	(Harris & Wanless 1993)
	Clyde Sea	Stomach contents**	Annual	1936-1939	*Ammodytes (78%)*	(Lumsden & Haddow 1946)

England	Farne Islands	Pellets**	Breeding	2014	*Ammodytes (71%), Gadidae (16%)*	This study
		Stomach contents	Non-breeding	1961-1963	*Ammodytes (81%)*	(Pearson 1968)
	Cornwall	Stomach contents**	Non-breeding	1929-1933	*Ammodytes (51%), Clupedidae (30%)*	(Steven 1933)
France	Chausey Islands	Pellets**	Breeding	1994-1995	*Ammodytes (87%)*	(Grémillet et al. 1998a)
	Mor Braz	Pellets	Breeding (annual)	2010-2011	*Gobiidae (33%), Gadidae (27%), Atherinidae (19%), Labridae (10%)*	(Fortin et al. 2013)
	Riou Archipelago	Pellets	Non-breeding	2004-2007	*Atherinidae (24%), Pomacentridae (23%), Labridae (14%), Centracanthidae (13%), Sparidae (13%)*	(Morat et al. 2011)
	Corsica	**	-	-	*Labridae (78%)*	(Guyot 1988)
Croatia	Oruda Island	Pellets	Breeding	2005	*Atherinidae (28%), Serranidae (16%), Labridae (12%), Gobiidae (18%)*	(Cosolo et al. 2011)
Spain	La Caladoria	Pellets	Breeding	1995-1996	*Labridae (52%), Atherinidae (35%)*	(Alvarez 1998)
	Isla de Ons	Pellets	Annual	1995-1996	*Ammodytes (38%), Gobiidae (30%), Atherinidae (20%)*	(Velando & Freire 1999)
	Islas Cíes	Pellets	Breeding	1994-1997	*Ammodytes (76%)*	(Velando & Freire 1999)
		Pellets**	Breeding	1992-2002	*Ammodytes (90%)*	(Velando et al. 2005)
		Pellets**	Breeding	2003 Δ	*Ammodytes (52%)*	(Velando et al. 2005)
	Mallorca	Pellets	Non-breeding	2009	*Sparidae (59%), Atherinidae (15%), Scorpaenidae (11%)*	(Al-Ismail et al. 2013)
Greece	Crete	Pellets**	Breeding	2010-2012	*Atherinidae (47%), Sparidae (25%), Pomacentridae (11%)*	(Xirouchakis et al. 2017)
Δ = post oil spill						

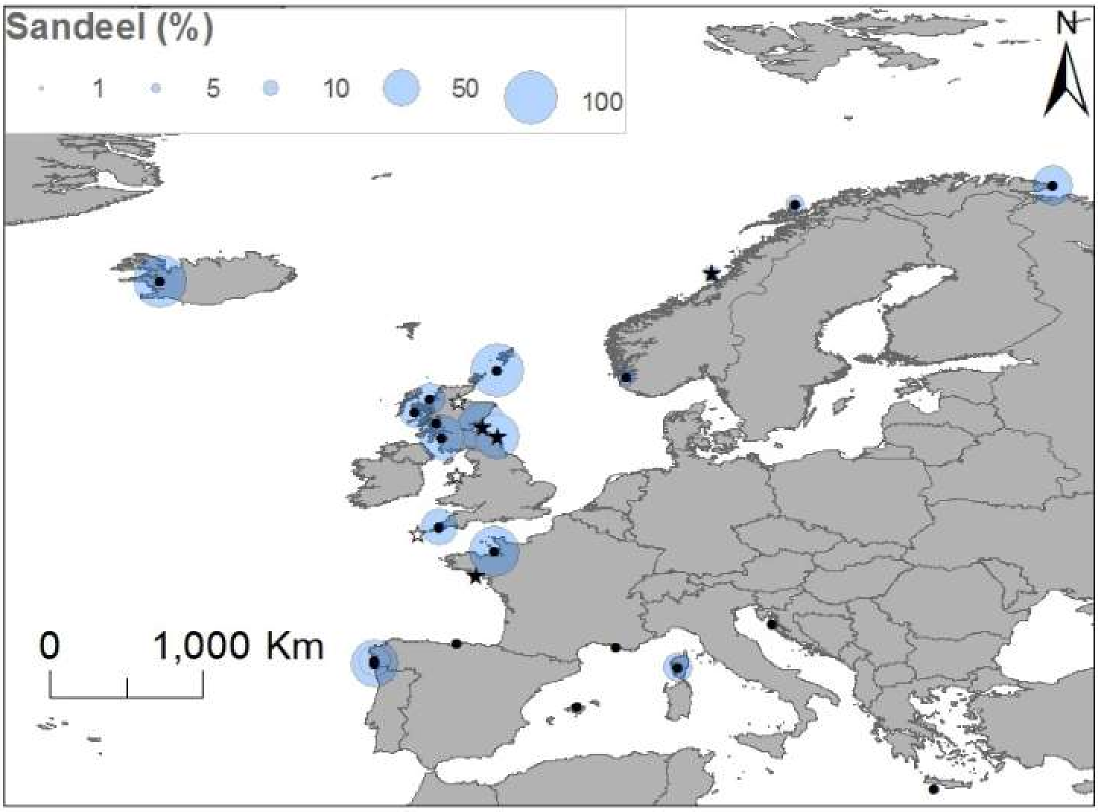


Figure 2-2. **Importance of sandeel (*Ammodytes* spp.) in the diet of *P. aristotelis* at sites where the species' foraging ecology has been intensively studied during the breeding season. Filled points represent sites where the species' diet has been quantified. Stars represent sites where bio-telemetry tracking data has been collected; filled stars indicate sites where both telemetry and dietary information were available. Proportional representation of sandeel in the diet is shown for each location based on frequency of occurrence or numerical frequency in the diet, dependent upon author's choice (for details, see Table 2-2 below).**

2.4 Discussion

2.4.1 Variation in foraging behaviour among colonies

Geographical variation in foraging behaviour occurs in many seabird species (e.g. Hamer et al. 2001, Hamer et al. 2006, Corman et al. 2016). Shags also showed substantial differences in foraging ranges and variation in diets between colonies. Together, these findings highlight the flexibility in the foraging behaviour of shags from site to site. Colony size, habitat availability and prey availability can explain some of the differences in foraging range and diet observed, however, socially mediated interactions, brood size and age could also influence foraging range (e.g. Soanes et al. 2014, Wakefield et al. 2013).

2.4.2 Parameters influencing variation

Prey availability, density-dependent competition and habitat availability can affect species' foraging ranges (Wright & Bailey 1993 , Monaghan 1996, Camphuysen et al. 2006, Wakefield et al. 2011, Cox et al. 2013, Angel et al. 2016). Colony-level distributions can also vary due to the combined effects of these factors e.g. regional habitat availability, coastal geomorphology and both parapatric and sympatric density-dependence (Wakefield et al. 2017). The distribution of available resources has previously been linked to shag foraging locations (Wanless et al. 1998) and in an analysis spanning 13 colonies in the UK, shags were found to have a preference for mixed waters close to the coast with warmer or cooler than average sea surface temperatures (Wakefield et al. 2017). This may explain the strong positive relationship between foraging range and distance of colony to the nearest large expanse of coastline found in this study. However, larger colonies also tended to be further offshore, so this result should be viewed with some caution. Corman et al. (2016) report similar findings from six colonies of lesser black-backed gulls, *Larus fuscus*, where foraging range increased with colony size and decreased with distance from the colony to the nearest shoreline. In contrast to shags, lesser black-backed gulls forage within both marine and terrestrial environments (Garthe et al. 2016), which may account for the relationship between colony size and distance to the nearest land mass in that species.

A positive relationship has been documented between foraging range and colony size in many seabird species, with birds breeding at larger colonies foraging further from the colony (Lewis et al. 2001, Ainley et al. 2003, Ballance et al. 2009, Oppel et al. 2015, Corman et al. 2016). Davies et al. (2013) found that in northern gannets, this density-dependence was stronger under adverse conditions. A similar relationship has been reported in shags, with a density-dependent relationship between foraging range and colony size only apparent in years with low prey availability (Bogdanova et al. 2014). The trend between population size and foraging range found in this study was weak, however a recent study (Wakefield et al. 2017) found density-dependent effects played a role in shaping at-sea distributions of shags. Annual changes in relationships between population size and foraging ranges were likely to have been masked in Wakefield et. al's dataset, as the population size dataset used was from the Seabird 2000 census (Mitchell et al. 2004); which could result in c. 12 years difference between tracking and population data, during this period shag populations in the UK have declined by as much as 34% (JNCC 2016).

Variation among colonies in geography, diet and habitat associations may modify density-dependent relationships. If shags derived a benefit from foraging socially, this could reduce density-dependent competition for food. For example, the Isles of Scilly hold the largest UK shag population (Heaney 2015), yet this population has one of the smallest foraging ranges, and birds here (and at a few other locations) are known to forage in large social groups (Velando & Freire 1999, Evans et al. 2016). Such groups are not commonly recorded off the Farne Islands during the breeding season but they are commonly seen in the autumn post fledging, when immature birds can form large rafts (Velando 2001), pers. obs.) and Watanuki et al. (2008) found that birds using sandy habitat around the Isle of May frequently fed with conspecifics.

2.4.2.1 Variation in diet

As previously reported (Velando & Freire 1999), shag diet varied across their geographic range. The main prey species taken differed between regions, changing from a heavy reliance on sandeel and/or gadids in the North Atlantic Ocean to a more varied diet in the Mediterranean region. The only location where the habitat use of European shags has been studied outside the North Sea is in the Bay of Biscay (Michelot et al. 2017). Here, birds showed a stronger preference for foraging in rocky areas and were primarily feeding on *Labridae* during the breeding season.

Regional differences are important drivers of variation in productivity and geographical location can alter birds' responses to environmental fluctuations (Frederiksen et al. 2007). Telemetry results presented in this study largely come from the North Atlantic region, where birds rely heavily on sandeels during the breeding season. However, gadoids predominate in the diet of birds breeding in Norway (Barrett et al. 1990, Hillersoy & Lorentsen 2012) and these data also fit the trend of increasing foraging range with distance to the shore and population sizes reported here. Gadoid prey are probably juvenile fish that are likely to have nursery areas associated with sheltered coastal regions (Ware 2009). Norwegian birds were associated primarily with areas of kelp (Rijcke 2015), which has a coastal distribution; hence, distance to the shore would also be a key factor in the location of this habitat.

No relationship was found between foraging range and the proportion of sandeel in shags' diet. Dietary differences largely mirror bio-geographical patterns of the abundance and distribution of fish species, especially sandeel (Froese & Pauly 2017), therefore foraging range is likely to be driven by the availability of suitable habitat for prey (i.e. kelp or sandy substrates) rather than prey type itself. Inference from these analyses are limited because there are comparatively few colonies with both foraging range and population data collected over a similar timescale. There were even fewer colonies with concurrent tracking data and dietary analyses. Mean foraging ranges were used in these analyses which could also limit the accuracy of this dataset, as does the fact there was a strong correlation between colony size and distance to coast. Further data are needed from multiple colonies with concurrent population size, diet and tracking data in order to test the aims of this chapter more comprehensively.

There is currently a lack of tracking data for birds from the Mediterranean region where diets are more varied and the habitat associations between birds and their prey are less well understood. Evidence suggests the foraging behaviour of shags in this region may differ from that of conspecifics breeding further North, with both benthic and pelagic foraging strategies (Grémillet et al. 1998a, Velando & Freire 1999, Velando et al. 2005, Cosolo et al. 2011, Al-Ismail et al. 2013, Fortin et al. 2013). It would be informative to examine the drivers of variation in foraging range, distribution and behaviour in this region.

2.4.3 Insights from studying within-colony foraging behaviour

Studying foraging behaviour on a colony by colony basis enables the impacts of anthropogenic or natural changes to be more accurately assessed at specific sites. Populations can be composed of specialised individuals or groups, where wide population-level niches may mask a subset of restricted individual niches (Bolnick et al. 2003, Araujo et al. 2011). It is important to examine foraging behaviour at a within-colony level, as these findings could enhance our understanding of factors associated with among-colony variation. For example, using data from shags on the Farne Islands (see supplementary material), I showed that trip duration may not be an adequate proxy for foraging range in this species. Although a positive relationship between trip duration and maximum distance travelled existed, it was much weaker than those reported in northern gannets (Hamer et al. 2001, Lewis et al. 2001) and in crested terns, *Sterna bergii* (McLeay et al. 2010). A positive relationship between trip duration and distance travelled has also reported in Adélie penguins (Ainley et al. 2004), but the strength of the relationship was not stated. Gannets and terns employ an aerial search strategy and have fully waterproof plumages, unlike shags which have partly wettable plumage (Grémillet et al. 2005). Consequently, shags need to leave the water in order to dry their feathers, so will often rest on land during a foraging trip before returning to the colony. This behaviour may explain why the relationship between trip duration and range is weaker in shags than in some other species.

During this study, birds on the Farne Islands experienced two years where breeding success was above average (2014 and 2015) and one year (2016) where breeding success was similar to the long-term average (see chapter 1). In 2016, birds increased their foraging range, but also increased their foraging intensity; i.e. they spent more time searching for prey on the seabed (Chapter 3). These findings suggest the species is able to respond to increasing competitive pressures in a similar manner to longer-ranging pelagic foraging species, i.e. by increasing trip distances and durations (e.g. Ashmole 1963, Furness & Birkhead 1984, Lewis et al. 2001, Lamb et al. 2017). This has also been the case in other diving seabirds (Ainley et al. 2004, Ballance et al. 2009, Wakefield et al. 2017). The fact that shags also increased time on the seabed could be indicative of a change in the density of prey within patches (Enstipp et al. 2007); however, foraging success can be high even at low prey densities in the closely related great cormorant, *Phalacrocorax carbo* (Grémillet et al. 2004b).

Data from the Farnes lie close to the regression lines of the relationship between colony size and distance to shore with foraging range. However, during years when population sizes were similar at the Isle of May and the Farne Islands, which are just 85 km apart, there was still a substantial discrepancy in birds' foraging ranges. The mean foraging range of Farne Island birds was much shorter, yet birds are largely reliant on the same species of prey. The bathymetry surrounding the Isle of May is deeper than that around the Farnes (Wanless et al. 1997a) and the colony lies approximately 6 km further offshore. In fact, the Isle of May has the largest recorded foraging range of any UK colony. Shag colonies further south seem to have much smaller foraging ranges (e.g. Fortin et al. 2013, Evans et al. 2016). Benthic habitats within a 15-km radius of the Isle of May consist of 18.4% sandy substrates, compared to 33.6 % around the Farnes (Daunt et al. 2015). Benthic habitats around the Scilly Isles (foraging range < 2 km) also largely comprise sandy substrates between the islands (Natural England 2010), however birds nesting here are also known to forage socially (Evans et al. 2016). These findings lend support to the idea that habitat availability may be more important than colony size in defining the foraging ranges of coastal foraging species such as shags.

Currently, the resolution of benthic substrate data available on a UK/Europe-wide scale (e.g. the European Marine Observation Data Network (EMODnet) Seabed Habitats project: www.emodnet-seabedhabitats.eu/ or British Geological Society sediment data (www.bgs.ac.uk/products/offshore.html) may be too broad to discern fine-scale distributions of benthic sediments at a level relevant to the foraging range of shags. Conversely, proximity to the coast seems to be a strong predictor of shag foraging range, and could be a good proxy for habitat accessibility.

2.4.4 Relevance of findings to conservation

The results presented in this chapter highlight that the way in which birds adjust their foraging behaviour may differ due to the location and size of their breeding colony (Davies et al. 2013). As information from tracking data is increasingly being used to identify potential marine protected areas (MPAs) (Ludynia et al. 2012, Thaxter et al. 2012, Chivers et al. 2013, Lascelles et al. 2016, Krüger et al. 2017) and to assess the potential impacts of marine renewable energy developments on seabirds (Soanes et al. 2013, Wade et al. 2014, Cleasby et al. 2015, Thaxter et al. 2015), it is important to develop effective ways to apply these data to conservation management and monitoring practices. For example, MPA designations could be improved if colony-specific distribution estimates were available (Perrow et al. 2015). Understanding the magnitude of colony-colony differences and the factors driving this variation would enable the potential impacts of natural and anthropogenic processes to be more accurately apportioned to specific colonies (Wakefield et al. 2017).

Here, I report substantial differences in shag foraging ranges between colonies, supporting recent findings by Wakefield et al. (2017). These could affect the accuracy of current recommended methods used to designate protected areas. For example, Thaxter et al. (2012) advocate a foraging-radius approach, stating the mean maximum foraging range for shags to be 14.5 km (mean: 5.9 km) based on three direct tracking studies; however, these studies only cover two different locations. In a more recent review, Soanes et al. (2016) report a mean maximum range of 9.21 km (mean: 5.9 km) for the species, based on GPS tracking studies from three separate geographical locations, i.e. colonies in north-east Scotland, northern Wales and France. With the addition of data from three more sites, I report values closer to those presented in Thaxter et al. (2012), with a mean maximum range of 13.19 km (mean: 6.64 km).

The accuracy of predictions made from mean foraging radii could be further improved by a more comprehensive knowledge of the factors that influence the species' foraging behaviour at both a local and global scale. The addition of basic habitat or bathymetric preferences to the foraging radius approach has been suggested as a way of improving this method (Soanes et al. 2016). My results suggest that distance to the shore might also be a useful parameter to add, improving capabilities to determine important marine areas for shags at colonies where tracking studies are not possible.

Recent telemetry data are becoming available from multiple colonies, which, along with the application of advanced modelling techniques, has enabled the at-sea distributions of certain seabirds to be predicted at a colony-level scale for the whole of the UK (Wakefield et al. 2017). The current study also highlights the importance of establishing and applying colony-specific distribution patterns to marine spatial management practices (see Chapter 6).

2.4.5 Conclusions

These results reveal a certain level of flexibility in birds' foraging behaviour from colony to colony. However, shags are strongly philopatric in their breeding locations (Aebischer 1995): birds are known to skip breeding seasons if they are in poor condition but are unlikely to move colonies once they reach breeding age (Potts 1969, Aebischer & Wanless 1992, Aebischer 1995, Barlow et al. 2013). As they are effectively constrained to specific areas, the resilience of each population to environmental changes will depend on the behavioural and/or energetic constraints associated with individual levels of plasticity.

Understanding heterogeneity within a species' foraging ecology and the scales over which these differences occur is important (Frederiksen et al. 2007), as it can affect the extent to which results from local-scale studies—i.e. individual study sites—could be extrapolated across a broader scale. My results show that the foraging ecology of shags breeding on the Farne Islands is comparable to birds at other North Sea colonies. Therefore, the findings presented within this thesis should be relevant to other shag populations, at least within this region. The results presented here also demonstrate how assessing biological responses at relevant scales, i.e. site specific, regional or global, could impact the accuracy of conservation measures, such as MPA designations, environmental impact assessments and predictions made to determine the effects of climate change or other anthropogenic impacts on marine ecosystems. This study also highlights the potential importance of studying populations across longer temporal scales in order to establish how species respond to annual variations in environmental conditions.

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2.6 Supplementary methods and results

2.6.1 Methods: Tracking data from shags breeding on the Farne Islands

Fieldwork was carried out on the Farne Islands, UK (55°36'57.30"N, 1°39'20.19"W). Adult shags were fitted with telemetry devices during the chick-rearing periods of three consecutive years (5th June to 8th July, 2014; 20th May to 20th June, 2015 and 21st May to 27th June, 2016). Birds were sampled on three of the main islands within the archipelago: one site on the Inner Farnes and two sites on the Outer Farnes (see Figure 2 in Chapter 1). Birds were caught at the nest using a 5-m telescopic pole with a wire noose or crook at the end. Some birds were also caught by hand.

Birds were individually colour ringed so they could be easily identified. GPS loggers (IgotU GT-120, Mobile Action Technology, Taipei, Taiwan) and time-depth recorders (TDRs: G5, CEFAS Technology, Lowestoft, UK) were combined into a single device using shrink wrap, cable ties and Tesa® tape (Milton Keynes, UK), then taped to the underside of the central tail feathers. The combined weight of these loggers was 34 g. Birds were weighed to the nearest gram upon capture to ensure devices did not exceed the 3% guideline recommended by Phillips et al. (2003), and devices on most birds were < 2% of body weight. GPS loggers were programmed to record locations every 60 seconds, and TDRs were set to record pressure when they were in water below 1.5 m deep. Tags were set to record at maximum resolution during diving activity (12 Hz) in 2014, however, this level of resolution was unnecessarily high and resulted in excessively large data files so in 2015 and 2016 the resolution was reduced to 2 Hz. Birds were re-captured four to five days after initial deployment, devices were carefully removed and biometrics (maximum chord wing length to the nearest millimetre using a slotted rule, weight as above, bill depth to the nearest millimetre using digital callipers) were collected from adults. Birds were sexed based on vocalisations and bill measurements during the initial capturing procedure (Baker 1993).

2.6.1.1 Tag effects

Trip durations of tagged and control (untagged) birds were examined in 2015 using five time-lapse trail cameras (Bushnell Outdoor Products, Utah, USA), each focused on a sample of nests with tagged and untagged birds. Cameras took three photographs every minute from 04:00 to 23:00 hours (approximately dawn to dusk), allowing calculation of trip durations from changes in nest attendance (Halvin 2015). Additional nest attendance data were collected at intervals (c. 5 days each season) throughout the duration of device deployments by visiting a sample of tagged and control nests on an hourly basis to determine the identity of the birds at each nest. In addition, potential effects of loggers on adult body condition were examined by comparing body mass on attachment and recovery of devices. A paired t-test was used to test the hypothesis that birds' mass during initial capture did not differ from mass upon device recovery. Birds were weighed at differing times of day therefore had unknown amounts of food in their stomachs, this could confound these results. To maximise the sample of tagged birds most accessible birds within the colony were caught and fitted with devices, therefore it was not possible to obtain weights from a control group of adults. I also assessed potential effects on breeding success, using productivity data (number of chicks fledged) obtained from National Trust nest monitoring data (collected for the BTO nest monitoring scheme). A linear mixed effects model was used to test whether productivity differed between nests with and without tagged birds (2014: n tagged nests = 14, n un-tagged nests = 25, 2015: n tagged nests = 12, n un-tagged nests = 21, 2016: n tagged nests = 10, n un-tagged nests = 30) and year was also added as a fixed effect in this model to see if productivity varied annually. In some cases both members of a pair were tagged, therefore nest identity was added as a random effect in these models to account for non-independence of data points. Productivity data for control nests included data from individuals which began nesting later in the season, whereas most devices were deployed on birds during the early part of the chick-rearing season. As birds which breed earlier tend to have higher breeding success (Potts et al. 1980, Aebischer 1993, Harris et al. 1994, Daunt et al. 1999) these results should be interpreted with caution.

2.6.1.2 Tracking data: Processing and analysis

Locational data were interpolated to 60 seconds to account for missing and duplicate locations recorded by the loggers. Dive data were zero offset to periods when birds were at the surface (i.e. the period between known dives identified from dive profiles) and dive parameters were extracted using the package DiveMove (Luque & Fried 2011). Calibrated dive data were then merged with locational data by matching date and time values to the nearest 60 seconds. Based on visual inspections of data, foraging trips were defined as successive locations where a bird spent over 30 minutes away from the colony and that also included at least one bout of diving activity to a depth > 1.5 m (the depth at which TDRs were triggered, confirming the bird had landed on the water). Shags often spend time at the colony but away from the nest (Grémillet et al. 1998b) and so I used a distance of 200 m from the central point of each island as the limit of each colony. This ensured that occasions when birds left the nest but stayed on land were excluded, while allowing the inclusion of data for locations at sea close to the colony. Complete trips were extracted from GPS tracking data using specifically written functions within the statistical software Rv3.0.2 (R Core Team 2013).

Behavioural states were assigned to each location during foraging trips using GPS and TDR data. To achieve this, the speed between successive locations was calculated from GPS distance and time data. Flight speeds of shags range from 8 to 20 ms^{-1} (Pennycuick 1987) and this range may be extended when using ground speeds calculated from GPS loggers (Kogure et al. 2016). Hence, speeds between 4 ms^{-1} and 30 ms^{-1} were classified as flight. Speeds of less than 2 ms^{-1} were initially classified as resting or foraging, with the latter then identified from TDR data (see Figure 1 for an example). For this, dives ≥ 5 m were classified as foraging dives, with shallower dives likely to be associated with washing and surface swimming (Watanuki et al. 2008). Bathymetry data were obtained from the SeaZone Solutions gridded bathymetry dataset (2015) at a resolution of 30 × 30 m (www.seazone.com). The benthic substrate type beneath each foraging location was extracted from benthic habitat maps, along with high-water depths beneath each location. Resting activity was further classified into resting on land (depth at high-water ≤ 0) and resting at sea (depth at high-water > 0). A small number of speeds (~2% of the total) were between 2 and 4 ms^{-1}, probably during take-off and landing, and these were excluded from the analysis.

The following variables were calculated for each foraging trip:

(1) Trip duration in minutes (taken as the time a bird crossed the 200m threshold until the time it returned to within 200m of the colony);

(2) Total distance travelled (km, as above);

(3) Maximum range (the greatest distance reached from the colony in km);

(4) Proportion of time spent resting per trip (calculated as the percentage of 60-second intervals with speed < 2m s^{-1} and depth <5m. This included both pauses at the sea surface between dives and occasions when birds rested on land away from the colony during a trip).

(5) Proportion of time spent foraging per trip (calculated as the percentage of 60-second intervals with depth ≥ 5m);

(6) Number of dives per trip;

(7) Mean dive depth per trip (calculated from the greatest depth attained during each dive);

(8) Total time spent at the bottom phase of each dive per trip (indicative of time spent probing for or pursuing prey).

I also calculated Kernel Density (KD) estimates for all locations classified as foraging activity, with a grid size of 600 and an ad-hoc smoothing parameter in the R package adehabitatHR version 0.4.13 (Calenge 2006).

On a small number of occasions, TDRs malfunctioned resulting in no dive depths being recorded for all or part of a trip. On these occasions I assumed that periods of repeated slow speeds (< 2m s^{-1}) at distance >200m from the colony were associated with diving activity, as was the case for all trips with complete GPS and TDR data. These trips with partial data were included in the analysis of trip durations, distances and kernel densities, but in no other analysis.

Birds roosted on land away from the colony overnight on a few occasions (n = 8) and these were removed from the trip analyses. One nest failed during the tracking period in 2015, probably due to predation of the brood, as the exact date of predation was unknown all this bird's data were also removed from analyses.

GPS data were obtained from previous deployments during the chick rearing periods in 2009, 2010 and 2011 (R. Bevan unpublished data) and processed as above. TDR data were also obtained from 2002, 2003, 2004 and 2009 (R. Bevan unpublished data) but were not matched with locational data. These data were not included in habitat or colony comparison analyses (see below).

2.6.1.3 Habitat usage

Benthic substrate maps were obtained from SeaMap surveys carried out between 1993 and 1997 (Davies et al. 1997) at a resolution of 50 × 50 m (R. Bevan Pers. Comm.).

Habitat preference was determined by comparing the habitat used by birds with the habitat potentially available to them. As tracking data records presence-only data, in order to provide a measure of habitat usage, a set of pseudo-absence data was generated and modelled as a binary response variable in logistic mixed-effects models to establish habitat use versus habitat availability (Aarts et al. 2008, Wakefield et al. 2011). A set of random absences (pseudo-absence data) was generated within a buffer zone matching the maximum foraging range of birds at the Farne Islands. This buffer was restricted to areas with depth at high tide ≥5 m and ≤60 m within a radius of 15 km from the centre of the each colony. Random points were generated to match the number of dive locations in the dataset (c. 60,000). Points were assigned the same bird identity, colony and sex as presence locations, and habitat and bathymetry values were also extracted beneath these 'absence' locations (e.g. Aarts et al. 2008). I then used a generalised linear mixed model with presence/absence as the response variable and substrate type as a fixed effect to test for habitat preference. Bird identity was added as a random effect to account for multiple observations from the same individuals and the model was run with a binomial distribution and logit link function.

2.6.1.3.1 Diet

Recently regurgitated pellets from shags were collected from the study colony on Inner Farne almost every morning from 10th May to 10th June 2014. Pellets from other islands were collected on an ad-hoc basis throughout the breeding season (June to August). Trail-camera footage suggested the majority of birds roosting around the Inner Farne study colony were breeding adults with few non-breeders present. Pellets could not be reliably assigned particular individuals or nests. Samples were stored frozen at approximately -18°C prior to analysis. After thawing, pellets were digested in biological washing power (Biotex^{TM}) until the proteinaceous tissue was dissolved (Johnstone et al. 1990). Hard remains were identified to the lowest possible taxon and counted under a binocular microscope. Fish remains were identified primarily from otoliths and, where possible, were identified to at least family level (Harkonen 1986). No attempt was made to calculate fish age or size from otoliths. Results were expressed as the frequency of occurrence in samples and, for otoliths, the actual numbers present. No attempt was made to pair up otoliths; each was treated as an individual item. The presence of benthic sediments and parasites in samples was also noted.

2.6.2 Results: Foraging behaviour of shags from the Farne Islands

Between 2014 and 2016, biotelemetry devices were deployed and recovered from 80 birds breeding on the Farne Islands. An additional 4 devices were deployed but could not be retrieved due to birds evading capture (these devices all fell off the birds within a period of 4 weeks). Complete location and dive data were obtained from 56 unique individuals, of which 14 were tracked over multiple seasons. Tags had no discernible effects on bird behaviour at the nest; there was no difference in trip durations or nest attendance patterns of tagged and control birds (Halvin 2015). However, as shags spend time loafing on land, time away from nest may not be equal to trip duration (see figure 2-5).

There was no significant change in adult body mass between deployment and retrieval (difference in mass -22 g ±15 g SE; Paired t-test: $t_{,77} = 1.79$, $p = 0.08$).

Breeding success did not differ significantly between nests with tagged birds (mean = 1.9 chicks fledged per nest, SE ±0.12) and those without (1.8 SE ±0.12 chicks per nest; linear mixed-effects model; n.s.). There was, however, a significant difference among years ($F_{,3} = 156$, $p < 0.001$), with productivity significantly lower in 2016 (1.5 SE ±0.17 chicks per nest) than in the other two years (2.0 SE ±0.17 chicks per nest; Tukey test; 2014-2016: $z = -2.5$, $p = 0.04$; 2015-2016: $z = -2.3$, $p = 0.05$). Visual observations indicated that tagged birds were behaving in a similar manner to untagged conspecifics and no adverse effects were noted after removal of the tags.

During 2014-2016, birds made 3.3 trips per day (range: 1 to 6) and generally foraged within a 3 km radius of the colony (Table 2-3). The maximum foraging range was 14.1 km, although some birds foraged within 100m of their nest. Foraging trip durations ranged from 22-290 minutes, with birds travelling a mean distance of 6.7 SD ±0.2 km per trip (max distance 29.4 km). The maximum dive depth recorded from combined tag data was 44.7m; however, a dive of 50.7m was recorded from a bird without corresponding locational data (Figure 2-3). Most bird spent time resting on land during foraging trips before returning to the colony. On average 11% of the time birds spent resting during trips occurred over land, however, 35% of birds did not rest on land at all during trips.

Foraging trip data (GPS) were obtained, prior to this study, from four birds within the 2009, 2010 or 2011 breeding seasons (Table 2-4). TDR data were obtained from nine individuals between 2002 and 2009 (Table 2-3). Trip parameters were similar between the two study periods (2009-2011 and 2014-2016), however, maximum dive depths were greater in 2002-4 with a dive of 72.82m recorded in 2003.

Table 2-3. Foraging trip parameters for shags rearing chicks at the Farne Islands in each year 2014-2016. Mean values ± standard deviations are displayed for each variable. The number of trips included in these analyses are shown above each set of parameters with the number of individual birds shown in brackets.

	2014		**2015**		**2016**	
Trip parameter	**Mean**	**±SD**	**Mean**	**±SD**	**Mean**	**±SD**
n trips location only	358(32)		265(23)		152(14)	
Duration (mins)	78.66	±38.84	80.45	±32.66	117.06	±52.42
Total Distance (Km)	5.23	±4.23	7.30	±4.61	8.93	±5.17
Max Dist (Km)	2.51	±1.92	3.47	±2.16	4.13	±2.39
n trips location + dive data	341(32)		235(20)		150(12)	
% time foraging	43%	±16%	45%	±14%	37%	±19%
%time resting	41%	±17%	38%	±15%	51%	±18%
mean max dive depth (m)	17.82	±7.06	20.00	±7.67	24.09	±8.43
n dives per trip	33.74	±19.45	36.72	±20.45	47.36	±38.21
total bottom time per trip (mins)	19.46	±10.50	19.71	±9.59	34.25	±19.77
n trips per day	3.31	±0.96	3.37	±0.80	3.13	±0.79

Table 2-4. Foraging trip parameters for shags rearing chicks at the Farne Islands between 2009 and 2011. All data are from birds nesting on Brownsman Island (Outer Islands). Trip parameters were calculated using GPS data only and show mean values ± standard deviations. The number of complete foraging trips made in each year is shown with the number of individual birds sampled in brackets.

	2009		**2010**		**2011**	
Trip parameter	**Mean**	**±SD**	**Mean**	**±SD**	**Mean**	**±SD**
Duration (mins)	62.87	±31.56	46.00	NA	53.00	±15.91
Total Distance (Km)	3.77	±2.76	4.29	NA	6.35	±4.06
Max Dist (Km)	1.72	±1.20	2.22	NA	3.12	±1.79
n trips (individuals)	15(1)		1(1)		11 (2)	

Table 2-5. Dive parameters for shags rearing chicks on the outer group of Farne Islands between 2002 and 2009. Devices deployed in 2002-2004 were Lotek TDRs and in 2009 Star Oddi DST micros. The number of dives analysed is shown below each set of parameters with the number of individual birds sampled in brackets.

	2002	2003	2004	2009
Mean max dive depth (m) ±SD	38.04 ±8.51	35.28 ±20.05	33.20 ±4.51	18.23 ±3.22
Max depth (m)	44.00	72.82	41.43	23.80
n dives (individuals)	50(1)	1055(4)	258(2)	324(2)

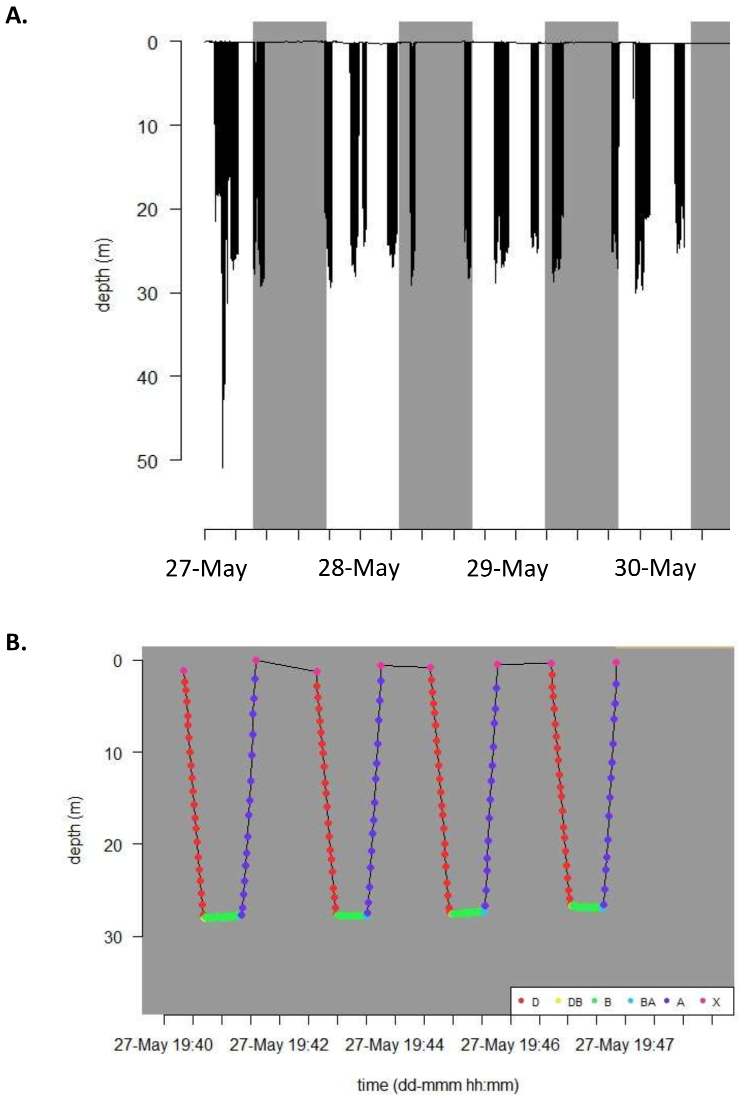


Figure 2-3. Example TDR data from one female shag (1407360) during the 2016 breeding season. (a.) Diving activity recorded over the duration of deployment (4 days - light and dark blocks represent day (6am-6pm) and night (6pm-6am) respectively), (b.) Traces of four dives showing the classification of dive phases- D (red dots) = descent, DB (yellow dots) = descent/bottom, B (green dots) = bottom phase, BA (blue dots) = bottom/ascent, A (purple dots) = ascent, and X (pink dots) = surface.

2.6.2.1 Habitat usage

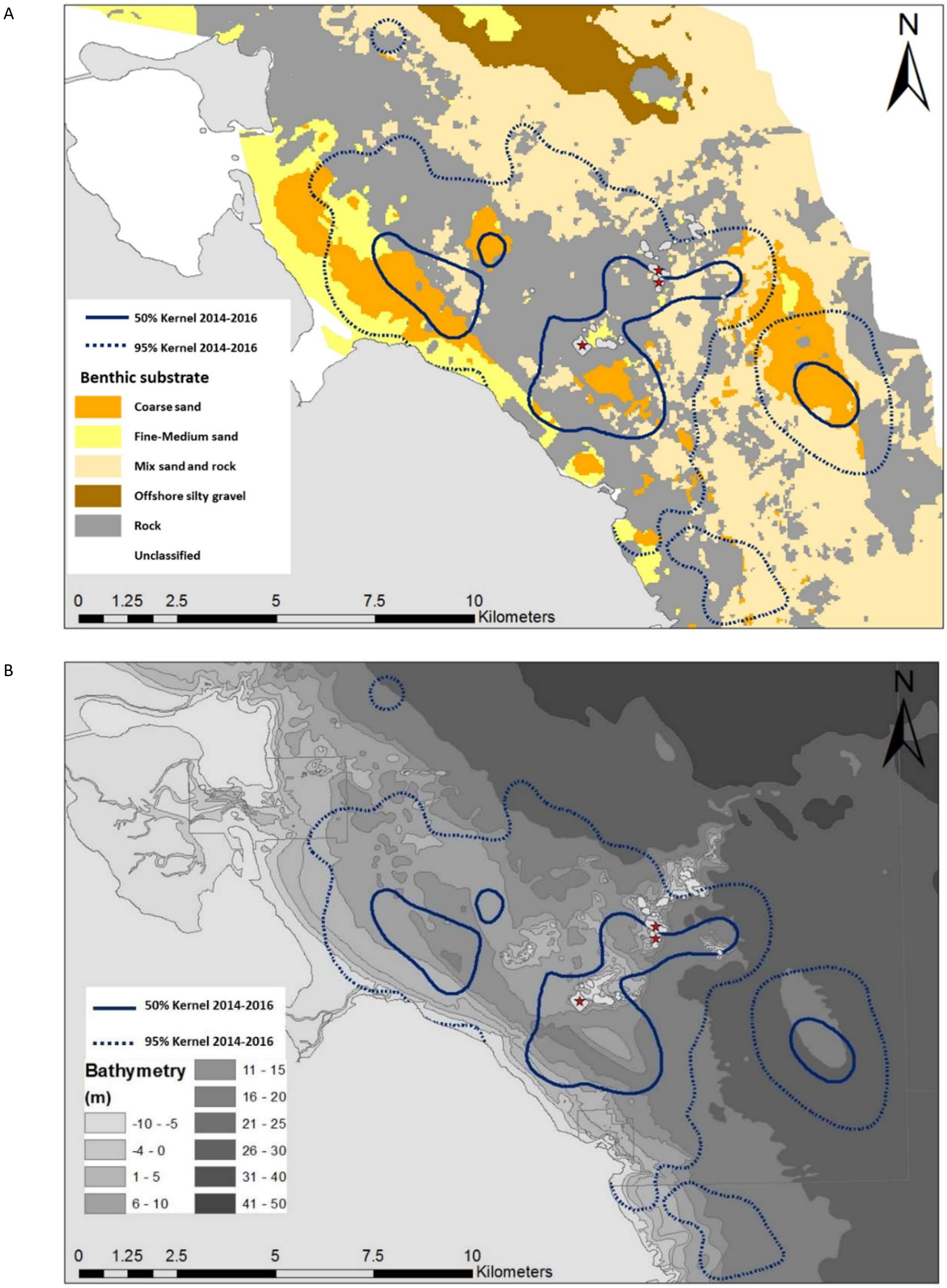


Figure 2-4. (A) Foraging areas of shags breeding on the Farne Islands over benthic substrate data; (B) Foraging areas of shags breeding on the Farne Islands over bathymetry data (depth at low tide). The core foraging areas (50% Kernel Density (KD)) and the area of active use (95% KD) are also shown on both maps. Red stars mark the locations of study colonies.

Birds utilised an area of approximately 85 km^2 around the islands across the three-year study, with foraging efforts primarily focused within four core areas (i.e. 50% Kernel Density) encompassing an area of around 18 km^2 (Figure 2-4). Birds showed a strong preference for shallow sandy substrates and also foraged over rocky substrates more than expected based on the availability of this biotope in the surrounding environment (Table 2-6). Nevertheless, the habitat below their core (50% UD) foraging areas was primarily shallow areas with coarse sandy substrates (Figure 2-4a). Birds actively avoided areas of mixed substrates (Table 2-6).

There was a significant positive relationship between the maximum distance birds reached from the colony (foraging range) and trip duration ($F_{1,773} = 234.54$, $p < 0.0001$, $R^2 = 0.23$) (Figure 2-5). However, this explained only 23% of the variance in the data and effect size was small: for every 1-minute increase in trip duration, distance increased by 0.025 km (mean, SE ±0.002 km).

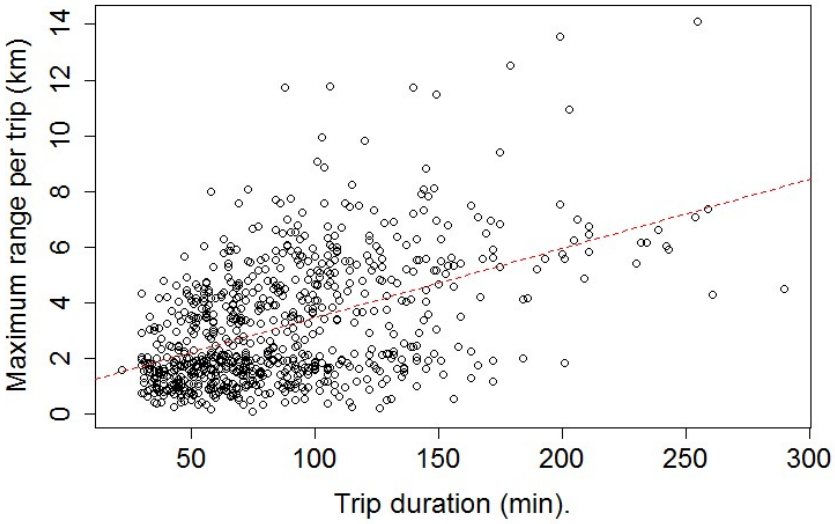


Figure 2-5. Relationship between trip durations and foraging ranges of birds breeding on the Farne Islands. Slope = 0.025 (SE ±0.002).

Table 2-6. Benthic habitat use versus availability for Farne Island birds. Preferences are shown as a percentage of total habitat used/available within the species' foraging range. Coefficients from model results are also shown for each substrate type. The habitats used that were significantly different from those expected based on their availability are marked with an asterisk.

Biotope	**Habitat availability**	**Habitat usage**	**Estimate**	**Standard error**	**z value**	**P**
Mixed sandy and rocky substrates	24.12%	3.12%	-2.05	0.02	-83.91	<0.001*
Offshore silty gravel	7.23%	0.00%	-16.57	36.16	-0.46	0.647
Rocky substrates	54.45%	61.45%	0.12	0.01	15.79	<0.001*
Sandy substrates	14.20%	35.42%	0.91	0.01	71.68	<0.001*

2.6.2.2 Diet

Pellets sampled in 2014 primarily contained fish remains (Table 2-7). Sandeel, *Ammodytes* spp., were the most frequent prey but small gadids (Family Gadidae) also comprised a high proportion of birds' diets (Table 2-8). Benthic sediments were found in the majority of samples, indicating that birds were likely to have fed at the sea bed.

Table 2-7. Contents of pellets regurgitated by shags breeding on the Farne Islands in 2014. Most pellets contained more than one type of prey; as a result, percentages of occurrence may sum to greater than 100%.

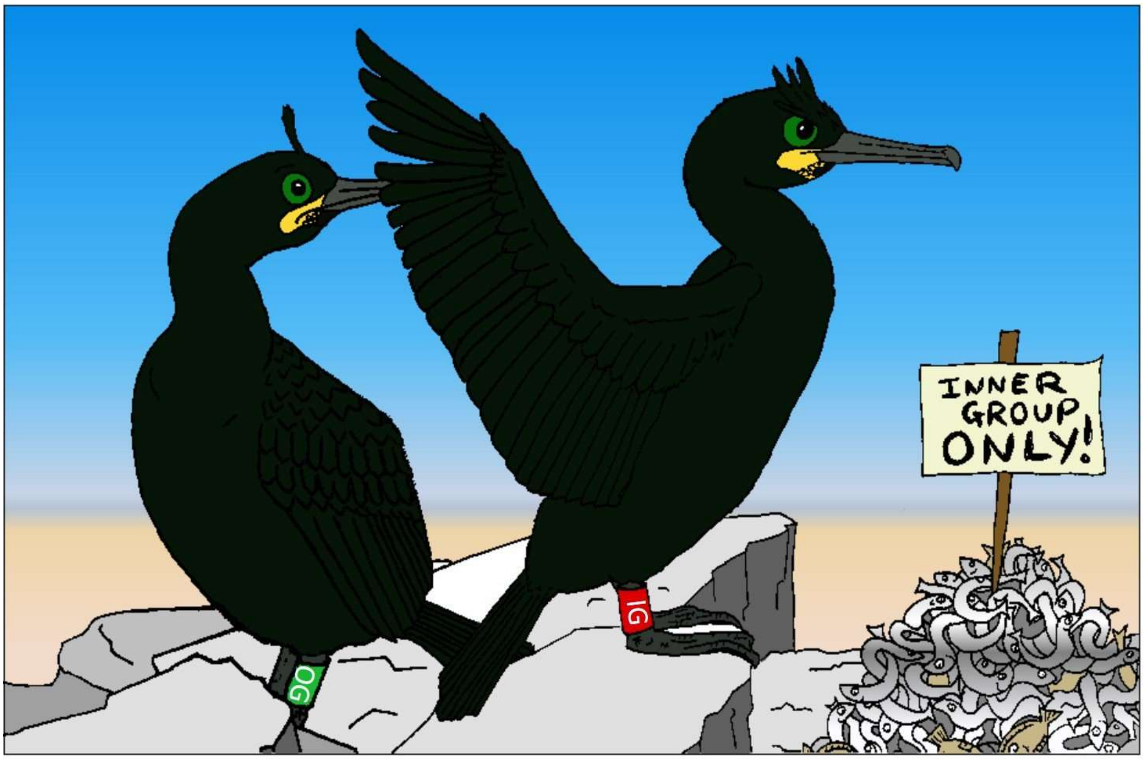
Contents	**frequency of occurrence (total = 51)**	**% occurrence**
Fish otoliths	50	98
Misc. fish remains	37	73
Crustacea	21	41
Polychaetes	8	16
Shell fragments (urchins)	11	22
Shell fragments (molluscs)	19	37
Benthic sediments	42	82

These results are similar to those found at other North Sea colonies (Harris & Wanless 1991, 1993, Wanless et al. 1997a). The primary component of birds' diet on the Farnes was sandeel and key foraging areas were associated with sandy benthic sediments, consistent with sandeel habitat preference (Wanless et al. 1997a, Holland et al. 2005). Foraging trip parameters were consistent with findings from other UK colonies (Wanless et al. 1991b, Bogdanova et al. 2014, Soanes et al. 2014, Evans et al. 2016) and previous research at this site (Pearson 1968, R. Bevan unpublished data). In general, birds showed similar dive depths to those found at other sites (Wanless et al. 1991a, Wanless et al. 1993). However, the previous maximum dive depth recorded for the species was 61m off Sumburgh head, Shetland (Wanless et al. 1997b); Dives of over 70m were recorded from more than one bird foraging around the Farne Islands in 2003 (Table 2-5 and see Appendix A).

Table 2-8. Families and species of fish in the diet of shags breeding on the Farne Islands in 2014. Data show fish families (in bold). Where positive identification could be made, genera are also shown.

Family	**Pellets containing fish remains (n = 50)**		**Number of otoliths (n = 4,143)**	
	n	% occurrence	n	% occurrence
Ammodytidae	**33**	**66**	**2934**	**70.82**
Sandeel, Ammodytes spp.	33			
Gadidae	**29**	**58**	**642**	**15.50**
Rockling, Gaidropsarus/Ciliata spp.	5		13	
Tadpole-fish, *Raniceps raninus*	1		5	
Gobiidae	**3**	**6**	**65**	**1.57**
Pleuronectidae	**14**	**28**	**42**	**1.01**
Cottidae	**19**	**38**	**133**	**3.21**
Bullrout, *Myoxocephalus scorpius*	9		31	
Pholidae	**18**	**36**	**89**	**2.15**
Butterfish, *Pholis gunnellus*	18		89	
Zoarcidae	**9**	**18**	**21**	**0.51**
Eelpout, *Zoarces viviparous*	6		10	
Labridae	**4**	**8**	**4**	**0.10**
Callionymidae	**1**	**2**	**0**	**0.00**
Dragonet spp.	1			
Cyclopteridae	**2**	**4**	**0**	**0.00**
Lumpsucker, Cyclopterus lumpus	2			
Unknown	**17**	**34**	**215**	**5.19**

Chapter 3 - Segregation of foraging distribution in a short-ranging marine predator



'Keep Out!' Illustration by Liz Morgan 2017 (from prize winning series of tweets for the third world seabird twitter conference)

Abstract

Intra-specific competition for food resources plays a key role in determining colony sizes and spatial distribution patterns in seabirds. Some species have colony-specific foraging areas because of competition with individuals from other colonies. Most studies showing this kind of spatial partitioning involve long-ranging marine predators across relatively narrow timescales and the extent to which these patterns are maintained under differing environmental conditions has received little attention. This study aimed to increase our understanding of flexibility in inter-population resource partitioning across different spatial and temporal scales, using the European shag, *Phalacrocorax aristotelis*, as a model short-ranging species. Strategies for efficient foraging could be more pronounced in this species as their movements are confined to smaller areas. Tracking data (location and diving activity) were obtained from birds nesting on separate islands within a small North Sea archipelago across three breeding seasons with different environmental conditions. Annual variation in the size and overlap of colony-specific foraging areas was examined and compared to annual variation in weather conditions and reproductive success. Shags showed flexibility in their foraging behaviour by adjusting their foraging patterns in response to spatial and temporal variation in their environment. The foraging areas of birds breeding within different sub-colonies overlapped less than expected by chance, despite breeding sites being much closer to each other than the average foraging range of the species. However, the degree of overlap between sub-colonies varied from year to year. Birds showed much stronger segregation between colonies in years with higher productivity than in a year when productivity was poor. Shags from both sub-colonies also increased their foraging effort when breeding conditions were less favourable, presumably due to lower prey availability. This inter-annual variation suggests the extent of spatial partitioning between sub-colonies varies with local environmental conditions; i.e. it is context dependent. Exploring the circumstances associated with such changes could potentially increase our understanding of how and why species segregate and allow us better to predict how they will respond to environmental change.

3.1 Introduction

Animals with similar dietary and habitat requirements occupying the same geographic locations at the same time are expected to compete when resources are limited (Begon et al. 2006). Individuals could reduce this pressure and increase individual fitness by segregating resources either spatially or temporally (Wilson 2010, Thiebot et al. 2012, Navarro et al. 2013). In non-territorial species such as colonial breeders, intra-specific competition for food resources plays a role in determining colony size and spatial distribution patterns (Furness & Birkhead 1984, Wakefield et al. 2009). The 'Hinterland' model (Cairns 1989) predicts that foraging ranges of colonies in close proximity should segregate along equidistant colony boundaries in order to reduce energy costs associated with travelling to and from foraging areas (Cairns 1989). Food availability is then assumed to be proportional to foraging area, limiting colony size. Some species seem to conform to this distribution pattern (Wanless & Harris 1993, Grémillet et al. 2004). However, density dependent effects are also known to limit population growth between neighbouring colonies (Furness & Birkhead 1984, Davies et al. 2013). Individuals from larger colonies have to travel further to find food (Lewis et al. 2001, Ainley et al. 2004, Ballance et al. 2009, Jovani et al. 2016) due to density dependent depletion (or disturbance) of prey around breeding sites (Ashmole 1963, Lewis et al. 2001). Colony-specific home ranges probably develop due to a combination of these processes, e.g. 'a density-dependent hinterland' (Wakefield et al. 2013). Due to these density-dependent effects, larger colonies generally have a greater influence on the degree of spatial divergence in foraging grounds than small colonies (Ainley et al. 2004, Grémillet et al. 2004, Thiebot et al. 2012, Wakefield et al. 2013).

Colony-specific foraging patterns could also arise indirectly because of individual-based memory processes (Riotte-Lambert et al. 2015). For instance, if individuals experience foraging success at a particular location, they may remember the location and return to it. If other individuals arrive at the same location after the prey have been disturbed or depleted, they may perceive the area as unproductive and, consequently, seek out alternative 'successful' locations, which they then remember and re-visit. This passive process could eventually lead to the avoidance of resource patches used by others (Riotte-Lambert et al. 2015). Resource partitioning can also occur as a result of factors associated with intrinsic differences in individual foraging capabilities or resource requirements, e.g. sex (Phillips et al. 2004, Page et al. 2005, Quintana et al. 2011, Wilson et al. 2015, Beerman et al. 2016, Rosciano et al. 2016), age (Pelletier et al. 2014, Weimerskirch et al. 2014, Fayet et al. 2015), breeding stage (Gonzalez-Solis et al. 2007, Campioni et al. 2016), social dominance (Pelletier & Festa-Bianchet 2004), health status (Pelletier & Festa-Bianchet 2004, Patrick & Weimerskirch 2014, Hicks et al. 2016) or 'personality' traits such as boldness (Patrick & Weimerskirch 2014).

Ecosystems are rarely static: the availability of resources fluctuates temporally and spatially and this environmental variability in turn affects species' distribution patterns (Pitois et al. 2015, Russell et al. 2015). The availability and distribution of resources are likely to affect the degree of overlap between individuals' (or groups') foraging sites (Warwick-Evans et al. 2016).

Therefore, the level of segregation observed between conspecific foraging areas could change on account of environmental and seasonal factors (Gonzalez-Solis et al. 2007, Kappes et al. 2011) and could also differ with geographic location. Despite this, few studies have examined foraging-area segregation across a range of environmental conditions.

In situations where food resources are plentiful, competition is likely to be negligible (Sale 1974); hence, species' foraging areas could overlap without detrimental effects on individual fitness. For instance, black-browed albatrosses *Thalassarche melanophrys* from two sub-Antarctic colonies were found to have site-specific foraging areas, yet they overlapped around an area of intense trawler activity (Weimerskirch et al. 1988, Cairns 1989). When food is limited, strategies such as resource partitioning could strengthen in order to reduce competitive pressure. For example, Angel et al. (2015) found that Australasian gannets *Morus* serrator from two colonies in close proximity increased their foraging effort within restricted ranges during times of poor prey availability. Conversely, many seabirds are known to increase their foraging range during times of poor prey availability (Hamer et al. 2007, Burke & Montevecchi 2009, Hennicke & Weimerskirch 2014), and so segregation could break down under unfavourable foraging conditions. Moreover, if individual foraging efficiency is increased through the use of social information, this could also result in a higher degree of overlap in foraging areas when food availability is low (Evans et al. 2016).

Foraging-area segregation and colony-specific foraging strategies have been documented in a number of colonial central-place foragers (Grémillet et al. 2004, Robson et al. 2004, Page et al. 2006, Wakefield et al. 2013, Kuhn et al. 2014, Ceia et al. 2015, Angel et al. 2016, Mott et al. 2016). Among these, seabirds may experience intense competition for food resources during the breeding season, when parents are constrained to nest sites and must provide food for offspring as well as themselves. The foraging decisions they make during this time can have important fitness consequences (Lewis et al. 2004, Kidawa et al. 2017). Accordingly, foraging-area segregation during the breeding season has been documented in a number of seabirds, including procellariiform species such as black-browed albatrosses *Thalassarche melanophris* (Wakefield et al. 2011), southern and northern giant petrels, *Macronectes* spp. (Forero et al. 2005), and shearwaters (Paiva et al. 2010, Afan et al. 2014, Ceia et al. 2015, Dean et al. 2015, Paiva et al. 2016). Colony-specific foraging areas also seem to be the norm in gannets, *Morus* spp. (Grémillet et al. 2004, Wakefield et al. 2013, Angel et al. 2016). Close colonies of lesser frigatebirds *Fregata ariel* (foraging range c. 100 km) also display segregation in their foraging resources and locations (Mott et al. 2016). Recent work suggests adjacent colonies of kittiwakes *Rissa tridactyla* and common guillemots *Uria aalge* (foraging ranges; 120 km and 135km, respectively) around the UK coastline also seem to have colony specific foraging areas (Wakefield et al. 2017).

In addition to these species with long foraging ranges (> 100 km), some shorter-ranging species have been recorded as segregating in a similar way (Wanless & Harris 1993, Sapoznikow & Quintana 2003, Lescroel & Bost 2005, Masello et al. 2010, Bogdanova et al. 2014, Corman et al. 2016). The majority of studies which have examined these kinds of segregation patterns have done so within a single breeding season or pooled results from multiple seasons, few studies have examined the persistence of segregation patterns over longer timescales. However, Ainley et al. (2004) found annual variation in the degree of segregation between Adélie penguin *Pygoscelis adeliae* (foraging range < 30 km) colonies, although colony segregation was limited to large colonies, with high levels of overlap observed between small colonies in all years. Similarly, no previous evidence has been found of spatial segregation among adjacent colonies of European shags *Phalacrocorax aristotelis* (hereafter shags; foraging range < 25 km)) (Evans et al. 2016, Wakefield et al. 2017). Further work is therefore needed to better understand the context under which foraging segregation occurs or is maintained among neighbouring colonies, particularly in such short-ranging species.

In these species it may be difficult to establish whether segregation patterns occur between parapatric colonies as inter-colony spacing may exceed the species maximum foraging range. This seems to be the case for shags nesting along the UK coastline (Wakefield et al. 2017). The shag colonies included in Wakefield et al. (2017)'s study where mostly small and sparsely distributed, hence this may account for the lack of spatial overlap between breeding sites. Where this species breeds in larger numbers, contrasting segregation patterns have been observed (Bogdanova et al. 2014, Evans et al. 2016). Bogdanova et al. (2014) documented partial segregation between the foraging distributions of shags around the Isle of May (N. Sea; population size*: 401 AON), whereas Evans et al. (2016) found birds from different islands within an archipelago in the English Channel (Scilly Isles; population size: 1010 AON (Heaney 2015)) foraged in common areas. The spatial extent of a 'colony' may be an arbitrary definition which may not respond as a functional unit, so it is unclear whether nesting aggregations (i.e. birds nesting within sub-colonies, colonies, archipelagos) function independently or as groups over different scales (Wakefield 2014). Here I define separate colonies as breeding aggregations of a species which are geographically distinct i.e. they lie further apart than the mean foraging range of the species.

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* Population size = Apparently Occupied Nests in 2015, data from JNCC seabird monitoring program database (http://jncc.defra.gov.uk/smp).

Segregation patterns in accordance with the density-dependent hinterland hypothesis (Wakefield et al. 2013) are more likely to occur at large and closely adjacent breeding sites. Although the Scilly Isles has a relatively large population of breeding shags (Heaney 2015), their nesting density on islands where tracking work has been possible is low (Evans et al. 2016, Wakefield et al. 2017). The Farne Islands, is an archipelago comprising 15 islands in the North Sea situated between 2 and 7 km from the mainland UK coast. The Islands have a relatively large (c.700 AON*) breeding shag population distributed fairly evenly between adjacent islands (see Figure 2 in Chapter 1). The main shag breeding areas on the islands are <3km apart (i.e. less than the average foraging range of the species), providing an opportunity to test among 'colony' foraging segregation patterns in this species and to explore the scale over which colonies and sub-colonies may act as separate functional units.

Shags are a species of conservation concern in the UK (Eaton et al. 2015): their global population is decreasing (BirdLife International 2017) and they may be particularly susceptible to the effects of climate change (Lewis et al. 2015, Russell et al. 2015). Foraging effort has been linked to state-dependent differences in survival, phenology and breeding success in shags (Potts et al. 1980, Aebischer 1993, Harris et al. 1994, Daunt et al. 1999, Daunt et al. 2006). Hence, a better understanding of the factors that can affect foraging behaviour in this species could improve predictions of its future demographic trends.

Here, I examine colony-specific foraging patterns in shags, aiming to increase our understanding of their flexibility with regard to foraging patterns across spatial and temporal scales. Using biotelemetry data, I explore differences in spatial distribution patterns between birds breeding on closely adjacent islands, testing the following hypotheses: (i) foraging areas between islands in close proximity are segregated at this site, and; (ii) the size and degree of overlap in sub-colony specific foraging patterns varies among breeding seasons. I then aim to investigate the mechanisms underpinning inter-annual variation in overlap by comparing foraging behaviours and distribution patterns with annual fluctuations in environmental conditions and changes in reproductive success.

3.2 Methods

3.2.1 Data collection

Fieldwork took place on the Farne Islands, N.E. England, UK (55°36'57.30"N, 1°39'20.19"W), over three breeding seasons (2014 to 2016). Catching efforts were focused on three of the main islands within the archipelago: one site on Inner Farne (IF) and two sites within the Outer Farnes (OF) (See Chapter 1). Birds were caught at the nest, using a noose, crook or by hand, during the early chick-rearing period in 2014 (5th June to 8th July), 2015 (20th May to 20th June), and 2016 (21st May to 27th June).

To determine foraging locations, GPS loggers (IgotU GT-120, Mobile Action Technology, Taipei, Taiwan) and time-depth recorders (TDRs: G5, CEFAS Technology, Lowestoft, UK) were combined into a single device using shrink wrap, cable ties and Tesa® tape (Milton Keynes, UK) and taped to the underside of birds' central tail feathers. Loggers weighed 34 g, which is < 2% of the average body weight of European shags (Robinson 2005), below the maximum of 3% recommended by (Phillips et al. 2003). Loggers were programmed to collect fixes every 60 seconds, with TDRs set to take regular readings throughout the day (once per hour in 2014 and every 20 minutes in 2015 and 2016) and at maximum resolution (12 Hz in 2014 and 2 Hz in 2015) when submerged below 1.5 m. Birds were re-captured 4 to 5 days after initial deployment, devices were carefully removed and biometrics (maximum chord wing length to the nearest millimetre using a slotted rule, weight to the nearest gram, bill depth to the nearest millimetre using digital callipers) were collected from adults. All adult measurements were taken by the same person. Birds were sexed based on vocalisations and biometric measurements (Baker 1993).

Visual observations were carried out during tag deployments. Where possible, nests were checked on an hourly basis from dawn until dusk and the identity of the adult(s) present was noted (see Chapter 2 for details). Tags had no discernible effects on adult body condition, behaviour at the nest or reproductive success (Chapter 2). In 2015, one nest failed during the duration of tracking, presumed to be a result of predation at young chick stage. Consequently, this individual's data were removed from analyses.

3.2.2 Telemetry data filtering

Data were processed as described in Chapter 2. The following variables were calculated for each foraging trip:

(1) Trip duration in minutes (taken as the time a bird crossed the 200m threshold until the time it returned to within 200m of the colony);

(2) Maximum foraging range (the greatest distance reached from the colony in km);

(3) Mean dive depth per trip (calculated from the greatest depth attained during each dive);

(4) Total time spent at the bottom phase of each dive per trip (indicative of time spent probing for or pursuing prey).

3.2.3 Spatial usage and overlap

Kernel density (KD) estimates were calculated for GPS locations classified as foraging activity using the R package adehabitatHR version 0.4.13 (Calenge 2006). Core foraging areas (50% utilisation distribution (UD)) plus the area of active use (95% UD) were calculated over a grid size of 600 with an ad-hoc smoothing parameter. On a small number of occasions, TDRs malfunctioned (n=5) resulting in no dive depths being recorded for all or part of a trip. On these occasions I assumed that periods of repeated slow speeds (< 2m s^{-1}) at distance >200m from the colony were associated with diving activity, as was the case for all trips with complete GPS and TDR data. These trips with partial data were included in kernel density analyses. The accuracy of GPS locations was approximately ±10m. The degree of overlap for the core (50%) foraging areas of birds from the two neighbouring sub-colonies was calculated using the function kernel overlap within adehabitatHR version 0.4.13 (Calenge 2006). Two indices were considered:

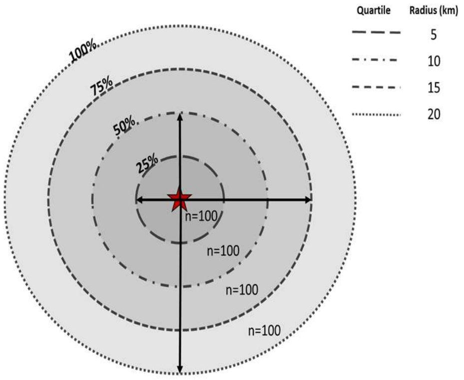
1.) The proportional overlap (PO), which denotes the proportion of the core foraging area of one colony covered by the core foraging area of the other, i.e.

$$\boldsymbol{PO[i,j] = \frac{A[i,j]}{A[i]}}$$

where A[i,j] is the area of the intersection between two colonies (i and j), and A[i] is the area of the home range of colony i (Fieberg & Kochanny 2005). The overall value for this statistic was calculated by taking a mean of the PO for colony [i,j] and [j,i];

2.) The Utilisation Distribution Overlap Index (UDOI), which is a measure of space-use sharing and ranges from zero (no overlap in home ranges) to 1.0 (complete overlap)(see Fieberg & Kochanny 2005 for details). Overlap indices were calculated based on dive locations with corresponding GPS data, i.e. kernels of foraging locations only. Calculations were carried out independently for each year for both 50% and 95% utilisation distributions.

Figure 3-1. Schematic example of how random GPS coordinates were allocated in null models. The same number of point locations were added within each quartile to represent the decreasing probability of birds foraging at distant locations. The radii shown in this diagram represent a simplified example of those used in the study.



To compare observed overlap distributions with a null or “expected” set of distributions, sub-colony overlap (PO and UDOI) were calculated for 100 sets of simulated foraging locations. For each sub-colony, randomised pairs of coordinates were generated within a bounded zone based on the maximum foraging distance recorded for the study site as a whole (c. 14 km) and the availability of suitable foraging habitat. Suitable habitat was identified as benthic substrate types that were used in > 5% of all recorded dives and fell within the known diving depth range for the species (5 m to 50 m) (Watanuki et al. 2008). Within each iteration, coordinates were generated to match the total number of GPS foraging locations in the original data set (37,220 for Inner Farne and 23,704 for the Outer Farnes). Individual foraging locations tend to be spatially auto-correlated within a trip; therefore, random coordinates were clustered into groups based on the total number of trips recorded at each sub-colony.

Habitat accessibility declines with distance from the colony during the breeding season (Wakefield et al. 2009). To simulate this distance-decay process, potential foraging zones were separated using increasing radii based on the quartiles of shags’ maximum foraging distances for the whole site. One quarter of the total number of randomised coordinates was assigned to each quartile radius, so the same number of points was confined to the smallest surface area (the 25% quartile, i.e. closest to the colony) as was spread across a larger surface area (the 75% and 100% quartiles) (Figure 3-1). Population size can affect foraging range in other seabird species (Lewis et al. 2001), but this effect was assumed to be negligible as similar numbers of shags were breeding on each island group (See Chapter 1). A one-sample t-test (or Wilcoxon Signed-Rank test, where appropriate) was used to compare the expected random distributions with the observed levels of sub-colony overlap. All statistics were calculated at both the 50% and 95% utilisation distribution levels.

3.2.4 Differences in foraging behaviour between islands

Descriptive statistics, i.e. mean and standard deviation, were calculated for each foraging parameter (e.g. dive depths, trip distance and duration etc.) for each individual bird in each year, and for each individual trip. To test whether spatial segregation could be linked to differences in foraging behaviours between the two sub-colony groups, each foraging parameter was tested as the response variable in mixed models using the mean values for each individual trip. Sub-colony and year plus an interaction between these two variables were included in all maximal models to explore how spatial and annual variation affected birds’ foraging behaviour. Environmental variables, i.e. tidal state, hourly wind speed and direction, are known to affect shag foraging behaviours (Daunt et al. 2006, Chapter 5) and so these variables were also included in all models. To account for seasonal changes across the study period, the date (Julian day) was also included as an explanatory variable.

Previous research indicates sex and brood size can affect foraging behaviour (Soanes et al. 2014, Lewis et al. 2015) so these were also added as fixed factors in all models. Brood size was taken as the number of chicks during the tracking period. Lewis et al. (2015) found significant interactive effects of sex and brood size associated with the time spent foraging across the annual cycle, along with differential responses of males and females to wind conditions. Therefore, I also tested for interactive effects of sex*wind speed, sex*wind direction, and sex*brood size in the models. To account for pseudo-replication of individual birds tracked over multiple years, bird identity and year were fitted as a random effects in all models.

Trip parameters were transformed where necessary to improve model fit and analysed using a Gaussian distribution. Parameters that required accurate TDR data, i.e. max depth and bottom time were examined only on complete trips with both TDR and GPS data (n = 708 trips), whereas trip distance and duration were examined using all available data (n = 755 trips). The influence of testing multiple trip variables was accounted for using false discovery rate (FDR) control (e.g. Verhoeven et al. 2005).

3.2.5 Model selection

Linear mixed effects models (LMMs) were constructed in the R package lme4 v.1.1-7 (Bates et al. 2015). All fixed effects were standardised using the 'arm' package v.1.7-07 (Gelman & Su 2014) to ensure they were on a common scale and to increase the interpretability of parameter estimates (Schielzeth 2010). Model simplification and selection were performed using a multi-model inference approach based on the methods and recommendations of Grueber et al. (2011) using the 'MuMIn' package v.1.13.4 (Barton 2015). Where there was no clear best model (i.e. ΔAICc <2) in the candidate model set, the top models (ΔAICc <2) were selected and parameter estimates and the relative importance (RI) of each parameter were averaged (Burnham & Anderson 2002). Predicted values for each factor were extracted for each individual trip from averaged coefficients from unstandardized models and back-transformed where necessary. As the principle aim of this paper was to explore the effect of colony location on foraging parameters and to ensure the model would pick up any weak effects of this factor compared to other covariates, the natural average method was used to avoid shrinkage towards zero (Grueber et al. 2011).

3.2.6 Environmental data

Environmental variables used in models were obtained from Boulmer weather station (55°25'N, 01°36'W, 23 km south of the colony; www.badc.nerc.ac.uk). Hourly weather variables (average wind speed and direction) were matched with the start times of trips (to the nearest hour) to establish how birds were responding to current weather conditions. The time to/since midday (to the nearest hour) was calculated from the start time of each foraging trip, and hourly wind data were then assigned to these times. Wind directions were sine transformed (following Daunt et al. 2006) to remove circularity, giving easterly winds a maximum value of 1 and westerly winds the minimum value of −1. Tidal state at the time of departure was calculated for each trip by extrapolating tide table data for North Sunderland harbour (55° 34'57"N, 1° 39'7"W, 3.5 km south of the colony). States were classified as high water/slack (+1 hour to −2 hours after high water), ebb (from 2 to 6 hours after tide where tide height was decreasing), low water/slack (+1 hour to −2 hours after low water) and rising (from 2 to 6 hours after tide where tide height was increasing).

To examine annual variations in weather conditions during the breeding season (May to July), daily values for each variable were calculated. Hourly wind and visibility data were averaged for each day. Rainfall and amount of sunshine were summed to give daily totals. To test for differences in weather conditions between years, Kruskal-Wallis tests were carried out on daily weather data. Post-hoc Nemenyi tests were then used to examine which years varied significantly from each other (see appendix D).

Breeding success in seabirds is strongly linked to prey availability (Monaghan 1996, Croxall et al. 1999). Therefore, productivity in each season should highlight how annual changes in weather or prey availability are affecting birds' fitness. Productivity (mean number of chicks successfully fledged per nest) for each island and the Farne Islands as a whole was determined using individual nest productivity data collected annually by National Trust wardens.

3.3 Results

Combined tracking and dive data were obtained for 443 trips by 34 birds (24 unique individuals; 11 females and 13 males) around the inner islands and 332 trips by 31 birds (28 unique individuals; 13 females and 15 males) around the outer islands (Table 3-1). This yielded ≈ 61000 geo-referenced foraging locations. The UD of all birds' foraging locations in each year revealed an increase in the size of foraging areas across the three years studied (figure 3-2).

Table 3-1. Number of complete foraging trips sampled from shags breeding on the Farne Islands each year, split by sex and sub-colony. IF = Inner Farne; OF = Outer Farnes.

	Year					
	2014		2015		2016	
Sub-colony	**IF**	**OF**	**IF**	**OF**	**IF**	**OF**
Females	87	65	73	78	52	0
Males	107	99	86	28	38	62
Total	194	164	159	106	90	62

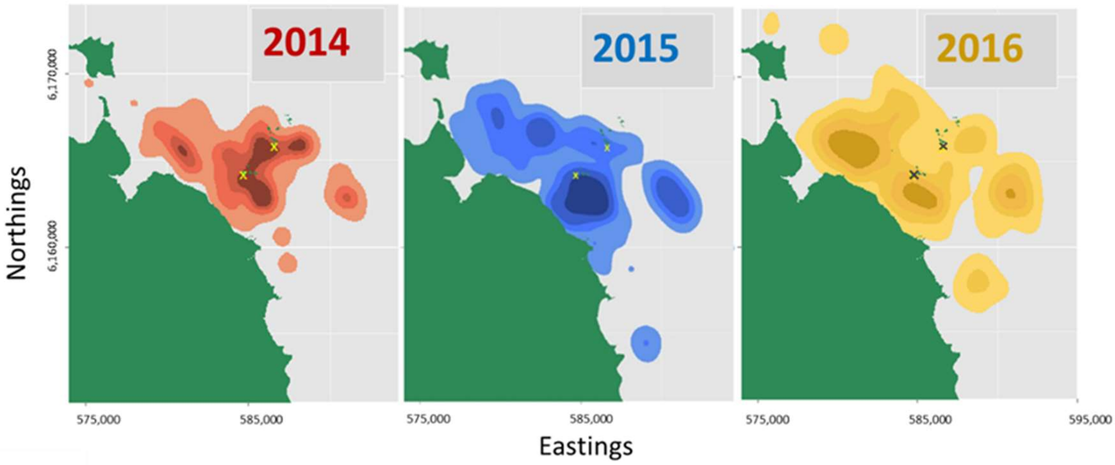


Figure 3-2. Foraging areas of shags studied each year. Crosses indicate the two breeding sites where birds were sampled. Distributions show 95%, 75%, 50% and 25% kernels graded by colour intensity.

3.3.1 Space partitioning between sub-colonies

In all three years, the foraging areas of birds (95% UD) from each group of islands overlapped significantly less than null models predicted (2016-$t_{99} = 40.5$; 2015-$t_{99} = 57.6$; 2014-$t_{99} = 63.0$, $p < 0.001$ in all years). In 2014 and 2015, core foraging areas (50% UD) overlapped between the inner and outer groups by a mean of 7.3% and 8.8% respectively, whereas the expected values from null models predicted mean overlap values of around 34% in both years. This low degree of overlap was reflected in low UDOI (utilisation distribution overlap index) scores (2014 = 0.001, 2015 = 0.002), which were significantly lower than the null model predicted (UDOI = 0.023 (+- 0.001), $V_{99} = 5050.0$, $p < 0.001$). In 2016, overlap between the sub-colonies' core foraging areas was more pronounced (mean overlap = 31.5%, UDOI = 0.035) and was not significantly different from null predictions ($V_{99} = 507.0$, $p = 1$) (Figures 3-3 and 3-4). At the 95% UD level, birds showed a higher level of space-use sharing (UDOI = 0.7). The mean overlap between the area of active use for birds from Inner and Outer Farnes was 64.5%. Overlap scores increased slightly from 2014 to 2016 (Figure 3-4), but were significantly less than null distributions predicted in all three years (Figures 3-3 and 3-4).

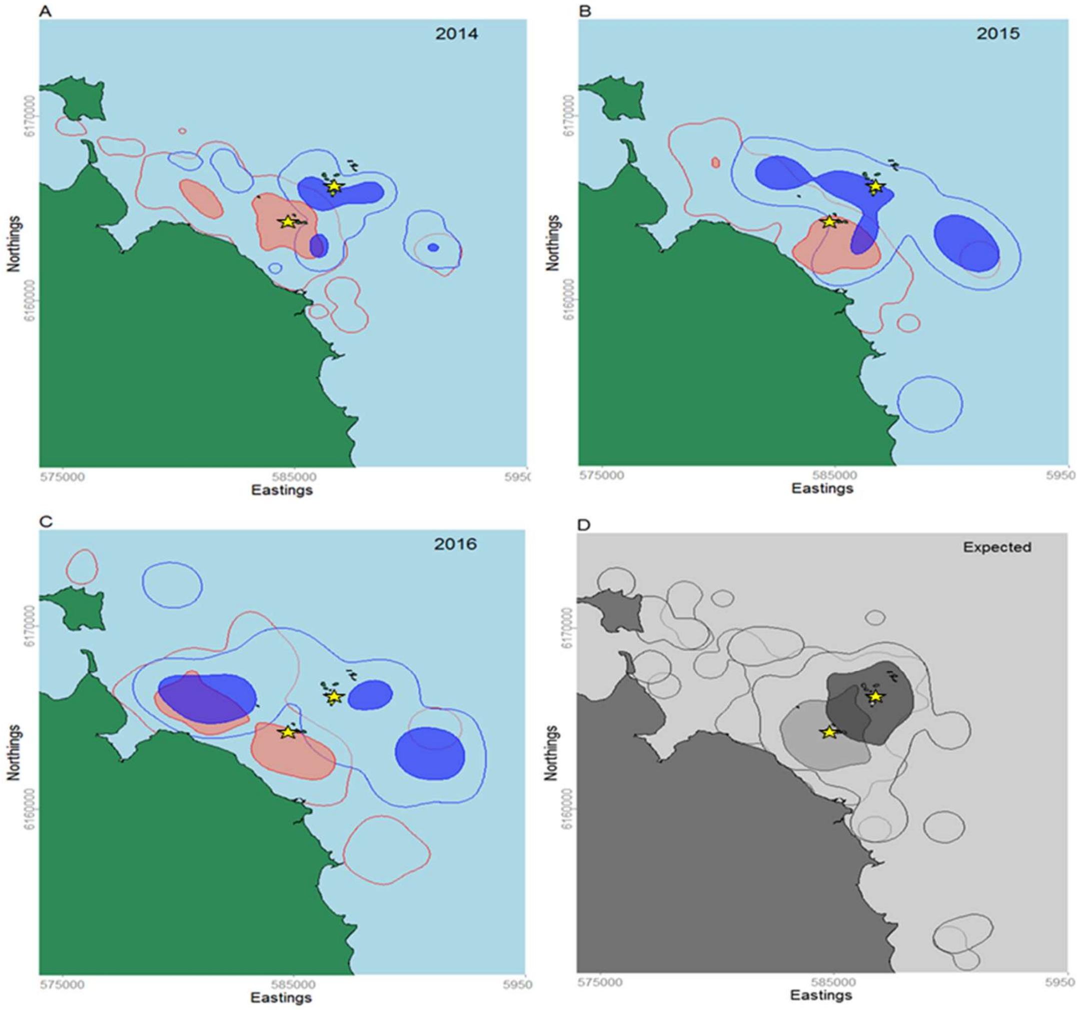


Figure 3-3. Overlap in the foraging distributions of shags breeding at Inner and Outer Farnes in (A) 2014, (B) 2015, and (C) 2016. (D) Null foraging distribution: an example plot from one iteration of the randomisation procedure used to generate expected foraging distributions for each sub-colony. Filled areas represent the core foraging zones (50% contours). Lines represent 95% contours. Red = Birds nesting on the inner group; Blue = Birds nesting on the outer group. Kernel density parameters were calculated from foraging locations using an ad-hoc smoothing parameter and grid size of 600 m. Stars indicate sub-colony locations.

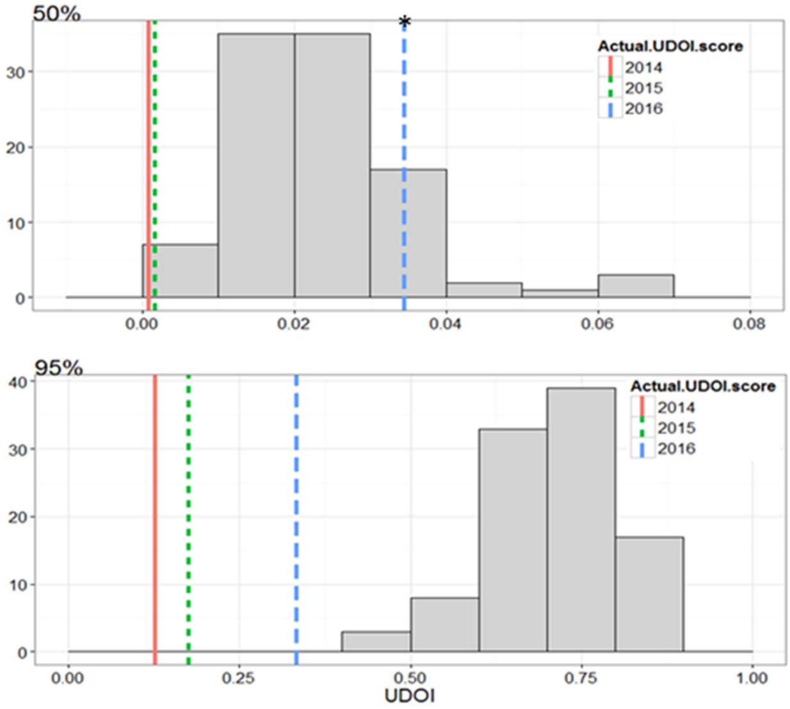


Figure 3-4. Comparisons of the observed UDOI scores in each year with the expected distribution of overlap in foraging areas between the two sub-colonies. Histograms show results from 100 randomised simulations of sub-colony foraging distributions and their associated overlap values. Lines represent actual UDOI scores in each year for 50% UD (upper panel) and for 95% UD (lower panel). Asterisk indicates overlap values that were not significantly different from the null distribution.

3.3.2 Mechanisms driving inter-annual variation in overlap

Sub-colonies showed slight differences in their mean foraging trip metrics and these varied between years (Table 3-2). Birds breeding on the Outer Farnes made shorter trips with fewer but deeper dives compared to birds nesting on Inner Farne (Table 3-2). Birds on the Outer Farnes spent on average 32% less time at or near the seabed per trip than those on Inner Farne (Table 3-2). There was also annual variation in the size and location of birds' core foraging areas (Figure 3-3). The area of active use (95% UD) increased across the duration of the study in both sub-colonies (Table 3-2). The foraging areas of birds on Inner Farne were 42% larger than those on the Outer Farnes in 2014; however, they were 15% and 19% smaller than those on the Outer Farnes in 2015 and 2016 respectively (Table 3-2). Across the study period, birds breeding at the Outer Farnes foraged over a total area of 131.2 km^2 comprising 4 to 5 distinct core foraging areas (50% UD area = 11.3 km^2), whereas those breeding on Inner Farne concentrated their foraging within two main hotspots (Figure 3-3) over an area of 182.4 km^2 (50% UD = 13.1 km^2).

Table 3-2. Mean trip metrics of birds nesting on the Inner Farne (IF) and Outer Farne (OF) Islands in each year of the study. Standard errors are shown in brackets alongside each value.

Year	Sub colony	Duration (mins)	Max range (km)	Mean max dive depth (m)	Total bottom time per trip (mins)	Foraging area (95% KD) (km^2)
2014	**IF**	84.15(±3.08)	2.78(±0.15)	14.30(±0.45)	22.73(±0.89)	48.72
	OF	72.15(±2.53)	2.18(±0.12)	21.88(±0.47)	15.68(±0.52)	28.46
2015	**IF**	84.88(±2.74)	2.99(±0.16)	17.46(±0.47)	22.41(±0.85)	51.96
	OF	73.79(±2.77)	4.20(±0.21)	23.10(±0.86)	16.42(±0.82)	61.57
2016	**IF**	118.78(±5.50)	3.91(±0.26)	19.38(±0.89)	39.08(±2.38)	71.48
	OF	114.56(±6.75)	4.45(±0.29)	30.06(±0.86)	26.34(±2.04)	82.07

Model results indicated that colony location within the archipelago and year were important factors in shaping foraging trip characteristics (Table 3-3). Year was retained in the majority of top models for all foraging parameters (Tables 3-3 and 3-4). Compared to previous years, in 2016, birds' trips were 50% longer (by approximately 33-36 mins); they spent 12-13 minutes longer at or near the seabed per trip; and they were diving deeper (c. +6 m). Overall, foraging ranges increased across the study period, with birds travelling around 1.6 km further in 2016 compared to 2014. However, there were interactive effects between year and sex, and between year and sub-colony (Table 3-4). The foraging ranges of males increased by 54% (2.5 km) from 2014 to 2016, whereas those of females remained stable (between 2.6 km and 2.9 km). In addition, the increase in foraging range across years was much greater at the Outer Farnes than at Inner Farne (Table 3-2). In 2014, foraging ranges were similar for both islands, with the outer group making slightly shorter trips (432 m: 19% shorter). There was a significant interaction between sub-colony and year; in 2015 and 2016, foraging ranges were greater at the Outer Farnes than at Inner Farne, in 2014 this situation was reversed (Table 3-4).

Table 3-3. Relative importance of fixed effects contained in the top model sets for each trip parameter tested. Values show proportional representation in the top model set (i.e. a value of 1 indicates the fixed effect was included in 100% of models). The number of models comprising the top model set (i.e. ΔAICc < 2) is shown in brackets below each response variable. X's indicate fixed effects which were not present in the top model sets. The structure of each model included in the top model sets are shown in Appendix B.1.

	Response variable (n best models)			
fixed effects	**Trip duration (12)**	**Foraging range (28)**	**Max dive depth (11)**	**Time on seabed (10)**
Year	1	1	1	1
Sub-colony	1	1	1	1
Sex	0.06	1	1	0.68
Time of day^2	0.58	1	0.35	1
Time of day	1	0.39	x	1
Date	0.34	0.53	0.32	0.19
Wind speed	0.2	0.39	1	0.18
Wind direction	0.19	0.34	1	0.07
Brood size	0.06	x	1	0.09
Tidal state	x	x	1	X
Sub-colony*Year	x	1	x	0.61
Sub-colony*Sex	x	0.62	x	0.1
Sex*Year	x	1	1	0.68
Sex*Wind speed	x	0.34	0.31	X
Sex*wind direction	x	x	0.3	X

Table 3-4. Model averaged coefficients for each trip parameter. Effect sizes have been standardized to two standard deviations following Gelman et al. (2014). Asterisks indicate significance at p<0.05 level. P values in bold represent significant results after false discovery control for multiple tests (m = 1-4, a = 0.05, adjusted P = 0.050–0.013).

Response variable	fixed effects	Estimate	2.5% C.I.	97.5% C.I	z value	p
Trip duration	(Intercept)	4.436	4.350	4.522	101.114	**<0.001***
(mins) [log]	Sub-colony	-0.172	-0.306	-0.038	2.518	**0.012***
	Year-2015	0.031	-0.074	0.135	0.576	0.564
	Year-2016	0.268	0.164	0.372	5.064	**<0.001***
	Time of day	-0.025	-0.096	0.012	0.830	0.407
	Time of day^2	-0.508	-0.638	-0.379	7.685	**<0.001***
	Date	0.030	-0.045	0.218	0.520	0.603
	Wind speed	0.006	-0.037	0.093	0.302	0.762
	Wind direction	0.005	-0.036	0.084	0.281	0.779
	Sex	0.002	-0.094	0.164	0.117	0.907
	brood size	-0.001	-0.101	0.066	0.094	0.925
Max range	(Intercept)	0.807	0.653	0.960	10.284	**<0.001***
(km) [log]	Sub-colony	-0.186	-0.470	0.099	1.280	0.201
	Sex	-0.254	-0.527	0.019	1.824	0.068
	Year-2015	0.302	0.106	0.499	3.017	**0.003***
	Year-2016	0.525	0.350	0.701	5.860	**<0.001***
	Time of day^2	-0.432	-0.630	-0.234	4.275	**<0.001***
	Sub-colony*Sex	-0.242	-0.877	0.094	0.888	0.375
	Sub-colony*Year-2015	0.508	0.184	0.832	3.071	**0.002***
	Sub-colony*Year-2016	-0.230	-0.692	0.232	0.977	0.329
	Sex*Year-2015	0.398	0.123	0.673	2.837	**0.006***
	Sex*Year-2016	0.666	0.269	1.062	3.293	**0.001***
	Date	0.090	-0.055	0.391	0.760	0.447
	Wind speed	-0.010	-0.126	0.076	0.288	0.774
	Sex*Wind speed	0.055	-0.020	0.341	0.589	0.556
	Time of day	0.020	-0.033	0.135	0.549	0.583
	Wind direction	0.019	-0.038	0.148	0.492	0.623
Max dive depth	(Intercept)	2.764	2.661	2.867	52.534	**<0.001***
(m) [log]	Sub-colony	0.414	0.244	0.585	4.767	**<0.001***
	Wind direction	-0.054	-0.101	-0.007	2.229	0.026*
	Sex	-0.129	-0.309	0.051	1.406	0.160
	Tidal state-HWSLACK	0.109	0.045	0.173	3.344	**0.001***
	Tidal state-LWSLACK	-0.005	-0.065	0.055	0.150	0.881
	Tidal state-RISING	0.096	0.034	0.159	3.034	**0.002***
	Year-2015	0.140	0.041	0.240	2.771	**0.006***
	Year-2016	0.164	0.065	0.262	3.264	**0.001***
	brood size	0.091	0.005	0.177	2.085	0.037*
	Wind speed	0.081	0.030	0.133	3.085	**0.002***
	Sex*Year-2015	0.124	-0.032	0.280	1.564	0.118
	Sex*Year-2016	0.384	0.177	0.592	3.629	**<0.001***
	Time of day^2	-0.026	-0.185	0.038	0.529	0.597
	Date	0.028	-0.056	0.229	0.481	0.630
Total time on seabed	(Intercept)	6.983	6.885	7.082	138.725	**<0.001***
(secs) [log]	Sub-colony	-0.387	-0.554	-0.220	4.546	**<0.001***

Sex	0.016	-0.148	0.196	0.223	0.823
Year-2015	0.036	-0.098	0.170	0.529	0.597
Year-2016	0.510	0.361	0.658	6.714	**<0.001***
Time of day	-0.095	-0.165	-0.025	2.651	**0.008***
Time of day^2	-0.228	-0.394	-0.061	2.672	**0.008***
Sub-colony*Year-2015	-0.072	-0.352	0.117	0.656	0.512
Sub-colony*Year-2016	0.206	0.003	0.668	0.979	0.328
Sex*Year-2015	-0.023	-0.246	0.178	0.253	0.800
Sex*Year-2016	-0.337	-0.849	-0.140	1.227	0.220
Date	0.018	-0.080	0.268	0.337	0.736
Sub-colony*Sex	-0.016	-0.462	0.150	0.231	0.818
Wind speed	0.007	-0.042	0.125	0.306	0.760
brood size	0.004	-0.062	0.155	0.194	0.846
Wind direction	0.001	-0.058	0.098	0.119	0.905

3.3.3 Annual variation in productivity

Table 3-5. Productivity of shags at Inner Farne and Outer Farnes in each year of the study. Data courtesy of the National Trust. Productivity was calculated as the number of chicks fledged per nest divided by the number of nests where birds were definitely or probably incubating.

	Productivity			
	2014	**2015**	**2016**	**20-year mean** (± SE)
Inner Farne	1.83	1.96	1.14	1.21 (± 0.10)
Outer Farnes	1.68	1.34	1.26	0.92 (± 0.09)
Total	1.76	1.67	1.19	1.04 (± 0.09)

Productivity (mean number of chicks fledged per nest) was lower in 2016 than in previous years (Table 3-5), especially at Inner Farne. Respectively, 2014 and 2015 were years with good breeding success, with 2016 a moderate year based on the long-term average (Table 3-5). However, visual nest observations showed chicks were left unattended on Inner Farne in 2016, whereas this behaviour was not recorded during either of the previous two breeding seasons. In general productivity is usually higher at Inner Farne than at the Outer Farnes (Table 3-5).

3.4 Discussion

This study set out to test whether foraging areas of birds breeding on islands in close proximity are segregated in a short-ranging central place forager. The foraging areas of shags breeding in neighbouring sub-colonies on the Farne Islands overlapped less than expected by chance. However, the degree of overlap between sub-colonies varied between years. Birds showed much stronger segregation patterns in the two years with higher productivity than in a year with moderate productivity. Segregation in foraging areas was accompanied by differences in the foraging behaviour of birds from the two island groups, largely due to birds from Inner Farne foraging in shallow coastal areas whereas those from the Outer Farnes foraged predominantly in deeper offshore areas. Shags increased their foraging effort across years, most likely as a result of changes in prey abundance or availability, with both sub-colonies responding in a similar way to these annual fluctuations. These data suggest that spatial partitioning occurs in shags but may be dependent on environmental conditions.

Colony segregation in short-ranging seabirds

Colony-specific foraging strategies seem to be common in colonial central-place foragers (Robson et al. 2004, Page et al. 2006, Wakefield et al. 2013). Though the majority of studies documenting spatial segregation among colonies refer to species that travel hundreds of kilometres in a single trip (Grémillet et al. 2004, Gonzalez-Solis et al. 2007, Paiva et al. 2010, Wakefield et al. 2011), some evidence that short-ranging species also show similar segregation patterns among close colonies exists (Wanless & Harris 1993, Ainley et al. 2003, Ainley et al. 2004, Lescroel & Bost 2005, Masello et al. 2010, Corman et al. 2016, Wakefield et al. 2017, This Study).

Intra-specific segregation in foraging sites has been documented in other members of the *Phalacrocoracidae* (Wanless & Harris 1993, Sapoznikow & Quintana 2003). Yet there appears to be a general lack of spatial segregation between foraging areas of shags breeding around the UK coastline (Wakefield et al. 2017). However, the authors note that the colonies studied were small and sparsely distributed, with inter-colony distances beyond the maximum foraging range for the species. By examining foraging area segregation between two relatively large populations of shags nesting on separate islands in close proximity, I provide the first evidence that spatial segregation occurs among sub-colonies of shags. My results contrast with those found on the Scilly Isles (an archipelago in the Celtic Sea with inter-island distances similar to those at the Farnes): there, birds showed an almost complete overlap in foraging sites between islands (Evans et al. 2016). These high levels of overlap could be due to low population densities, insufficient to induce density-dependent intra-specific competition (Wakefield et al. 2017). However, individuals seemed to benefit from using social information and were frequently observed foraging in large rafts during chick rearing, so a lack of segregation in foraging areas could also be attributed to shags deriving a benefit from foraging socially at this site (Evans et al. 2016). This kind of rafting behaviour is not commonly observed around the Farnes—or elsewhere (Velando 2001)—until later in the season, after chicks have fledged (pers. obs.).

Segregation patterns between sub-colonies breeding on the Isle of May (S.E. Scotland) were similar to those documented on the Farne Islands. Foraging areas were partially segregated, notably in areas close to birds’ nesting sites; however, birds shared foraging areas in certain locations further from the colonies (Bogdanova et al. 2014). These findings suggest environmental context may be an important driver in shaping spatial resource partitioning in shags, as it is in other seabirds (Mott et al. 2016).

Annual variation in the extent of overlap between sub-colonies

Seabirds can respond to dynamic changes in the marine environment by adjusting their foraging behaviour and distributions to match changing resources (Pinaud et al. 2005, Ballance et al. 2006, Hamer et al. 2007, Pettex et al. 2012). Yet, only a few studies have considered how these annual variations affect foraging distributions of conspecifics from neighbouring colonies/sub-colonies (Ainley et al. 2004, Bogdanova et al. 2014, Dean et al. 2015, Corman et al. 2016). Most studies present overlap calculations within a single year or pool results from multiple years (Masello et al. 2010, Wakefield et al. 2013, Evans et al. 2016).

Bogdanova et al. (2014) documented annual variations in the foraging distributions of shags around the Isle of May, but found little annual variation across two years in spatial overlap between sub-colonies. Here, I found the size of the core foraging areas of shags and the degree of overlap among colonies varied between years. Similar annual changes have been documented in Adélie penguins with increased overlap among colonies in years where food availability appeared low (Ainley et al. 2004). In contrast, however, Mott et al. (2016) found spatial segregation was maintained from year to year in the foraging areas of lesser frigatebirds from two colonies, despite declines in prey availability. When resources are scarce, seabirds could either switch to more abundant prey (Suryan et al. 2000, Wanless et al. 2005) or increase their foraging effort (Hamer et al. 1991, Hamer & Hill 1993). They may do this by travelling further to locate prey (Monaghan et al. 1994, Hamer et al. 2007, Garthe et al. 2011) or by increasing the amount of time spent foraging within a restricted range (Angel et al. 2015).

Direct data on prey abundance could not be obtained for this study, but foraging range, food availability and productivity are linked in most seabird species (Cairns 1988, Croxall et al. 1999, Lewis et al. 2001, Davies et al. 2013, Daunt et al. 2014). Reduced prey availability generally results in longer foraging trip durations, greater ranges and an increase in the size of core foraging areas (Monaghan et al. 1994, Suryan et al. 2000, Hamer et al. 2007, Burke & Montevecchi 2009). Thus, in 2016, the longer foraging trips and larger foraging areas, alongside the shags' decreased productivity, is indicative of lower prey availability. In this study, I found that birds maintained sub-colony-specific foraging areas in years where foraging behaviours were consistent with favourable conditions, but when conditions appeared less favourable, these segregation patterns broke down.

Birds might show segregation under some conditions and not others due to changes in resource availability and/or resource patchiness (see Figure 1 in Warwick-Evans et al. (2016)). In situations where prey is abundant and evenly distributed, birds are likely to perform short-range trips close to their nesting sites; therefore, while individuals are not actively segregating, foraging areas are unlikely to overlap. Conversely, if there is only a single profitable patch, all birds are likely to use that patch irrespective of the distance of the area from their home colony (within their foraging capabilities), which would result in considerable overlap in their foraging areas. If multiple prey patches exist that are equally profitable, birds could benefit by utilising the patches closest to their colony in order to minimise energy expenditure and reduce intra-specific competition. This kind of density-dependent competition is known to drive the formation of colony-specific home ranges in Northern gannet colonies around the UK (Wakefield et al. 2013).

Segregation patterns could be strengthened by birds using a combination of memory and public information, i.e. individuals observing and following other individuals from the colony and while at sea (Wakefield et al. 2013). Islands within the Farnes archipelago are only 2 km at most from their nearest neighbour. Consequently, most birds are nesting virtually within sight of one another, meaning individuals could potentially exploit public information even before setting off on a foraging trip. Foraging-site fidelity has been documented on the Farne Islands (see Chapter 4); therefore, learned preferences (memory) are likely to be playing a role in driving the observed distribution patterns between sub-colonies (Riotte-Lambert et al. 2015).

In 2014 and 2015, my findings support Wakefield et al. (2013)'s density-dependent hinterland model with birds maintaining colony-specific foraging areas. In these years, productivity and trip parameters indicated food availability was good—or, at least, adequate—and colony segregation patterns were strong, with birds foraging closer to their respective colonies. In 2016, however, trips were longer and many birds from both study groups used the same foraging areas, particularly the coastal area in the NW of the islands. This suggests prey patches and/or availability were more limited in that year. The increased overlap in foraging areas coupled with the fact that breeding success was reduced at both sub-colonies indicates prey availability may have been a limiting factor. This situation could have been exacerbated due to individuals experiencing increased levels of competition within these patches.

Wakefield et al. (2013)'s study was performed on data from a single season within each colony. How segregation patterns between neighbouring gannet colonies could change under times of environmental stress is yet to be established. Additional work covering a range of environmental conditions over a longer timescale is required to further explore the circumstances favouring or impeding spatial segregation. In addition, tracking work was not logistically possible on the smaller islands located between my study sites in the Farnes archipelago (See Chapter 1), and it would be useful to expand this study to see if segregation patterns persist across even smaller spatial scales than those recorded here.

Annual differences in foraging behaviour

In 2016, birds from both study colonies increased the size of their foraging areas and increased foraging effort, i.e. they made more dives and spent longer on/near the seabed. No dietary data were collected in 2016, so it is unknown if the prey taken were more diverse that year. Foraging-range expansions associated with low prey availability have been recorded in many other seabird species (Hamer et al. 2007, Burke & Montevecchi 2009, Hennicke & Weimerskirch 2014). Conversely, in Australasian gannets, *Morus serrator*, colony segregation patterns remained strong during years of poor prey availability, with individuals increasing foraging effort without expanding their range (Angel et al. 2015). In this case, intensified intra-specific competition due to limited resources seemed to strengthen segregation between sites. These processes could be driven by interference competition, where birds are excluded from other foraging areas due to the presence of neighbouring conspecifics (as opposed to exploitation competition, where birds compete directly for the same resources in the same areas), and this may be heightened if nearby colonies are particularly large (Wakefield et al. 2013).

My results suggest shags breeding on the Farne Islands are less constrained to mutually exclusive foraging areas. There are no geographic/oceanographic boundaries that would restrict birds from one colony from extending their range and birds cannot and do not directly exclude conspecifics from areas in times of poor prey availability. The populations on each island may be small enough to accommodate additional foragers (Ainley et al. 2004, Wakefield et al. 2017), though my results suggest this may have detrimental effects on annual productivity.

Shag foraging behaviour is closely linked to benthic substrates (Wanless et al. 1998, Chapter 2); and so the location of potential prey patches should remain static between years. In this study, the areas of overlap between the two sub-colonies were primarily associated with shallow areas (10-30 m deep) of coarse/medium-grained sand (see Chapter 2). This is the preferred habitat of sandeels, *Ammodytes* spp. (Wright et al. 2000, Holland et al. 2005), which are important prey for shags, especially during chick rearing (Wanless et al. 1991). Sandeels burrow into benthic sediments and spend most of their time associated with these areas (Macer 1966). Hence, patches of coarse sandy substrates are likely to provide predictable foraging areas for shags and are potentially areas of high food abundance.

Annual changes in resource availability between patches may be evident from shifts in the foraging distributions of birds from each colony. In a year where breeding success was comparatively lower than the previous two years (i.e. 2016), birds from the Outer Farnes were using a coastal patch to the west of the islands that was primarily only used by birds from Inner Farne in previous years. The habitats associated with birds' core foraging areas throughout the study tended to be course sandy sediments which tended to be bordered by rocky substrates (see Chapter 2, Figure 2-2). As sandeel burrow into sediment to evade predators, if birds could drive fish towards rocky substrates prey may be less likely to evade capture and birds could potentially increase their foraging success. The shared use of one of these core sandy areas seems to account for much of the increase in overlap seen in 2016, if prey densities were lower in other patches in this year, then this could explain why many birds from both sub-colonies were foraging in the same patch. In a poor year (i.e. low productivity due to prey availability) I would expect the degree of overlap to increase further, as all birds are likely to increase the spread of their search areas to all potential prey patches. Productivity is generally higher for birds nesting on the Inner Farne islands (see Chapter 1). In 2016, this pattern was reversed, with birds at the Outer Farnes experiencing higher breeding success than the inner group. In 2016, Inner Farne birds' productivity was lower than the 20-year mean, whereas that of birds at the Outer Farnes remained slightly above average. Nevertheless, factors such as weather, predation, and parental quality and experience are also likely to affect productivity (Clutton-Brock 1988, Baird 1990, Aebischer 1993, Jones et al. 2008, Daunt et al. 2014) and could affect each island differently. For instance, on the Farne Islands, shags on the Outer Farnes seem to experience more predation pressure from large gulls due to the flatter topography of nesting sites (Wilson & Noble-Rollin 2008).

3.4.1 Conclusions

So far, few seabird foraging studies have examined how spatial distribution patterns between neighbouring colonies differ in response to environmental variation. Even fewer have examined how these patterns might change over time. I found shags breeding on the Farne Islands displayed flexibility in their foraging behaviour, with inter-annual variation in the degree of spatial segregation between sub-colonies in close proximity, which I attribute to changes in local environmental conditions. The use of data from multiple years to more accurately represent species' foraging ranges has previously been advocated (Bogdanova et al. 2014, Soanes et al. 2016) and I suggest the degree of segregation in other species is also likely to be affected by annual variations in prey availability and environmental conditions. Hence, where long-term data sets exist, this should be tested more widely.

Birds from different island groups appeared to be acting as separate functional units (or 'colonies') under certain (favourable) environmental conditions, but birds within the archipelago may all act as the same unit under different (less favourable) conditions. Therefore, the functional unit birds operate over may not only vary with scale (Wakefield et al. 2014) but can also be altered by environmental conditions. The scale of these functional units are likely to be linked to birds' foraging ranges (e.g. Frederiksen et al. 2004).

To conserve species and their habitats effectively, it is important to understand what constrains populations to specific areas, and the scales over which they occur. Comparison between and within populations may increase our understanding of the adaptive capabilities within a species (Tremblay & Cherel 2003). Finding out where, how and why differences in colony foraging distributions arise could help predict how species will respond to environmental or anthropogenic change. This information could also improve marine spatial management decisions (Thaxter et al. 2012, Jovani et al. 2016).

In this study I show that segregation can drive differences in foraging behaviour between sub-colonies, forcing birds to adapt their behaviour to match habitat availability, and that this could potentially have fitness consequences for birds restricted to certain breeding sites. Many seabirds, including shags, are site faithful and are unlikely to change their nesting areas after their first successful breeding attempt (Potts 1969, Aebischer 1995). These constraints could therefore have differential consequences between populations. Ultimately, this could result in certain colonies or even sub-colonies being more susceptible to change than others. Such findings are becoming increasingly evident (Bogdanova et al. 2014, Thaxter et al. 2015, Wakefield et al. 2017). The findings of this study reiterate this notion, highlighting the importance of long-term studies and site-specific considerations in relation to advising marine conservation management decisions.

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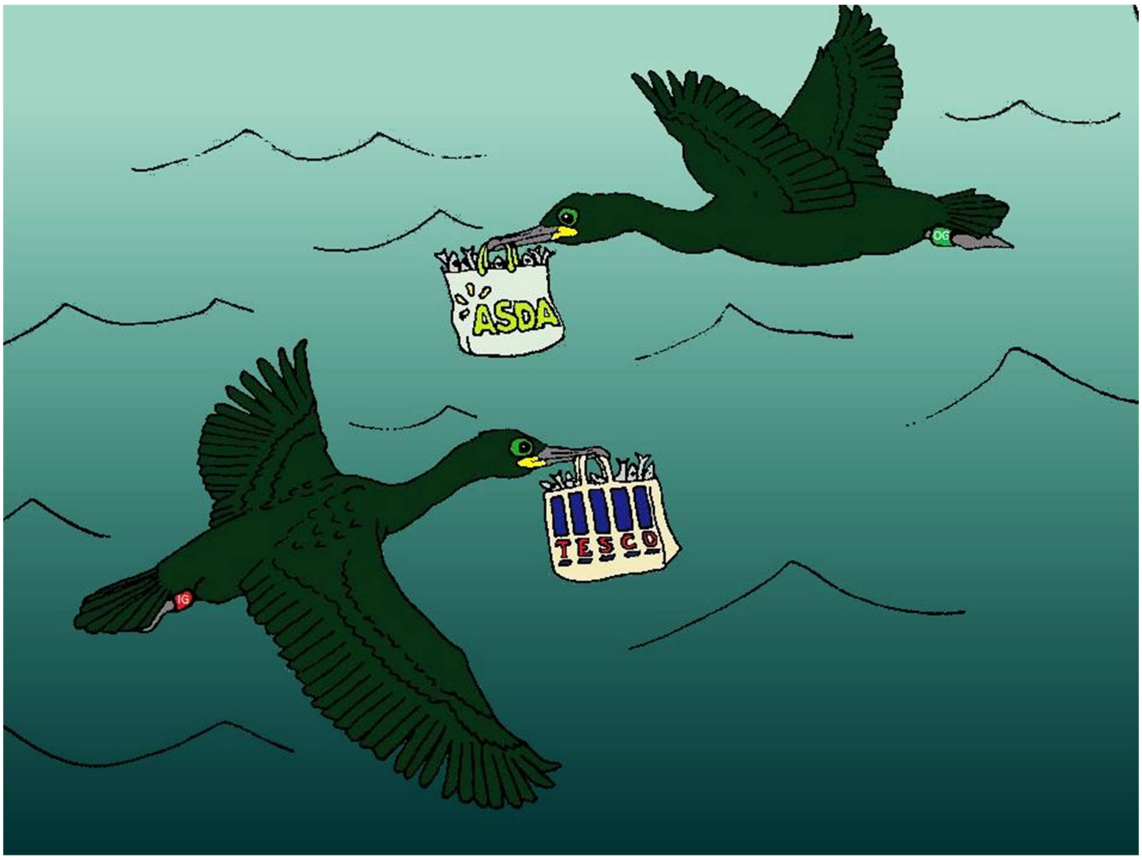
Chapter 4 - Individual foraging-site fidelity in European shags: incidence and implications



'Supermarket preferences' Illustration by Liz Morgan 2017 (from prize winning series of tweets for the third world seabird twitter conference)

Abstract

Consistency and flexibility in foraging behaviour play vital roles in species' responses to variable and changing environments. A growing body of work has revealed high levels of individual consistency in certain behaviours in a wide range of taxa. However, few studies have been able to link this inter-individual variation to fitness consequences in wild populations. Using combined GPS and dive data, I estimated consistency in the foraging behaviour of a short-ranging benthic predator, the European shag (*Phalacrocorax aristotelis*). I quantified individual-level spatial consistency alongside repeatability at the population level within and across three consecutive breeding seasons. Shags were highly repeatable in location-based foraging parameters (e.g. departure angle, mean foraging latitude and maximum dive depth), which was most likely driven by individual foraging-site fidelity (IFSF). Individuals varied in the levels of IFSF expressed both within and between seasons. Some birds were highly consistent in the locations they visited, foraging in similar areas over multiple breeding seasons, but others changed their foraging locations between trips. Inter-annual consistency was generally higher than within-season consistency, with most birds retaining similar levels of consistency from year to year. Females with higher levels of spatial consistency bred earlier and were in better condition than birds with lower consistency. This suggests that IFSF may provide fitness benefits, presumably through enhanced foraging success, although overall breeding success (number of chicks fledged) was not affected and no relationship was found between male foraging consistency and condition over the same time period.

4.1 Introduction

Understanding the degree of consistency and flexibility in individuals' behaviour is key to understanding population-level responses to environmental change. If individual niche widths are narrower than the population's niche as a whole, individuals may not be ecologically equivalent (Bolnick et al. 2003). Understanding the level of consistency in a population is an essential step towards assessing behavioural flexibility, i.e. the capacity to alter behaviour based on external factors. For instance, how dependent individuals are on specific locations may determine how susceptible or resilient a population is to the loss or alteration of those areas, and such information could be used to enhance predictive modelling scenarios and better inform conservation management strategies.

In a behavioural context, repeatability, measured by the ratio of the variance between and within individuals (Lessells & Boag 1987, Nakagawa & Schielzeth 2010), is the most common measure used to assess individual consistency (Hayes & Jenkins 1997, Bell et al. 2009). This method gives an indication of repeatability within a population. When repeatability is high, most individuals behave differently from each other in a consistent way. Low repeatability, however, could either indicate that all individuals are behaving in the same way as each other, or that individuals are acting differently each time they perform a behaviour (i.e. inconsistently). These estimates do not provide information about how each individual differs in their level of behavioural consistency in space or time (Réale & Dingemanse 2001).

Individual consistency in traits such as diet and foraging behaviour has been documented in a wide range of species (Bolnick et al. 2003, Araujo et al. 2011), including air-breathing marine vertebrates such as seabirds (reviewed by Ceia & Ramos 2015). For example, yellow-eyed penguins *Megadyptes antipodes* show consistency in their foraging areas and in the routes used to travel to and from them (Mattern et al. 2007). Crozet shags *Phalacrocorax melanogenis* also display consistency in the timing of foraging bouts and dive depths (Tremblay & Cherel 2005). However, individuals may also vary in the level of consistency and repeatability they express (e.g. Kato et al. 2000, Potier et al. 2015) and only recently have studies started to explore the variation within or between populations in levels of individual consistency in spatial habitat usage (Baylis et al. 2012, Arthur et al. 2015, Wakefield et al. 2015) or foraging behaviour (Harris et al. 2014, Potier et al. 2015, Wakefield et al. 2015).

In addition, while short-term consistency in foraging behaviour within populations has been well documented, longer-term consistency is less well understood; some studies recorded little or no consistency between years (Ceia et al. 2012, Granadeiro et al. 2014, Harris et al. 2014) whereas Woo et al. (2008) found dive depths of Brünnich's guillemots *Uria lomvia* were consistent over successive years. Individual repeatability in other behavioural traits, such as boldness, also seems to be conserved between years and has been linked with consistent foraging traits (Patrick & Weimerskirch 2014). Consistency should benefit fitness in order to be maintained within a population (Marra et al. 1998, Vander Zanden et al. 2014) and there is some evidence to suggest consistency may increase individual fitness over decadal timescales (Bradshaw et al. 2004, Patrick & Weimerskirch 2014). However, over short timescales, links between consistency and individual condition seem weak (Wakefield et al. 2015) and overall fitness consequences are far from clear (Woo et al. 2008, Ceia et al. 2012, Patrick et al. 2014).

One common form of consistency in foraging behaviour is individual foraging-site fidelity (IFSF), where an individual repeatedly uses the same foraging location. Site familiarity can increase an individual's fitness as a result of previous experience of the location of resources and threats (Piper 2011). IFSF has been frequently recorded in marine birds (Hamer et al. 2001, Weimerskirch 2007, Woo et al. 2008, Montevecchi et al. 2009, Schwemmer & Garthe 2011, Baylis et al. 2015) and other colonial central-place foragers such as pinnipeds (Bradshaw et al.

2004, Call et al. 2008, Baylis et al. 2012, Arthur et al. 2015), bats (Kerth et al. 2001, Hillen et al. 2009) and ants (Beverly et al. 2009). IFSF could arise as a result of fitness advantages associated with increased foraging efficacy, achieved by learning the location of productive foraging sites (Hamer et al. 2001, Weimerskirch 2007), or as a mechanism to limit intra-specific competition (Wilson & Yoshimura 1994). For instance, Patrick and Weimerskirch (2017) demonstrated that IFSF was linked to breeding success in black-browed albatrosses *Thalassarche melanophris* both within a single breeding season and across years. In environments where prey patches are predictable, IFSF could be apparent if individuals employ 'win-stay, lose-shift' foraging tactics (Switzer 1993). The processes generating and maintaining IFSF are, however, not well understood (Piper 2011, Votier et al. In Press) and the extent of IFSF is likely to depend upon the spatial and temporal scales examined (Wakefield et al. 2015).

Previous studies of IFSF have primarily focused on mid- to long-ranging species, which often spend days away from their breeding sites, travelling hundreds to thousands of kilometres in order to provide food for their offspring. For these species, knowing where profitable foraging areas are likely to occur could greatly reduce the energetic costs of locating prey and increase foraging trip success. The energetic consequences of foraging decisions might not be as costly for short-ranging species, so they may be more likely to change foraging locations even within a single trip. However, recent research is beginning to reveal that repeatability may also occur in short-range foragers (i.e. range < 50 km) (Harris et al. 2014, Potier et al. 2015).

Here, I use tracking data from a short-ranging species, the European shag *P. aristotelis* (hereafter shag), to investigate IFSF and repeatability of foraging behaviour both within and between breeding seasons. Shags are coastal foragers and have a particularly short foraging range compared to most seabird species: their median foraging range is 3.4km, IQR 1.6-7.5 (Wakefield et al. 2017)). During the breeding season, shags make multiple (on average, 3 to 4) foraging trips per day (Wanless et al. 1993). This makes them a useful model for studying repeatability, as low-cost telemetry devices can be used to gather data for multiple trips from the same individual.

Their short-ranging nature could enable greater flexibility in foraging locations; birds have been recorded foraging in two different habitats (and, presumably, locations) within a single trip (Watanuki et al. 2007, 2008). At certain sites, birds forage virtually within sight of their nests; therefore, they could potentially assess patch quality even before leaving the colony. However, as a benthic diving predator, it may be difficult for birds to assess prey availability before initiating a dive-bout other than through prior experience. Birds could increase foraging efficiency by learning from previous foraging successes (Irons 1998, Grémillet et al. 1999). Improved foraging success has been linked to age in shags (Daunt et al. 2007b). Observational studies have documented shags using landmarks to keep their surface position whilst foraging, presumably allowing them to maintain sub-surface locations (Citrynell & Lea 1996). Repeatability has been documented in the closely related great cormorant, *P. carbo*, where certain individuals appear highly consistent in their foraging behaviour, while others were more plastic (Potier et al. 2015). Shags are known to exhibit strong site fidelity with regard to breeding (Aebischer et al. 1995) and wintering locations (Grist et al. 2014), and they show repeatable traits in winter foraging activities (Daunt et al. 2014). Therefore, they may show similar repeatability in their foraging behaviour during the breeding season. They have particularly high foraging costs and a restricted foraging range because of poor plumage insulation (Grémillet et al. 1998). They also exhibit state-dependent differences in survival, phenology and breeding success, which can be linked to foraging effort (Potts et al. 1980, Aebischer 1993, Harris et al. 1994, Daunt et al. 1999, Daunt et al. 2006). Generally, birds that breed earlier tend to be older, higher quality individuals that spend less time foraging during the late winter/pre-breeding period (Daunt et al. 2006).

The overall aim of this chapter is to explore the causes and consequences of consistency in shag foraging behaviour across varying timescales. The following hypotheses are tested: (i) Shags show IFSF within a breeding season; (ii) IFSF could be responisble for individual repeatability in variables such as foraging range, trip duration and dive depths; (iii) Birds retain similar levels of repeatability and IFSF over multiple breeding seasons; and (iv) IFSF is associated with increased fitness (namely adult body condition, higher breeding success and earlier hatching dates).

4.2 Methods

4.2.1 Study site and data collection

Fieldwork was conducted on the Farne Islands, UK (55°36'57.30"N, 1°39'20.19"W) across three breeding seasons (2014 to 2016). The study site consists of 15-28 islands (depending on tidal state) in the North Sea stretching between 2 km and 7 km from the north-east coast of the UK (see figure 1-2, Chapter 1). Catching efforts were focused on three of the main islands within the archipelago, one site on the Inner Group (c. 2 km from the shore) and two sites within the Outer Group (c. 5 km from the shore) of islands. Birds were caught at the nest, using a noose, crook or by hand, during the early chick-rearing period (May to July).

GPS loggers (IgotU GT-120, Mobile Action Technology, Taipei, Taiwan) and time-depth recorders (TDRs: G5, CEFAS Technology, Lowestoft, UK) were combined into a single device using shrink wrap, cable ties and Tesa® tape (Milton Keynes, UK), then taped to the underside of the central tail feathers. Loggers weighed 34 g, < 2% of the average body weight of European shags

(Robinson 2005), which is within the recommended 3% guideline (Phillips et al. 2003). Loggers were programmed to collect fixes every minute, with TDRs set to take regular readings throughout the day (once per hour in 2014 and every 20 minutes in 2015 and 2016) and at maximum resolution (12 Hz in 2014 and 2 Hz in 2015 and 2016) when submerged below 1.5 m. Birds were re-captured 4 to 5 days after initial deployment, devices were carefully removed and biometrics (maximum chord wing length to the nearest millimetre using a slotted rule, weight to the nearest gram, bill depth to the nearest millimetre using digital callipers) were collected from adults. Birds were sexed based on vocalisations and bill measurements (Baker 1993).

4.2.2 Telemetry data filtering

Data were processed as described in Chapter 2. The following variables were calculated for each foraging trip:

(1) Trip duration in minutes (taken as the time a bird crossed the 200m threshold until the time it returned to within 200m of the colony);

(2) Total distance travelled (km, as above);

(3) Departure angle in degrees (calculated by averaging the first ten bearings that were > 50 m from the colony);

(4) Return angle to the colony in degrees (calculated by averaging the last ten bearings of a trip);

(5) Longitude and latitude (UTM projection) at the terminal point of a trip, i.e. the maximum distance from the colony;

(6) Bearing from the terminal point to the colony.

(7) Maximum range (the greatest distance reached from the colony in km);

For trips where TDR and GPS data could be matched, I also estimated:

(8) Number of dives per trip;

(9) Mean dive depth per trip (calculated from the greatest depth attained during each dive);

(10) The location of all foraging dives, calculating the mean foraging location per trip (latitude and longitude);

(11) Total time spent at the bottom phase of each dive per trip (indicative of time spent probing for or pursuing prey).

(12) Proportion of time spent resting per trip (calculated as the percentage of 60-second intervals with speed < 2m s-1 and depth <5m. This included both pauses at the sea surface between dives and occasions when birds rested on land away from the colony during a trip)

(13) Proportion of time spent foraging per trip (calculated as the percentage of 60-second intervals with depth ≥ 5m);

On a small number of occasions, TDRs malfunctioned resulting in no dive depths being recorded for all or part of a trip. As shags are unlikely to spend time resting on water when they are not foraging (Daunt et al. 2007a), on these occasions I assumed that periods of repeated slow speeds ($< 2\text{m s}^{-1}$) at distance >200m from the colony were associated with diving activity, as was the case for all trips with complete GPS and TDR data. These trips with partial data were included in the analysis of trip durations, distances and utilisation distributions (UD), but in no other analysis.

Birds roosted on land away from the colony overnight on a few occasions (n = 8) and these were removed from the trip analyses. One nest failed during the tracking period in 2015, probably due to predation of the brood, as the exact date of predation was unknown all this bird's data were also removed from analyses.

4.2.3 Individual foraging-site fidelity (IFSF)

To explore spatial consistency in individual foraging behaviour, I utilised functions within the R package adehabitat v.0.4.13 (Calenge 2006). In order to avoid pseudoreplication of the same individuals across multiple years, these analyses were performed on each year separately. Kernel density estimates (KD) were calculated for each bird using all locations classified as foraging activity.

4.2.4 Within-season IFSF

Within-individual spatial consistency (or IFSF) between individual KD's were quantified using Bhattacharyya's affinity (BA) (Fieberg & Kochanny 2005). BA gives a measure of spatial similarity, with scores bounded between 0 (no overlap, i.e. no spatial consistency) and 1 (complete overlap, i.e. perfect spatial consistency). With this method, the choice of smoothing parameter (h) can greatly influence the results obtained (Worton 1989). Quantitative sensitivity analyses showed this to be the case regarding shag foraging areas (Appendix C.2). In order to choose a biologically relevant h value, minimum convex polygons (MCPs) were calculated for each bird to obtain the mean size of the area used by birds within a single trip. The radius of a circle with the area of the mean MCP was then calculated and used as the smoothing parameter in kernel estimations. KD estimates were generated using bivariate normal kernels with a fixed bandwidth (h) of 340 m over a 1 km × 1 km grid.

To determine levels of within-season repeatability, mean overlap scores were calculated using pairwise combinations of the 95% KD between individuals' trips. The mean number of trips recorded per bird was 8 trips (which should equate to two or three days foraging effort). Therefore, to standardize sample size for this analysis only the first eight foraging trips made by a bird in each year (for birds who made ≥ 8 trips). In order to test whether levels of within-individual spatial consistency were greater than expected population level consistency, I used a randomisation procedure to generate a null distribution (as per Wakefield et al. 2015). Bird identity was randomly re-assigned to trips in each year. Mean overlap scores were then calculated for each individual and the mean population overlap scores extracted. This was repeated for 100 permutations in each year.

4.2.5 Individual repeatability in the population

Repeatability (r) values for each trip parameter and their associated standard error and p-values were calculated based on the ratio of between-group and within-group variance components from a GLMM structure using the R package "rptR" v.0.6.405 (Nakagawa & Schielzeth 2010). Three birds where only a single trip was recorded were included in these analyses. As bearings are circular measures, bounded by 0 and 360, I used a circular ANOVA (R package "circular" v.0.4-7 (Agostinelli & Lund 2013)) and calculated repeatability using Lessells and Boag (1987)). Standard errors for these values were calculated using equations from Becker (1984). P-values are not available using this latter method; therefore, they are not reported for bearings. Repeatability scores were classified as highly repeatable ($r > 0.50$), moderately repeatable ($0.25 < r < 0.50$) and poorly repeatable ($r < 0.25$) (Potier et al. 2015).

4.2.6 Variation in individual repeatability between seasons, sexes and sites.

To test for overall consistency between years at the population level, I calculated the difference in Z-transformed repeatability estimates (McGraw & Wong 1996). This method uses the difference in r values—i.e. population-level repeatability—and the associated standard errors to assess whether repeatability differs significantly between groups; If 95% confidence intervals do not overlap zero, the difference is significant at the 0.05 level (English et al. 2010). This method was also used to test for differences in r values between sexes and sub-colonies.

4.2.7 Persistence of IFSF between seasons

To test whether levels of within-season spatial consistency are retained across years, paired t-tests were carried out using within-season overlap scores for birds with two or more years' data. For individuals tracked over two or more years, I also pooled data from the first eight trips that a bird made in each year and calculated annual or between-season overlap scores using all pairwise combinations of years. Paired t-tests were then used to see if annual levels of overlap were retained between consecutive and non-consecutive years (2014/2015, 2015/2016, and 2014/2016). Birds could have similar levels of repeatability between breeding seasons, but may be switching the locations they use each year. To test for this, I compared the within-season overlap scores and between-season scores of repeat birds.

4.2.8 Fitness consequences of IFSF

Mixed-effects models were used to investigate whether individuals with strong IFSF (i.e. high BA scores) could have a fitness advantage over less consistent birds. Three models were constructed to examine the effect of repeatability on adult condition and breeding success, using the following response variables:

1) Body condition index. This was calculated using the residuals from an ordinary least squares (OLS) linear regression of adult body mass against wing length. Though condition indices have certain limitations (Green 2001), the correlation between mass and wing length was high for both males (Pearson's corr = 0.43, p = 0.01) and females (Pearson's corr = 0.48, p = 0.01). Confounding effects of sex on mass/structural size (Ormerod & Tyler 1990) were accounted for by calculating and analysing values for each sex separately.

2) Timing of breeding (hatching dates). Foraging ability has been linked to breeding phenology in shags (Daunt et al. 2006). Young, inexperienced birds lay significantly later in the season than older, more experienced birds (Potts et al. 1980, Aebischer 1993). Younger birds are also known to have lower foraging efficiency irrespective of the time of season (Daunt et al. 2007a). Assuming consistency (IFSF) during chick-rearing is indicative of foraging consistency during the pre-laying period, then advanced breeding phenology could signify bird quality/age or experience. To account for differences in environmental conditions between years, hatching dates were standardised by calculating the time difference from the earliest recorded hatching date each year.

3) Productivity, i.e. the number of chicks fledged from each nest. This was used as an indicator of short-term reproductive success. Individual nest productivity data are collected annually by National Trust wardens.

Generalised linear mixed models (GLMMs) were constructed within the R package lme4 v.1.1-7 (Bates et al. 2015). All fixed effects were standardised using the 'arm' package v.1.7-07 (Gelman & Su 2014) to ensure they were on a common scale and to increase the interpretability of parameter estimates (Schielzeth 2010). Model simplification and selection were performed, using a multi-model inference approach based on the methods and recommendations of (Grueber et al. 2011), using the 'MuMIn' package v.1.13.4 (Barton 2015). A set of candidate models were identified for each response variable, with all possible subsets of the variables in the global model considered. Support for different candidate models was assessed using Akaike's information criterion adjusted for small sample size (AICc) and Akaike weights. Model sets representing the 95% confidence intervals (C.I.) of the summed weights were selected and parameter estimates and the relative importance (RI) of each parameter were averaged (Burnham & Anderson 2002). A single best model was identified when summed model weight >95% C.I., P values and test statistics were then extracted from the best model results using the package "LMERConvenienceFunctions" (Tremblay et al. 2015).

All global models included year and repeatability (individual BA score) as fixed effects, with bird identity as a random effect to account for pseudoreplication of repeat individuals in multiple years. In some cases, both members of a pair were tagged within the same season. To account for the non-independence in nest/chick data, sexes were analysed separately. Models, including hatching-date data, were performed on a subset of data where exact hatching dates were known (n = 13). Body condition models were carried out on all data; therefore, sub-colony was also added as a fixed factor and models were analysed using a Gaussian distribution. Productivity models were analysed with a Poisson distribution and hatching date was also included as a fixed factor in this model.

4.3 Results

GPS-based foraging trip data were obtained from 70 birds (52 unique individuals; 29 males and 23 females) over the three-year study. Combined TDR and GPS data were recorded for fewer birds; therefore, parameters including dive data represent 66 birds (51 unique individuals; 28 males and 23 females). Multiple foraging trips were recorded for most birds, mean = 8 trips per bird (range: 1-21). Fourteen individuals were successfully tracked over two or more breeding seasons. Tags had no discernible effects on adult body condition, behaviour at the nest or reproductive success (see Chapter 2 for details). The productivity of shags on the islands was 1.76, 1.67, and 1.07 chicks per nest in 2014, 2015 and 2016, respectively. Year had a significant effect on breeding success at the Inner Farne sub-colony ($F_{,3}$=156, p<0.001) with productivity significantly lower in 2016 (1.5±1.1 SD chicks per nest, Tukey test; 2014-2016 z=-2.5, p=0.04, 2015-2016 z=-2.3, p=0.05) than other years (mean 2.0±0.9 SD chicks per nest) (see Chapter 2 for details).

4.3.1 Individual foraging-site fidelity

4.3.1.1 Within a breeding season

Shags showed IFSF within a single breeding season. Mean within-season foraging overlap scores greatly exceeded those expected by chance (Table 4-1). The level of spatial repeatability expressed within a season varied between individuals but was similar across years (Table 4-1). Individual BA scores ranged from 0.06 to 0.75, with a mean score of 0.32 (SD ± 0.18). Birds with repeatability scores above the 75th percentile were classified as having high IFSF and birds with scores below the 25th percentile as having low IFSF. Individuals with high IFSF (n = 15) foraged in a small number of different areas across successive trips (Figure 4-1a), whereas individuals with comparatively low IFSF (n = 13) used multiple different locations from trip to trip. Nevertheless, there was still a degree of overlap between certain trips (Figure 4-1b and Appendix C.1).

Table 4-1. Spatial consistency estimates (BA scores) within a breeding season. Mean values for birds with eight or more foraging trips were calculated from mean overlap scores of the first 8 trips made by individuals in each year. Null estimates from the randomisation procedure are shown for comparison.

Year	**n individuals**	**Mean within season overlap (range)**	**Null distribution expected overlap (range)**
2014	26	0.330 (0.113-0.742)	0.016 (0.013-0.020)
2015	20	0.326 (0.093-0.751)	0.016 (0.012-0.020)
2016	12	0.301 (0.060-0.687)	0.007 (0.005-0.009)

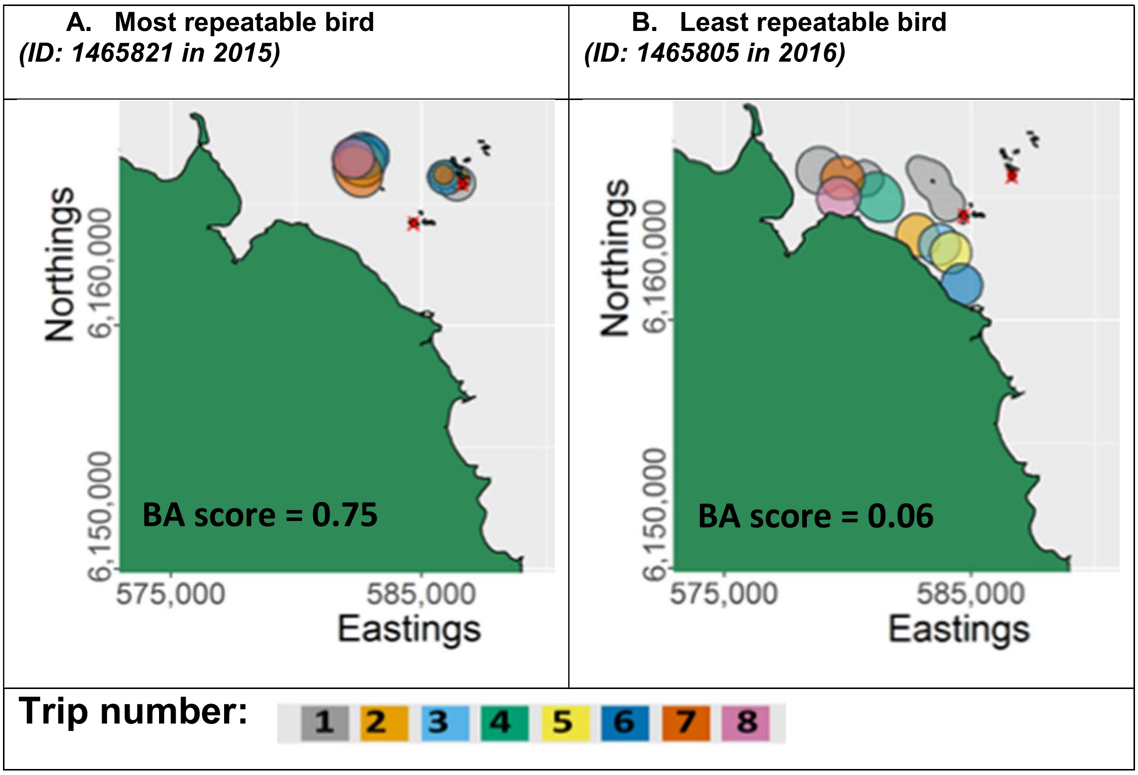


Figure 4-1. Foraging areas used in successive trips by A. the most repeatable bird in the dataset and B. the least repeatable bird. Colours represent 95% kernel of active foraging areas for each trip.

Table 4-2. Repeatability of foraging-trip parameters across all three years. Repeatability values (r) are shown along with 95% confidence intervals for each parameter. P-values were not available for parameters involving bearings.

Trip parameter	r	(95% CI)	P
Mean foraging longitude	0.665	(0.559-0.749)	<0.01*
Mean max dive depth (m)	0.639	(0.522-0.726)	<0.01*
Bearing to mean foraging location	0.595	(0.494-0.696)	N/A
Departure angle	0.563	(0.460-0.667)	N/A
Proportion of time resting (%)	0.554	(0.438-0.643)	<0.01*
Mean foraging latitude	0.515	(0.403-0.611)	<0.01*
Max distance from colony (km)	0.448	(0.331-0.544)	<0.01*
Total distance (km)	0.430	(0.311-0.526)	<0.01*
Proportion of time foraging (%)	0.369	(0.253-0.470)	<0.01*
Total time at seabed (seconds)	0.333	(0.225-0.435)	<0.01*
Total duration (minutes)	0.304	(0.197-0.402)	<0.01*

4.3.2 Individual repeatability

Individual repeatability scores for latitude and longitude were high-moderate at the terminal point of the trip (latitude: r = 0.51 ± 0.07, p < 0.01; longitude: r = 0.64 ± 0.05, p < 0.01) and at mean foraging (dive) locations (latitude: r = 0.52 ± 0.05, p < 0.01; longitude: r = 0.67 ± 0.05, p < 0.01) (Table 4-2). Birds also expressed a high level of repeatability in departure angle and bearing from the terminal point of the trip to the colony, indicative of high IFSF. Birds also had high repeatability in dive depth and were moderately repeatable in the time spent resting per trip, but were less consistent in the time spent in foraging behaviour per trip. Birds were least repeatable in foraging-trip duration, time spent at the sea bed and total trip distance, although these metrics were still significantly more repeatable than expected by chance (Table 4-2).

4.3.2.1 Consistency across seasons

Levels of repeatability in locational parameters are retained between seasons

Individual repeatability at the population level was broadly similar between years (Figure 4-2), sexes, and sub-colonies. There was no significant change in any of the locational parameters, i.e. mean foraging longitude, mean foraging latitude, bearing to mean foraging location, departure angle, mean maximum dive depth (m), maximum distance from colony (km) or total distance travelled (km). However, activity budgets did change from year to year. Birds spent more time foraging and less time resting in 2015 and 2016 compared to 2014, with greater repeatability in these parameters in 2016 (foraging: r = 0.70, $p < 0.001$; resting: r = 0.81, $p \leq 0.001$) compared to 2015 (foraging: r = 0.35, $p < 0.001$; resting: r = 0.53, $p \leq 0.001$). Birds also spent consistently longer at the bottom phase of dives, i.e. at the seabed, in 2016 (time = 34.2 ± 1.6 mins, r = 0.55, $p < 0.001$) compared to 2014 (time = 19.5 ± 0.57 mins, r = 0.20, $p < 0.001$) (Table 4-3).

No significant differences were found between sexes or sub-colonies in any of the trip parameters tested. Overall, birds were consistent in the locations they used but showed plasticity in the time they allocated to foraging activities.

Retention of IFSF across consecutive breeding seasons

IFSF was retained across years in the majority of birds, with some birds showing much higher IFSF than others (Figure 4-3, Table 4-4). Most birds tracked in successive years showed similar levels of IFSF within and among years (Figures 4-4 and 4-5, Appendix C). There was no significant difference between within-season overlap scores for 2014 to 2015 (paired t-test; t_9 = -0.39, p = 0.71), 2015 to 2016 (t_3 = 0.21, p = 0.85) or 2014 to 2016 (t_4 = -1.27, p = 0.27).

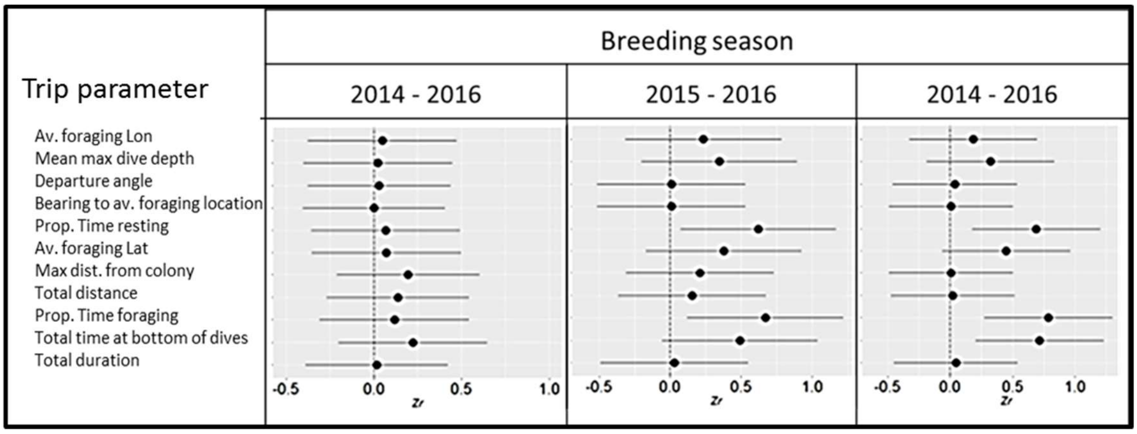
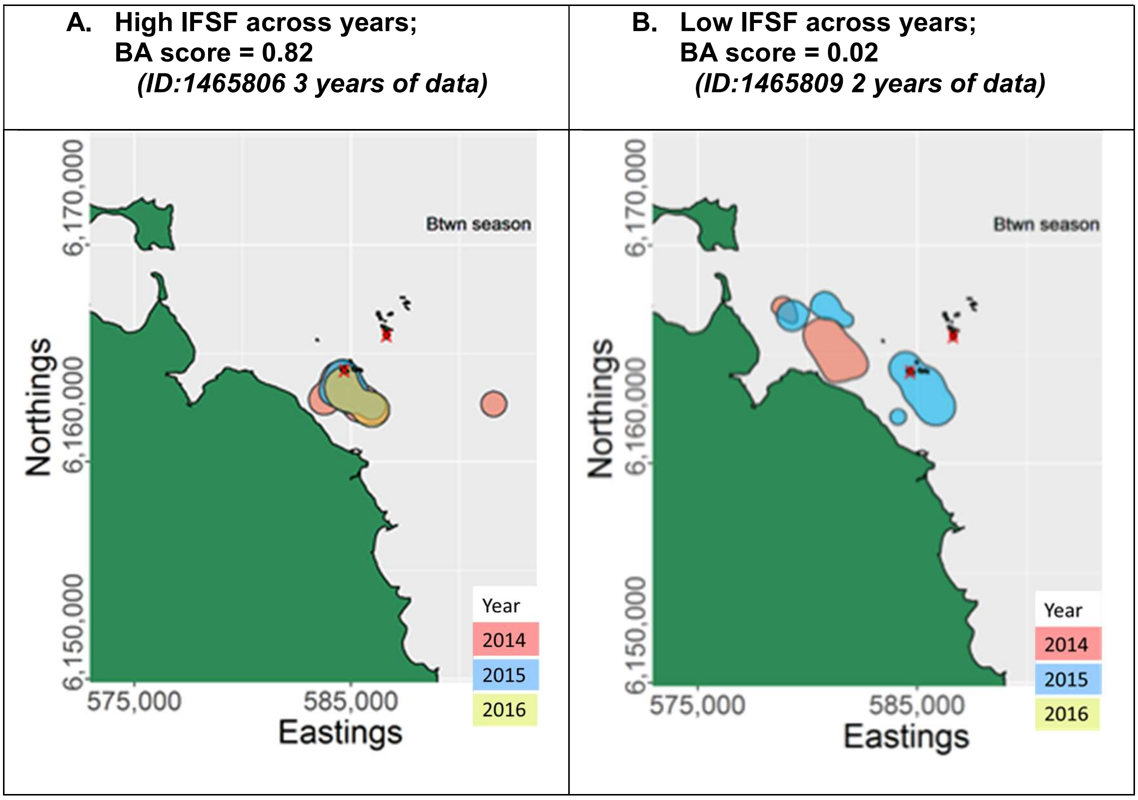


Figure 4-2. **Differences between z-transformed repeatability estimates and their confidence intervals for each parameter across breeding seasons. Values that do not cross zero are significant at the p = 0.05 level.**

Table 4-3. Differences in repeatability of trip parameters across years. Mean values (± standard errors) for each parameter in each year are shown alongside repeatability estimates (r).

	Proportion of trip spent foraging		Proportion of trip spent resting		Time at sea bed (mins)	
Year	**Mean (±SE)**	**r (C.I.)**	**Mean (±SE)**	**r (C.I.)**	**Mean (±SE)**	**r (C.I.)**
2014	0.43 (±0.01)	0.31 (0.16-0.44)	0.41 (±0.01)	0.52 (0.36-0.65)	19.46 (±0.57)	0.20 (0.08-0.31)
2015	0.45 (±0.01)	0.35 (0.16-0.50)	0.38 (±0.01)	0.53 (0.34-0.67)	19.71 (±0.63)	0.28 (0.13-0.44)
2016	0.37 (±0.02)	0.70 (0.43-0.83)	0.51 (±0.01)	0.81 (0.60-0.90)	34.25 (±1.61)	0.55 (0.29-0.73)



A. High IFSF across years; BA score = 0.82 ***(ID:1465806 3 years of data)***

B. Low IFSF across years; BA score = 0.02 ***(ID:1465809 2 years of data)***

Figure 4-3. **Foraging areas used in successive breeding seasons by an individual with (A) high and (B) low IFSF across years. Colours represent 95% kernel of active foraging areas for each year. BA score is the mean Bhattacharyya's affinity (see Methods for further explanation).**

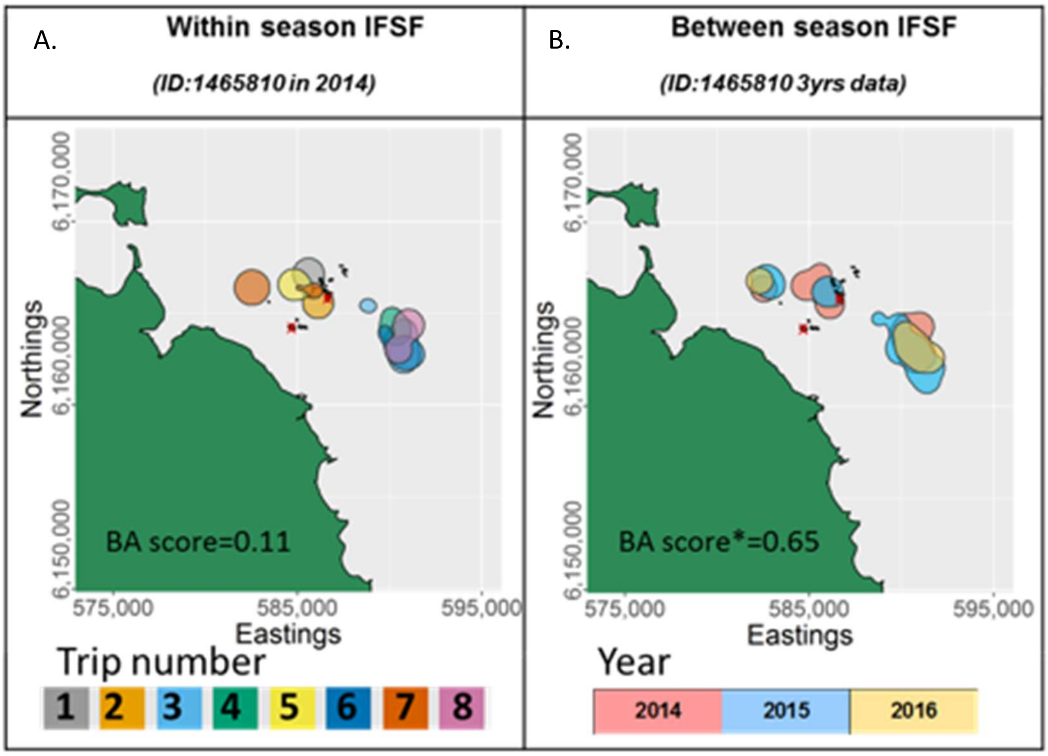


Figure 4-4. Example of IFSF for the same individual both within and between breeding seasons. A. shows low repeatability within a single season, while B. shows high repeatability between seasons. Colours represent 95% kernel of active foraging areas for each trip or year, respectively. * indicates the mean BA across three consecutive years.

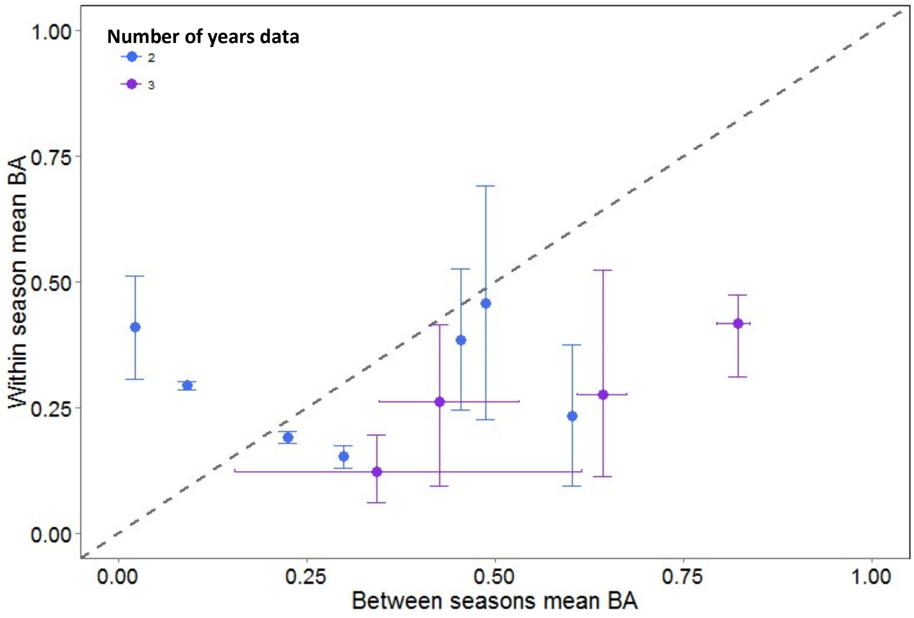


Figure 4-5. The relationship between an individual's spatial repeatability score (mean BA) within a single breeding season and between breeding seasons. The dashed line indicates a 1:1 relationship. X-axis error bars show the range of within-season BA scores. Y-axis error bars show the range between years. BA is Bhattacharyya's affinity (see Methods for explanation)

Table 4-4. Levels of spatial consistency of individual birds between different breeding seasons A.) shows BA overlap score between pairs of years for each repeat individual. B.) T-test statistics for birds with three years of data tests show differences between consecutive and non-consecutive pairs of years. BA is Bhattacharyya's affinity (see Methods for explanation).

A.)	**Overlap between pairs of years**			
Bird ID	**2014-2015**	**2015-2016**	**2014-2016**	**3-year mean**
1465680	0.57	0.41	0.37	0.45
1465805	0.62	0.17	0.27	0.35
1465806	0.83	0.82	0.80	0.82
1465810	0.61	0.67	0.68	0.65
1407272	0.09	-	-	
1465802	-	-	0.49	
1465807	0.61	-	-	
1465808	0.32	-	-	
1465809	0.01	-	-	
1465813	0.47	-	-	
1465814	0.24	-	-	

B.) t-test results	**Years**	**Test statistics**	**P value**
	2014-2015 to 2015-2016	$t_3 = 1.2$	p = 0.32
	2015-2016 to 2014-2016	$t_3 = -0.25$	p = 0.85
	2014-2015 to 2014-2016	$t_3 = 1.2$	p = 0.32

Repeatability did not differ significantly between seasons and levels of repeatability were similar between consecutive and non-consecutive pairs of years (Table 4-4).

Most birds expressed lower levels of IFSF within seasons than between seasons (Figure 4-5); i.e. they were using multiple foraging areas within a season but were reusing the same areas in subsequent years (Figure 4-4, Appendix C.1). The few birds with high within-season and low between-season scores seemed to be faithful to different sites each year (Appendix C.1).

4.3.3 Fitness consequences

The level of individual IFSF expressed within a season was linked to female condition (Figure 4-6, Tables 4-5 and 4-6). IFSF (within-season BA score) was the only variable contained in the top model set for hatching date (Table 4-5), showing a significant negative relationship between hatching date and consistency in females ($F_{1,12} = 8.35$, conservative p value = 0.01). BA is measured on a 0-1 scale; therefore, a 0.1 increase in repeatability score would equate to chicks hatching 2.8 days earlier (mean, 95% C.I.: 0.6 to 4.6 days). This relationship was reversed in males with a slight positive trend, however, the relationship was not significant.

The repeatability score was positively associated with female body condition index; i.e. females in better condition showed higher levels of IFSF (Figure 4-6). No significant trends were found between IFSF and condition measures for males (Figure 4-6) but males from the outer group of islands were generally in poorer condition than males from the inner group (z = 2.14, p = 0.03). The overall number of chicks fledged was not significantly associated with the IFSF score for either sex (Table 4-5). Although repeatability scores were retained in the top 95% of models for females (Table 4-8), its relative importance was low (16%) and its average effect was not significant (p = 0.46). For both sexes, hatching date was found to be a more important factor in determining fledging success, as it was retained in the best candidate models (Table 4-7).

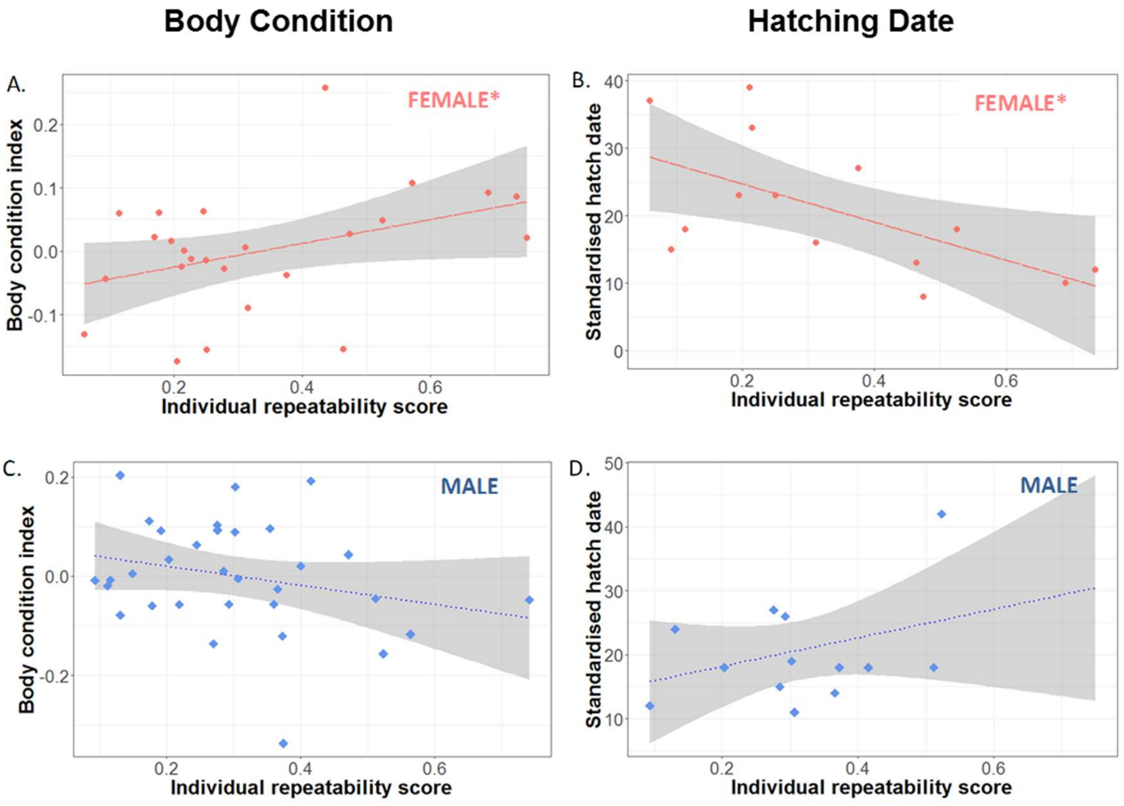


Figure 4-6. Relationship between repeatability (IFSF) score and (A, C) adult body condition (A, Females; C, Males), and (B, D) hatching date (B, Females; D, Males). Lines represent linear regression trends. Significant relationships are marked with an asterisk.

Table 4-5. Model selection results for each sex (A, Females; B, Males). Candidate models were included if the summed AICc weights > 95%.

A.) Females

Response variable (n individuals)	**Rank**	**Best model(s)**	**Df**	**logLik**	**AICc**	**ΔAICc**	**Weight**
Number of chicks fledged ***(n = 13)***	1	(Null)	2	-20.31	45.70	0	0.59
	2	Hatch Date	3	-19.5	47.39	1.69	0.25
	3	Repeatability	3	-19.96	48.33	2.63	0.16
Adult body condition ***(n = 25)***	1	Repeatability	4	25.87	-41.73	0	0.38
	2	(Null)	3	23.81	-40.49	1.25	0.2
	3	Repeatability + Year	5	26.67	-40.17	1.56	0.17
	4	Sub-colony + Repeatability	5	26.2	-39.23	2.5	0.11
	5	Sub-colony	4	24.2	-38.41	3.33	0.07
	6	Year	4	24.15	-38.3	3.44	0.07
Hatching date ***(n = 13)***	1	Repeatability	4	-48.21	108.86	0	0.73
	2	(Null)	3	-51.28	110.95	2.09	0.26

B.) Males

Response variable (n individuals)	**Rank**	**Best model(s)** **(sum weights > 95%)**	**df**	**logLik**	**AICc**	**ΔAICc**	**Weight**
Number of chicks fledged ***(n=12)***	1	(Null)	2	-20.17	45.43	0	0.83
	2	Hatching date	3	-20.13	48.66	3.23	0.17
Adult body condition ***(n = 32)***	1	Sub-colony	4	27.88	-46.28	0	0.34
	2	Sub-colony + Year	5	28.51	-44.72	1.57	0.16
	3	(Null)	3	25.54	-44.23	2.06	0.12
	4	Sub-colony + Repeatability	5	28.22	-44.13	2.16	0.12
	5	Year	4	26.53	-43.57	2.71	0.09
	6	Repeatability + Year	5	27.94	-43.57	2.71	0.09
	7	Repeatability + Year	4	26.46	-43.44	2.84	0.08
Hatching date ***(n = 12)***	1	(Null)	3	-48.62	105.64	0	0.72
	2	Repeatability	4	-47.61	107.67	2.03	0.26

Table 4-6. Model-averaged estimates for factors affecting the fitness of female shags.

Response variable **(n = number of individuals)**	**N models**	**Parameters in best model(s)**	**Estimate**	**Confidence Interval**	**P value**	**Relative importance**
Number of chicks fledged ~ **(n = 13)**	3	Hatching Date	-0.52	(-1.45 to 0.41)	0.273	0.25
		Repeatability Score	0.31	(-0.51 to 1.13)	0.458	0.16
Adult body condition ~ **(n = 25)**	6	Repeatability Score	0.21	(0.01 to 0.15)	0.042*	0.66
		Year	-0.04	(-0.12 to 0.03)	0.287	0.24
		Sub-colony	0.03	(-0.05 to 0.11)	0.427	0.18

◦Effect sizes have been standardized on two SD following Gelman (2008). *indicates significance at $p < 0.05$ level

4.4 Discussion

To my knowledge, this is the first study to examine individual consistency in the foraging behaviour of European shags during the breeding season. It is also one of the first to document potential fitness consequences of consistent foraging behaviours over a short timescale.

Shags showed spatial consistency in foraging sites at an individual level (IFSF). This was reflected in high repeatability in location-related foraging-trip parameters at a population level. These levels of repeatability were largely maintained from year to year; however, I found evidence that birds may adjust their foraging effort—i.e. time spent foraging—on an annual basis. Certain birds showed greater levels of consistency than others, with individuals visiting areas they had previously used both within a single breeding season and from one breeding season to the next. Strong individual site fidelity was found to be advantageous for female shags: birds that expressed higher levels of spatial consistency were in better condition and their broods hatched earlier in the season compared to less consistent birds.

Individual foraging-site fidelity

Significant IFSF was found in shags both within and between breeding seasons, with individuals varying in the degree of fidelity they expressed. Similar findings have been reported in other seabird species (Potier et al. 2015, Wakefield et al. 2015, Patrick & Weimerskirch 2017). However, all individuals showed greater spatial consistency in their foraging areas than predicted by null models where individual identity was randomly assigned. Birds breeding at the Farne Islands nest virtually within sight of one another; thus, they potentially have access to the same food patches. This, coupled with the fact that levels of IFSF are maintained across seasons, indicates that birds must benefit from foraging consistently. I show that increased fidelity has sex-specific advantages associated with condition and reproductive success. Longer-term studies would be required to assess the impact of IFSF on survival and on the fitness component of recruitment of fledged young (e.g. Authier et al. 2012). Nonetheless these findings add to the growing body of evidence that long-term IFSF may be widespread in seabirds (Weimerskirch 2007, Harris et al. 2014, Potier et al. 2015, Wakefield et al. 2015). These results also corroborate the findings from Potier et al. (2015) and Harris et al. (2014), indicating that foraging-site fidelity could be just as advantageous to short-ranging seabird species as it is to longer-ranging species.

Individual repeatability in other trip parameters

Within-season fidelity

Repeatability in foraging behaviours seems to be widespread in the marine environment (Patrick et al. 2014, Ceia & Ramos 2015), yet few studies have quantified variation among individuals in the repeatability of these parameters (Potier et al. 2015, Wakefield et al. 2015, Patrick & Weimerskirch 2017). The average population-level repeatability value, reported for foraging behaviour from a wide range of taxa, is approximately 0.45 (Bell et al. 2009). I found that in addition to being highly repeatable in the location of and direction travelled to their foraging areas, birds showed high repeatability in maximum dive depths, which also has a spatial aspect due to the species' benthic foraging habits. However, parameters that were less influenced by location, such as total trip duration and time allocated to foraging activity, were less repeatable, akin to patterns reported for other seabird species (Patrick et al. 2014, Potier et al. 2015).

IFSF has also been documented in northern gannets, *Morus bassanus* (Wakefield et al. 2015). This species shows similarly high repeatability in terminal trip locations (longitude and latitude) and departure bearings (Patrick et al. 2014), and similarly low repeatability in trip durations and distances. In great cormorants at Chausey, France, high-moderate repeatability was found in departure angles, latitudes and trip durations, with much lower repeatability in foraging longitudes and maximum distances reached (Potier et al. (2015). This difference was attributed either to large tidal fluctuations affecting the availability of foraging locations or to birds responding to opportunistic foraging cues, such as the presence of feeding conspecifics. The tidal range around the Farnes (c. 5 m) is substantially lower than around Chausey (c. 14 m Grémillet et al. (1999)); the higher levels of repeatability reported here may be due to a greater stability or more constant accessibility of foraging sites around the Farnes. Higher levels of repeatability in foraging behaviours have been found in Imperial shags *P. atriceps* feeding off the Patagonian shelf (Harris et al. 2014), which is known to be a highly productive ecosystem (Song et al. 2016).

Retention of consistency in foraging locations from year to year

The levels of repeatability in trip parameters associated with foraging location were retained across multiple breeding seasons. Recurrent foraging success at specific locations is likely to contribute to the levels of repeatability observed. There is evidence that success reinforces stereotypical behaviour patterns in other species, with such patterns becoming more consistent over multiple years (Woo et al. 2008). So far, the persistence of spatial site fidelity across seasons has only been documented in a few mid to long-ranging (i.e. foraging range > 50 km) marine species, namely gannets (Wakefield et al. 2015) and pinnipeds (Bradshaw et al. 2004, Chilvers 2008). Generally, these studies have found that individuals maintain similarly strong foraging-site fidelity between and within years.

Patrick and Weimerskirch (2017) found that fidelity in black-browed albatrosses was stronger within years than between years, while I found that spatial consistency in shag foraging areas was stronger between seasons than within. These differences might arise due to the short-range foraging behaviour of shags, which may allow them to assess conditions at feeding sites, potentially without leaving the colony, and, if necessary, use alternative locations.

Some of the shags that used multiple foraging sites within a season (low IFSF) nonetheless re-visited the same locations that they had used in previous years. Conversely, in Imperial shags (foraging range < 55 km), levels of repeatability were found to be higher within a breeding season than between seasons (Harris et al. 2014). European shags retained similar levels of within-season repeatability across multiple years. Annual levels of repeatability also seem to persist; however, these results should be interpreted with caution due to the sample-size limitations of birds tracked over more than two years.

Spatial consistency is maintained over both short and long timescales in northern gannets (Wakefield et al. 2015), but was found to increase as the breeding season progressed in Imperial shags (Harris et al. 2014). Harris et al. (2014) tracked individuals during early chick rearing and again in the late chick-rearing stage, whereas Wakefield et al. (2015) and this study only examined foraging behaviour once within a season: during the early-mid chick-rearing period.

Annual variation in foraging behaviour

Although foraging locations remained fairly consistent from year to year, the time birds allocated to active foraging behaviours—i.e. the percentage of time spent resting, foraging and on/near the seabed—within a trip differed. Birds were presumably adjusting their foraging effort in response to annual fluctuations in environmental conditions and/or prey availability. A similar behavioural strategy has been found in Australasian gannets *Morus serrator* where, during years of poor prey availability, individuals increased the time spent foraging within a restricted range (Angel et al. 2015). However, in response to changing prey availability, individual northern gannets were found to increase the size of their core foraging areas rather than increasing foraging effort (Warwick-Evans et al. 2016). There appear to be two main strategies: (1) travel further to look elsewhere for prey; or (2) continue foraging in the same sites but work harder to find prey. Here, I found individual shags seemed to vary in which of these strategies they adopted.

The repeatability of migratory behaviours has been relatively well studied (Bell et al. 2009). Site fidelity of migration routes and timings, staging sites and wintering areas has been well documented in avian species (Wilson et al. 1991, Bêty et al. 2004, Phillips et al. 2005, Grist et al. 2014, Lourenco et al. 2016). The benefits to survival in these cases are likely due to site familiarity (Piper 2011) and the refinement of migration tactics (Sergio et al. 2014). However, many species also show flexibility in migratory behaviours, adapting to annual variation in environmental conditions (Vardanis et al. 2011, López-López et al. 2014, van Wijk et al. 2016). So far, few other studies have examined inter-annual changes in the repeatability of foraging behaviour within a population (Gray et al. 2005), or at an inter-individual level across years (Harris et al. 2014, Patrick & Weimerskirch 2014, Wakefield et al. 2015, Patrick & Weimerskirch 2017).

My findings support the notion that repeatability is context dependent, reflecting the stability of a particular habitat and the persistence of prey patches over time (Ceia & Ramos 2015). Differences in the extent of individual specialisation in seabirds may be related to temporal changes in the availability and predictability of resources (Hamer et al. 2001, Woo et al. 2008, Ceia et al. 2014, Ceia et al. 2015). Productivity is strongly linked to prey availability in seabirds (Monaghan 1996, Croxall et al. 1999); therefore, poor productivity at the study site—for instance, in 2016—could imply a lack of food availability. Alternatively, environmental conditions could alter the accessibility of prey by modifying prey and/or predator behaviour (Elkins 1988). Shags seemed to show lower levels of repeatability when foraging conditions were more productive, but repeatability was higher when feeding conditions appeared to be less favourable. When prey availability is plentiful, birds may be responding to opportunistic cues, e.g. the presence of prey at the water's surface or the feeding activity of conspecifics, rather than travelling to foraging areas further afield, which reduces repeatability (Potier et al. 2015).

Repeatability studies may be enhanced if data can be gathered over a wide range of environmental conditions at different locations to establish both an intrinsic level of consistency for a species and a measure of the flexibility in this consistency. This would provide a basis upon which to better understand flexibility within species, which could then inform predictive modelling scenarios and help evaluate conservation management practices under different environmental conditions.

Individual variation in IFSF

In this study, I found some individuals were more repeatable in their behaviour than others. Variation between individuals in the levels of consistency expressed has been documented in most studies quantifying individual-level consistency (Arthur et al. 2015, Potier et al. 2015, Wakefield et al. 2015, Patrick & Weimerskirch 2017). Multiple factors may contribute to the individual-level variability in foraging behaviours observed. Foraging efficiency in shags increases with age and experience (Daunt et al. 2007a, Daunt et al. 2007b). Foraging specialisations could arise from improvements in prey detection, capture and handling techniques as a result of increased experience (Bolnick et al. 2003). Individuals could also develop foraging preferences through increased familiarity with a site (Riotte-Lambert et al. 2015). Young shags form post-fledging crèches around their breeding colonies, where juveniles appear to learn and develop fishing skills from parents and conspecifics (Velando 2001). Wide-ranging pelagic predators show individual variation in the environmental cues used to detect foraging areas from the sea surface, i.e. sea-surface temperature, chlorophyll-a concentration and copepod abundance (Cox et al. 2013, Patrick & Weimerskirch 2014), and these can be linked to dietary specialisations (Votier et al. 2010). Environmental cues that are detectable from the sea surface may be less relevant for species that are unable to assess environmental conditions from a great distance and that rely on benthic prey. In short-ranging benthic foragers, bathymetric features may play a more influential role in locating foraging areas; for example, yellow-eyed penguins *Megadyptes antipodes* used distinct benthic features to navigate to foraging hotspots (Mattern et al. 2007).

Fitness consequences of IFSF

Previously, fitness consequences of IFSF have been difficult to establish over short timescales. Consistency of foraging behaviour has been weakly linked to fitness in northern gannets, where residual body mass of adults was found to be positively related to consistency in trip durations (Wakefield et al. 2015). Here, I present the first evidence that IFSF in short-ranging species can also have detectable consequences on an individual's condition within a single breeding season. Sex-specific fitness consequences associated with short-term persistence of IFSF have recently been found in black-browed albatrosses, with more consistent females showing higher reproductive success within a single season (Patrick & Weimerskirch 2017). Similarly, I found potential fitness benefits associated with IFSF in female shags within a single breeding season. However, Patrick & Weimerskirch (2017) also found birds which displayed stronger site fidelity had higher productivity across multiple years in both sexes. No overall effect of IFSF on productivity was found in this study; however, a negative relationship between breeding success and laying date has been found at other North Sea colonies (Daunt et al. 2006).

Experience seems to play a vital role in brood provisioning in shags: older parents deliver more food to chicks than young, naïve birds (Daunt et al. 2007b). In Adélie penguins, more efficient foragers are also known to have higher breeding success (Lescroel et al. 2010). Age-related effects are likely to contribute to some of the individual variation seen in this study. However, IFSF in albatross species does not seem to be linked to age (Patrick & Weimerskirch 2017). Shags cannot be aged beyond four years of age by plumage characteristics (Baker 1993) and most do not breed successfully until their third or fourth year (Robinson 2016); therefore, the age and previous breeding experience for most birds tracked in this study could not be ascertained. However, age seems to be connected with shag breeding phenology; thus, early breeders are likely to be older, more experienced birds (Daunt et al. 2007b). If the females that show high IFSF are more experienced birds, perhaps this increased foraging efficiency could be attributed to familiarity with particular locations and prey capture techniques (Piper 2011), i.e. learnt behaviours (Riotte-Lambert et al. 2015). Older birds also seem able to adjust their foraging effort to changing environmental conditions (Daunt et al. 2007b). It is possible that more experienced individuals have prior knowledge of alternative foraging sites and can adjust foraging locations or increase foraging effort more effectively. The development of migratory behaviour in birds seems to be a gradual process with cumulative effects of individual improvement and selective mortality (Sergio et al. 2014). Equivalent processes may also be involved in the development and maintenance of IFSF (Votier et al. In Press).

If the fitness consequences of foraging behaviour are sex- (Patrick & Weimerskirch 2014, This study) or age-dependent, individuals may respond differently to changing environments. Shags are already experiencing population declines due to an increase in the frequency of winter storms (Gunn et al. 2016). Females are more susceptible to these adverse winter weather conditions (Lewis et al. 2015). I show that they may also be more vulnerable to changes in food availability or accessibility during the breeding season. Strong IFSF could mean more experienced birds (i.e. those with higher breeding success) are at greater risk. If they are unable to switch foraging sites, this could cause detrimental population-level effects. In order to fully understand the conservation implications of intra-individual differences in foraging behaviour, future studies should therefore try to ascertain the level of flexibility in IFSF under varying environmental conditions.

4.4.1 Conclusions

This study highlights the importance to animal movement ecology of not only examining individual differences in behaviour but also considering variation among individuals in levels of consistency. I provide evidence that short-ranging seabird species can show strong IFSF, which indicates that the advantages of IFSF may be applicable to a wide range of seabird species, irrespective of their foraging range. Levels of consistency were maintained over time, which may be a result of spatially and temporally predictable prey patches. I suggest that site familiarity could lead to increased foraging success, with potential benefits for individual fitness. However, effects of IFSF on shags were sex-specific, indicating that females benefited more from IFSF than males.

Results of this study also have potential implications for conservation and management. For example, in the Mediterranean region, shags are particularly vulnerable to entanglement in gill-nets (Velando & Freire 2002). If birds there show similar patterns of IFSF to those in the Farne Islands, then bycatch-induced mortality could have a disproportionate impact on the survival of certain members of the population. IFSF could also influence which members of a population are best protected by Marine Protected Area designations or affected by anthropogenic developments. More studies should consider how factors such as sex, age and location may differentially affect the implications of behavioural responses and the adaptability of species to changes in their environment.

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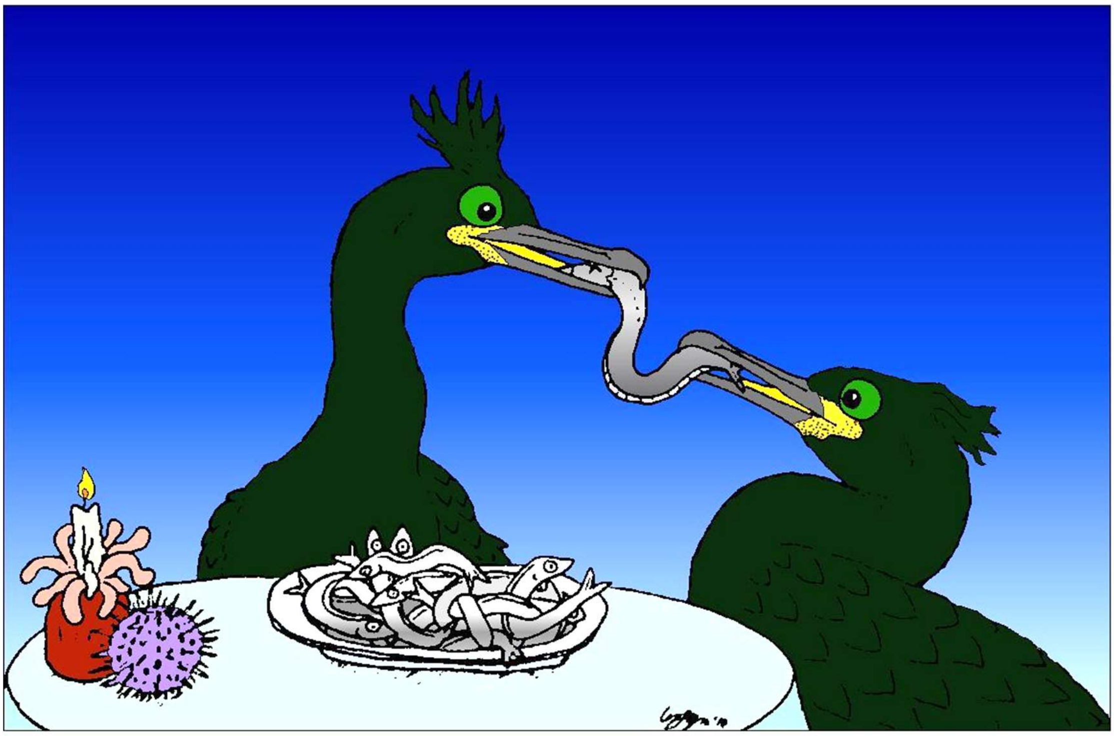
Chapter 5 - Intrinsic and extrinsic influences on three-dimensional foraging behaviour in shags



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Abstract

Intrinsic and extrinsic factors that influence foraging behaviour may play a key role in determining individual and population-level responses to environmental change. In populations where individuals show consistent variation in their foraging behaviour, intrinsic differences could result in differential responses to environmental variation, placing some members of a population at greater risk than others. In Chapter 4 I used bio-telemetry data to reveal that chick-rearing European shags show high repeatability in a number of different components of foraging behaviour. Here, I investigate how the characteristics of these trips differed in relation to individual traits and local environmental conditions. To characterise foraging trips, I used principal components analysis (PCA) to extract uncorrelated orthogonal factors that could explain the underlying patterns in three-dimensional foraging behaviour in an integrative way from multiple trip variables. PCA extracted three factors, together explaining 90% of the variation in trip data, and most strongly associated with: (i) dive frequency, bottom time and trip duration (PC1); (ii) dive depth, resting time and horizontal distance travelled (PC2), and; (iii) time spent resting, duration and horizontal distance (PC3). PC1 and PC2 were most strongly influenced by sub-colony location, year and time of day. Birds had higher PC1 values at nesting locations which were closer to shore (i.e. they foraged more intensively) whereas birds nesting further offshore had higher PC2 values (i.e. foraging behaviours associated with deep diving). Mean values of PC1 and PC2 were both higher in 2016 than in the previous two years. There was an accelerating decline in PC1 values associated with time of day, i.e. trips had higher PC1 values in the morning. PC2 Time of day also influenced PC2 with lower values around dawn and dusk. In addition, PC2 values were also higher at rising and high tidal states. PC3 did not differ significantly between colonies or years but was significantly affected by wind direction, wind speed and sex. Scores for PC3 were higher during westerly winds and stronger winds, with females showing a stronger response to increased wind speeds than males (i.e. females were not travelling as far and resting more). Individual birds had significant repeatability in all three factors (mean r values were between 0.39 and 0.45) across the three years of the study, but there was also evidence that individuals differed in the extent and direction of change from year to year, suggesting that not all birds responded similarly to annual variations in environmental conditions.

5.1 Introduction

Many species show plasticity in their foraging behaviour in response to changes in biotic and abiotic environmental conditions or to changes in their energy and nutrient requirements

(Rosalino et al. 2005, Beck et al. 2007, García-Navas & Sanz 2010, Hernandez-Pliego et al. 2017). This flexibility may be particularly important to central-place foragers such as seabirds during the breeding season, when parents need to provide food for dependent offspring in addition to themselves, and may face large spatial and temporal variation in prey abundance and availability (Hamer et al. 2007, Robertson et al. 2014, Angel et al. 2016, Mott et al. 2016). Diving species may face particular challenges in this respect because they must allocate their time between periods at the surface when they can acquire oxygen but cannot obtain food, and periods underwater when they can search for prey but cannot acquire oxygen (Cook et al. 2008, Wilson et al. 2011). Cormorants and shags are foot-propelled pursuit-divers that typically dive to the seabed to feed on benthic organisms but have short foraging ranges, little fat reserves and partially wettable plumage (Grémillet et al. 2005), all of which may constrain their ability to adjust their foraging behaviour in response to changing circumstances. Hence flexibility in foraging behaviour may be especially important for these species.

Recently there has been a rise in individual-based studies focusing on consistency and specialisations in foraging behaviour (Bolnick et al. 2003, Araujo et al. 2011, Harris et al. 2014, Patrick et al. 2014, Potier et al. 2015, Patrick & Weimerskirch 2017). This individual variation could become more distinct as environmental conditions deteriorate (Sydeman et al. 1991, Lewis et al. 2015). Therefore, a knowledge of which intrinsic and extrinsic factors have the strongest influence on an individual's behaviour and how they interact is needed to more accurately assess the potential impacts of future environmental change.

European shags *Phalacrocorax aristotelis* (hereafter shags) breed at colonies in the NE Atlantic Ocean (Hagemeijer & Blair 1997). At colonies around the UK, they feed mainly on sandeels (principally *Ammodytes marinus*; typically >80% of prey) obtained primarily at the seabed on short foraging trips (median foraging range 3.4km, IQR 1.6-7.5 (Wakefield et al. 2017)). However, in some years at some colonies, sandeels may comprise <30% of the diet and trips may exceed 20km in range (Bogdanova et al. 2014, Soanes et al. 2014, Chapter 2), and birds may also occasionally capture epipelagic prey within the water column (Grémillet et al. 1998a, Watanuki et al. 2008). Trip range and duration may increase slightly with increasing brood size and chick age (Soanes et al. 2014), while females make consistently longer trips than males in both distance and duration (Bogdanova et al. 2014, Soanes et al. 2014, Lewis et al. 2015). Across the year, birds also adjust their foraging behaviour in relation to local weather conditions, but in a manner that differs between sexes, resulting in sex-specific differences in foraging effort becoming more marked as wind conditions worsen (Lewis et al. 2015). On a finer scale, birds' dive depths also vary diurnally in relation to light attenuation levels, probably due to the species' reliance on vision to locate prey (Wanless et al. 1999). Diving behaviour and prey-capture techniques also differ between birds foraging over sandy and rocky substrates (Watanuki et al. 2008), but relatively little is known about the drivers of variation in shags' diving behaviour, in contrast to the wealth of information on their two-dimensional movements (Daunt et al. 2006, Daunt et al. 2014)

Shags show consistent individual variation in foraging behaviour, including individual foraging site fidelity (Daunt et al. 2014, Chapter 4) but it was not previously known to what extent this consistency could vary in response to changing circumstances. Hence, here I evaluate the relative importance of intrinsic (namely; sex and brood size) and extrinsic factors (including; weather, time of day, year and tidal state) influencing the individual foraging behaviours of shags. I then examine whether or not individual birds showed differences in the strength and direction of their behavioural responses to these factors.

5.2 **Methods**

Fieldwork was carried out on the Farne Islands, UK (55°36'57.30"N, 1°39'20.19"W). Adult shags were fitted with telemetry devices during the chick rearing period of three consecutive years (5th June to 8th July 2014, 20th May to 20th June 2015 and 21st May to 27th June 2016). Birds were sampled on three of the main islands within the archipelago, one site on the Inner Farnes and two sites within the Outer Farnes. Birds were caught at the nest using a 5m telescopic pole with a wire noose or crook at the end, some birds were also caught by hand.

Birds were individually-colour ringed so they could be easily identified. GPS loggers (IgotU GT-120, Mobile Action Technology, Taipei, Taiwan) and time-depth recorders (TDRs; G5, CEFAS Technology, Lowestoft, UK,) were combined into a single device (combined weight = 34g) using shrink wrap, cable ties and Tesa® tape (Milton Keynes, UK), then taped to the underside of the central tail feathers. Birds were weighed to the nearest gram upon capture to ensure devices did not exceed the 3% guideline recommended by (Phillips et al. 2003)devices on most birds were <2% of body weight). GPS loggers were programmed to record locations every 60 seconds, with TDRs set to take regular readings throughout the day (once per hour in 2014 and every 20 minutes in 2015 and 2016) and at maximum resolution (12Hz in 2014 and 2Hz in 2015 and 2016) when submerged below 1.5m. Birds were re-captured 4-5 days after initial deployment, devices were carefully removed and biometrics (maximum chord wing length to the nearest mm using a slotted rule, weight as above, bill depth to nearest mm using digital callipers) were collected from adults. Birds were sexed based on vocalisations and bill measurements during the initial capture (Baker 1993). Tags had no discernible effects on adult body condition, behaviour at the nest or reproductive success (see Chapter 2 for details).

5.2.1 Data processing

Data were processed as described in Chapter 2. The following variables were calculated for each foraging trip:

(1) Trip duration in minutes (taken as the time a bird crossed the 200m threshold until the time it returned to within 200m of the colony);

(2) Total distance travelled (km, as above);

(3) Maximum range (the greatest distance reached from the colony in km);

(4) Proportion of time spent resting per trip (calculated as the percentage of 60-second intervals with speed < 2m s^{-1} and depth <5m. This included both pauses at the sea surface between dives and occasions when birds rested on land away from the colony during a trip).

(5) Proportion of time spent foraging per trip (calculated as the percentage of 60-second intervals with depth ≥ 5m);

(6) Number of dives per trip;

(7) Mean dive depth per trip (calculated from the greatest depth attained during each dive);

(8) Total time spent at the bottom phase of each dive per trip (indicative of time spent probing for or pursuing prey).

On a small number of occasions, TDRs malfunctioned resulting in no dive depths being recorded for all or part of a trip. As no diving activity was recorded time-activity budgets could not be calculated therefore these trips were removed from this analysis.

5.2.2 Environmental data

To explore the environmental characteristics associated with key foraging areas, bathymetry data were obtained from the SeaZone Solutions gridded bathymetry data set (2015) at a resolution of 30x30m. In addition, hourly weather data were obtained from Boulmer weather station (55°25’22”N, 01°36’3”W, 23 km south of the colony; www.badc.nerc.ac.uk)., Wind directions were sine transformed (following Daunt et al. 2006) to remove circularity, giving easterly winds a maximum value of 1 and westerly winds the minimum value of −1. The time to/since midday (to the nearest hour) was calculated from the start time of each foraging trip, and hourly wind data (speed and direction) were then assigned to these times. Tidal state at the time of departure was also calculated for each trip, by extrapolating tide table data for North Sunderland harbour (55° 34'57”N, 1° 39'7”W, 3.5 km south of the colony). States were classified as high water/slack (2 hours before to 1 hour after high water), ebb (2-6 hours after high tide), low water/slack (2 hours before to 1 hour after low water) and rising (2-6 hours after low tide).

To examine annual variation in weather conditions during the breeding season (May-July), I calculated daily values for each variable by averaging hourly wind and visibility data and summing rainfall and hours of sunshine, I then used Kruskal-Wallis tests followed by post hoc Nemenyi tests to examine differences in weather conditions between years.

5.2.3 Data analysis

To examine how the characteristics of foraging trips were related to intrinsic and extrinsic factors, the eight foraging-related variables calculated for each trip (see above) were normalised where necessary, including arcsine-transformation of percentages, and analysed using a principal components analysis (PCA; Pettex et al. (2012), Patrick and Weimerskirch (2014)). The PCA allowed ordination of differences among trips in three-dimensional foraging behaviour, by generating a number of independent components comprising sums of weighted variables, with each variable standardised (i.e. mean across all trips = 0, SD = 1). Each component was then treated as the response variable in linear mixed effects models (LMMs) to assess the impact of intrinsic and extrinsic factors on three-dimensional behaviour. Models were constructed in the R package lme4 v.1.1-7 (Bates et al. 2015) using restricted maximum likelihood and a Gaussian error distribution (Zuur et al. 2009). To account for pseudoreplication of repeat individuals tracked over multiple years and multiple trips per year, bird identity and year were fitted as a random effects in all models.

Nesting colony and year were included as explanatory variables in all maximal models, together with date (Julian day) to account for seasonal changes within each year, for instance due to the increasing food requirements of offspring as they grew. To examine responses to weather conditions, mean hourly wind speed and direction during each trip (the latter a two-level factor; east or west) were added as fixed effects to all models, together with the interaction between wind speed and direction to test whether birds responded differently to onshore and offshore winds. Tidal state (4 level factor; high, falling, low or rising; see above) was also included, together with linear and quadratic terms for time of day (classified as hours since midday). In addition, sex (two level factor), brood size (taken as the number of chicks during the tracking period; range: 1-4) and their interactive effects (sex*brood size) were also fitted, together with interactions between sex*wind speed and sex*wind direction to account for potential sex-specific effects on foraging behaviour.

To summarise, the global model for each component of three-dimensional forging behaviour included the following explanatory variables; sex, brood size, date, year, sub-colony location, tidal state, time of day, time of day^2, wind speed, wind direction, and two-way interactive effects of sex with wind speed, wind direction and brood size, plus an interaction term between wind speed and direction, along with bird identity nested within year. PC models were run using only complete trips with both GPS and TDR data (n trips=708 from 50 birds; 396 trips from males and 312 from females).

5.2.4 Model selection

Model averaging was used to identify factors which had the greatest influence each component of behaviour. All fixed effects were standardised using the ‘arm’ package v.1.7-07 (Gelman & Su 2014) to ensure they were on a common scale, and to increase the interpretability of parameter estimates (Schielzeth 2010). Model simplification and selection were performed using a multi-model inference approach based on the methods and recommendations of (Grueber et al. 2011) using the ‘MuMIn’ package v.1.13.4 (Barton 2015). Akaike information criterion (AICc) was used in model selection procedures, where the best model had the lowest AICc value. Models within two AIC (ΔAIC < 2) were considered to have equal support and coefficients were averaged across these models (Burnham & Anderson 2002). Where there was no clear best model in the candidate model set, the top models were selected and parameter estimates and relative importance (RI) of each parameter were averaged (Burnham & Anderson 2002). The zero method of averaging was used to determine which factors have the strongest effect on the response variable (Grueber et al. 2011, Nakagawa & Freckleton 2011). Predicted values for each factor were extracted for each individual trip from averaged coefficients (from unstandardized models).

5.2.5 Individual repeatability

To examine the individual consistency in three-dimensional behaviour, I examined the repeatability in each principal component from the PCA, using methods described in Chapter 4. Though repeatability tells us whether individuals within a population show consistent variation in a given variable (e.g. PCs’), it does not tell us how individuals varied their responses in relation to specific factors e.g. year. Hence for each individual bird, I compared the annual means for each component of behaviour. To standardise the number of trips per individual only the first six trips a bird made in each year were included in this analysis. To increase sample size, six trips were used rather than the eight trip threshold (used in Chapter 4) as fewer repeat individuals had >8 trips in each year.

5.3 Results

The majority of trip parameters were significantly correlated with one another (Figure 5-1). In addition, examining individual dives in greater detail, there was a positive relationship between maximum dive depth and dive duration (Figure 5-2a) and between maximum dive depth and the duration of the subsequent period at the water surface (Figure 5-2b). Birds which made deeper dives tended to make fewer dives per trip and spent less time at the bottom phase of each dive (as shags are largely benthic predators this was presumably time spent probing for and capturing prey at the seabed), but spent more time resting after each dive and per trip, and hence spent less time foraging per trip (Figures 5-1 and 5-2). Conversely, shallow dives were strongly associated with more time foraging, due to an increase in the number of dives and longer time spent in the bottom phase of dives.

PCA extracted three principal components (PCs) which explained 90% of the variability in the data (Table 5-1). The first PC (PC1, eigenvalue =1.8) explained 41% of the variation in trip characteristics. PC1 increased with (in order from greatest to least importance) an increasing number of dives, higher dive bottom time, increasing trip duration, range and total distance travelled, more time spent foraging and less time spent resting, with birds also making slightly shallower dives (Table 5-1, Figure 5-3). PC1 hence indicated foraging intensity, with a high value for PC1 occurring when there were many dives and a high proportion of time presumably probing for prey at the seabed on trips of long distance and duration. PC1 tended to be highest for trips with terminal points along the coastline to the west of the Farne Islands (Figure 5-4a).

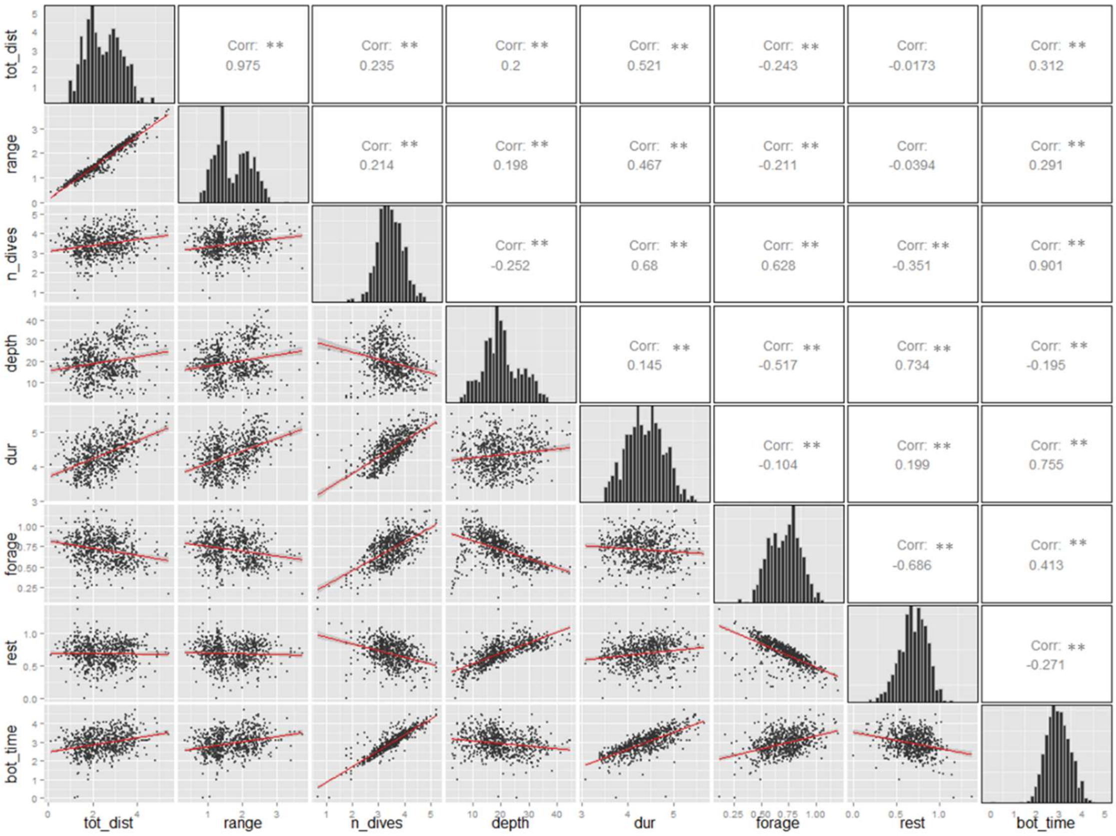

Figure 5-1. Correlation matrix between trip parameters. Scatterplots with linear trend lines are shown in the lower panels. Spearman's rank correlation coefficient for each pair are shown in the upper panels, significance at p<0.001 level is indicated by asterisks. Histograms for each parameter are shown on the diagonal axis. Abbreviations of trip parameters are as follows (data transformations performed shown in brackets); Tot_dist= total distance in km (sqrt), range= distance to furthest point from the colony in km (sqrt), n_dives=number of dives (log), depth= maximum dive depth in m, dur= trip duration in minutes (log), foraging= percent of trip spent foraging (arcsine sqrt), resting= percent of trip spent resting (arcsine sqrt), bot_time= cumulative time spent at the bottom phase of dives per trip in minutes (log).

The second PC (PC2, eigenvalue =1.7) explained 34% of the variation in trips. PC2 increased with increasing dive depths, less time spent foraging and more time spent resting, and with increasing trip duration, range and total distance travelled. PC2 thus indicated foraging depth, with a high value occurring when there were deep dives and a high proportion of time resting, on trips of long distance and duration. PC2 tended to be highest for trips with terminal points in deeper waters in offshore locations, e.g. to the east of the colony (Figure 5-4b).

The third PC (PC3, eigenvalue =1.1) accounted for only a small proportion (15%) of the variability in trip characteristics. High values of PC3 indicated trips that were of long duration despite short ranges and distances travelled, as a consequence of a high proportion of time spent resting.

Trips with the highest values of PC3 tended to have terminal points close to the Farne Islands (Figure 5-4c).

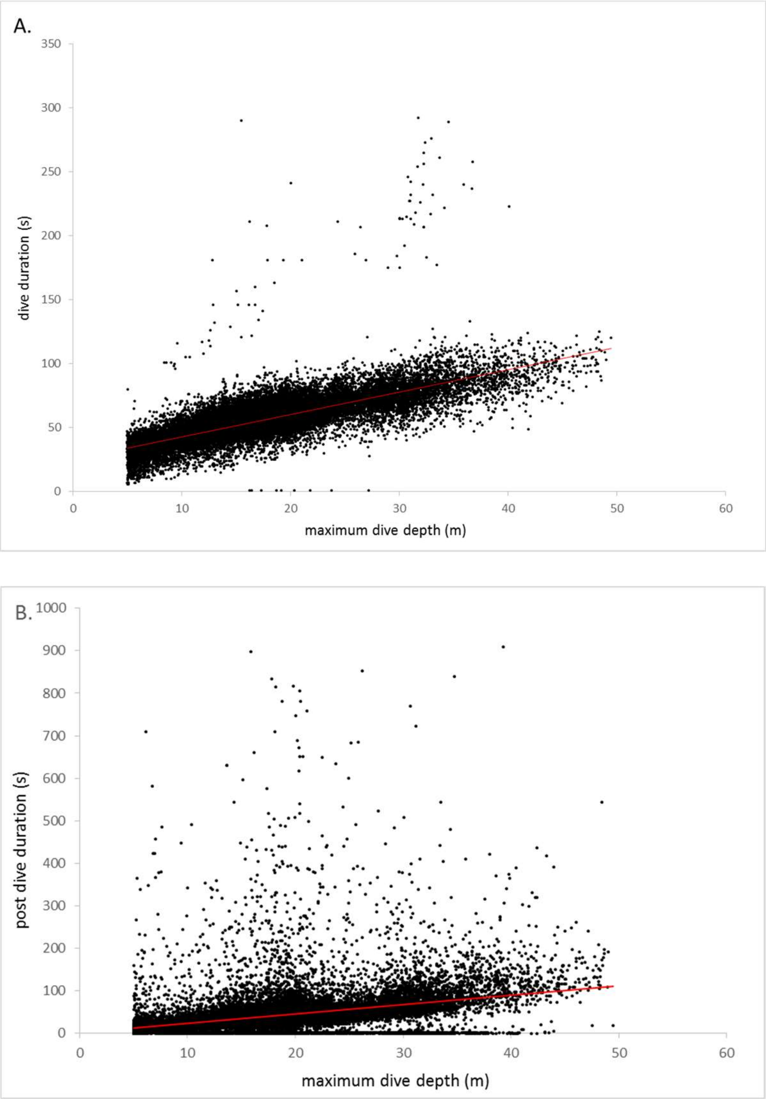

Figure 5-2. The relationships between: (A) Maximum dive depth and dive duration, and; (B) Maximum dive depth and duration of post-dive interval at sea surface. Dives <5m were excluded from analyses as they are unlikely to be associated with foraging activity. Post dive durations >5mins were also excluded as they were considered to represent the end of a diving bout.

PC1 and PC2 were most strongly influenced by year, sub-colony and time of day (Tables 5-2, 5-3 & 5-4). Birds nesting on the inner islands tended to forage more intensively (i.e. had higher PC1 values) whereas those nesting on the outer islands tended to forage at greater depths (i.e. had higher PC2 values). Mean values of PC1 and PC2 were also higher in 2016 than in the previous two years. In addition, PC1 showed a negative linear term and a negative quadratic term for time of day, indicating an accelerating decline, i.e. birds foraged more intensively (most likely at distant shallow locations) in the morning. In contrast, PC2 showed a positive linear and negative quadratic relationship with time of day, probably due to birds making shallower dives around dawn and dusk. PC2 was also influenced by tidal state (Tables 5-2 and 5-3), probably due to birds diving deeper around high tide (Table 5-4). PC3 did not differ significantly between colonies or years but was significantly affected by wind speed (Tables 5-2 and 5-3): scores for PC3 were higher during onshore (easterly) winds and increased with wind speed

Table 5-1. Contributions (correlation coefficients) of different variables to three principal components of variation in trip characteristics. Variables making main contributions to each principal component are indicated in bold.

Variable	**Weighting**		
	PC1	PC2	PC3
Total distance	**0.532**	**0.669**	**-0.465**
Max distance from colony	**0.510**	**0.649**	**-0.502**
Number of dives	**0.857**	-0.146	0.252
Max dive depth	-0.292	**0.738**	**0.309**
Trip duration	**0.706**	**0.527**	**0.330**
Time spent foraging	**0.475**	**-0.770**	0.025
Time spent resting	**-0.441**	**0.697**	**0.512**
Total dive bottom time	**0.846**	0.012	0.282
Prop. variance explained	*41%*	*34%*	*15%*

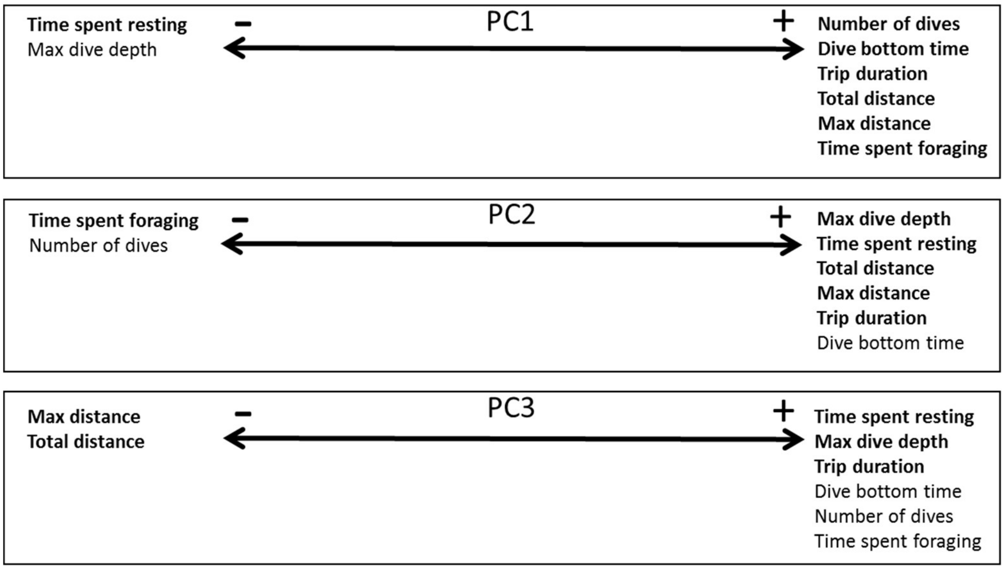

Figure 5-3. Schematic representation of the contribution and direction of variables making up each principal component. Variables are shown in increasing order of importance (top-bottom). Variables making main contributions to each PC are indicated in bold.

Table 5-2. Model selection tables for each response variable (i.e. principal component score). Only models within two AICc of the model with the lowest AIC are shown.

Response variable	**Factors included in top model(s) (ΔAICc <2)**	**AICc**	**ΔAICc**	**weight**
PC1 (shallow diving)	Sub-Sub-colony + time of day^2+ year + time of day	2578.18	0	0.21
	Sub-colony + wind direction+ time of day^2+ year + time of day	2578.47	0.29	0.18
	Sub-colony + wind direction+ time of day^2+ year	2578.55	0.37	0.17
	Sub-colony + time of day^2+ year	2579.77	1.59	0.09
	Sub-colony + wind direction+ sex+ time of day^2+ year + time of day+ sex*wind direction	2579.86	1.68	0.09
	Sub-colony + time of day^2+ year + time of day+ wind speed	2579.94	1.76	0.09
	Sub-colony + time of day^2+ year + date+ time of day	2579.97	1.79	0.09
	Sub-colony + wind direction+ sex+ time of day^2+ year + sex*wind direction	2580.11	1.93	8.00E-02
PC2 (deep diving)	Sub-colony +time of day^2+ tidal state+ year +brood size	2360.62	0	0.29
	Sub-colony +time of day^2+ tidal state +year +brood size +time of day	2361.4	0.78	0.2
	Sub-colony +sex +time of day^2 +tidal state +year +brood size	2361.97	1.35	0.15
	Sub-colony +time of day^2 +tidal state +year +date +brood size	2362.05	1.43	0.14
	Sub-colony +wind direction +time of day^2 +tidal state +year +brood size	2362.61	1.99	0.11
	Sub-colony +time of day^2 +tidal state +year	2362.61	1.99	0.11
PC3 (close to colony)	wind direction + date + time of day + wind speed	1917.87	0	0.11
	wind direction + sex + date + time of day + wind speed + sex*wind speed	1918.16	0.29	0.09
	wind direction + time of day + wind speed	1918.5	0.63	0.08
	wind direction + date + time of day + wind speed + wind direction*wind speed	1918.69	0.82	0.07
	wind direction + sex + time of day + wind speed + sex*wind speed	1918.78	0.91	0.07
	wind direction + sex + date + time of day + wind speed	1919.01	1.14	0.06
	wind direction + sex + date + time of day + wind speed + wind direction*wind speed + sex*wind speed	1919.05	1.18	0.06
	wind direction + sex + date + time of day + wind speed + sex*wind direction + sex*wind speed	1919.39	1.52	0.05
	wind direction + sex + time of day + wind speed	1919.4	1.52	0.05
	wind direction + time of day + wind speed + wind direction*wind speed	1919.51	1.63	0.05
	date + time of day + wind speed	1919.63	1.76	0.05
	wind direction + date + wind speed	1919.66	1.79	0.04
	sex + date + time of day + wind speed + sex*wind speed	1919.7	1.83	0.04
	date + wind speed	1919.79	1.92	0.04
	wind direction + date + brood size + time of day + wind speed	1919.79	1.92	0.04
	wind direction + sex + time of day + wind speed + sex*wind direction + sex*wind speed	1919.84	1.97	0.04
	Sub-colony + wind direction + date + time of day + wind speed	1919.85	1.98	0.04

Table 5-3. Relative importance of each variable (as a proportion of models containing each variable) for each PC model. Number of models making up the candidate model set for each PC are also shown in parentheses below.

Explanatory variables	Response variable:		
	PC1 (shallow diving)	**PC2 (deep diving)**	**PC3 (close to colony)**
Sub-colony	1	1	0.04
time of day^2	1	1	-
year	1	1	-
wind direction	0.52	0.11	0.87
date	0.09	0.14	0.71
sex	0.17	0.15	0.47
time of day	0.65	0.20	0.91
brood size	-	0.89	0.04
tide	-	1	-
wind speed	0.09	-	1
sex*wind speed	-	-	0.36
sex*wind direction	0.17	-	0.09
wind speed*wind direction	-	-	0.18
n models	***(8)***	***(6)***	***(17)***

Table 5-4. Model averaged coefficients from best candidate model set with PC's as the response variable in each case. Parameters which were significant at a 95% level are highlighted in bold. To determine which factors have the strongest effect on the response variable, estimates represent conditional averages with shrinkage taken into account (see Grueber et al. 2011).

Model	**Factors in top model set**	**Estimate**	**Confidence Interval**		**Z ratio**	**P**
PCA1 (shallow foraging)	**Sub-colony**	**-1.417**	**-1.970**	**-0.865**	**5.029**	**<0.001**
	year 2014	-0.051	-0.396	0.294	0.289	0.772
	year 2015	0.308	-0.070	0.687	1.596	0.111
	year 2016	**1.122**	**0.671**	**1.572**	**4.881**	**<0.001**
	time of day	-0.122	-0.403	0.029	0.969	0.332
	time of day^2	**-1.224**	**-1.732**	**-0.716**	**4.721**	**<0.001**
	wind direction	0.096	-0.051	0.418	0.763	0.446
	sex	-0.001	-0.570	0.558	0.008	0.994
	wind direction*sex	-0.062	-0.807	0.074	0.375	0.708
	wind speed	0.006	-0.179	0.319	0.143	0.886
	date	0.014	-0.431	0.747	0.137	0.891
PCA2 (deep diving)	**Sub-colony**	**0.981**	**0.444**	**1.519**	**3.580**	**<0.001**
	tide FALLING	0.024	-0.332	0.379	0.130	0.897
	tide HWSLACK	0.320	-0.037	0.678	1.755	0.079
	tide LWSLACK	0.034	-0.314	0.382	0.193	0.847
	tide RISING	**0.395**	**0.037**	**0.752**	**2.163**	**0.031**

	year 2015	0.054	-0.271	0.379	0.327	0.744
	year 2016	**0.925**	**0.541**	**1.308**	**4.726**	**<0.001**
	brood size	0.293	0.014	0.644	1.603	0.109
	time of day^2	**-1.212**	**-1.631**	**-0.793**	**5.668**	**<0.001**
	time of day	0.020	-0.074	0.279	0.355	0.722
	sex	-0.035	-0.767	0.301	0.259	0.795
	date	0.031	-0.318	0.757	0.243	0.808
	wind direction	-0.003	-0.221	0.162	0.095	0.924
PCA3 (close colony foraging)	wind direction	-0.122	-0.285	0.005	1.456	0.146
	date	0.164	-0.034	0.495	1.060	0.289
	time of day	-0.122	-0.269	0.002	1.601	0.109
	wind speed	**0.178**	**0.034**	**0.323**	**2.416**	**0.016**
	sex	0.100	-0.202	0.622	0.557	0.577
	sex*wind speed	-0.088	-0.520	0.034	0.608	0.543
	wind direction*wind speed	0.028	-0.129	0.438	0.328	0.743
	wind direction*sex	0.012	-0.144	0.415	0.214	0.831
	brood size	0.002	-0.193	0.277	0.068	0.946
	Sub-colony	0.002	-0.369	0.478	0.049	0.961

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A.

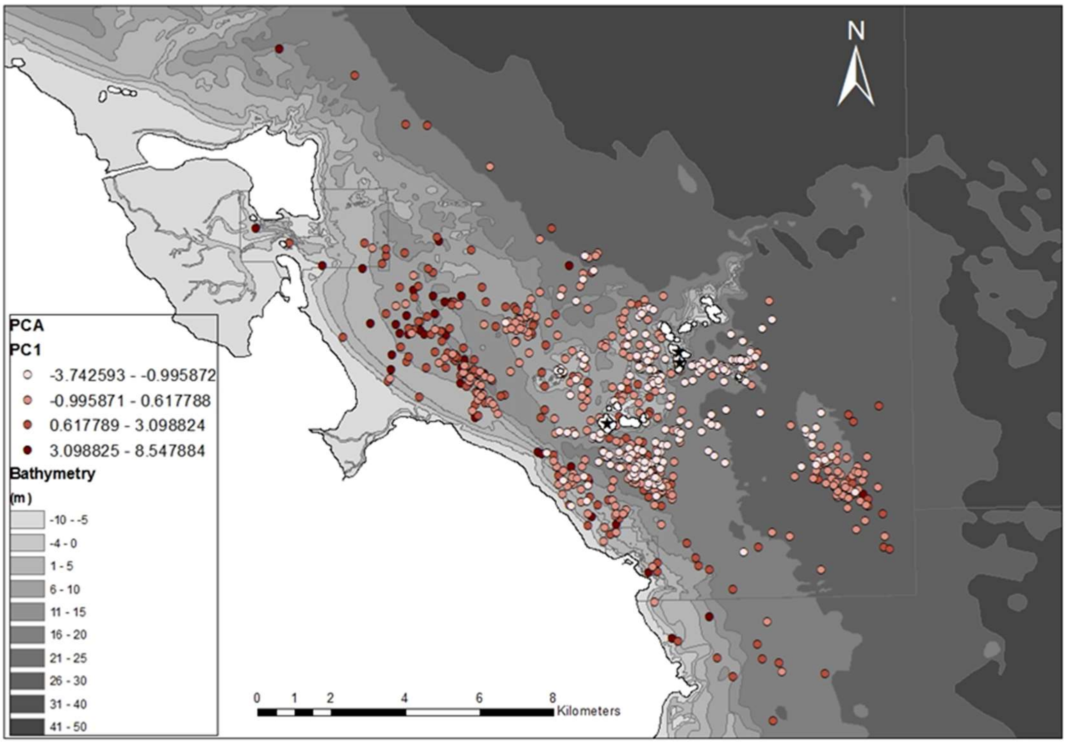
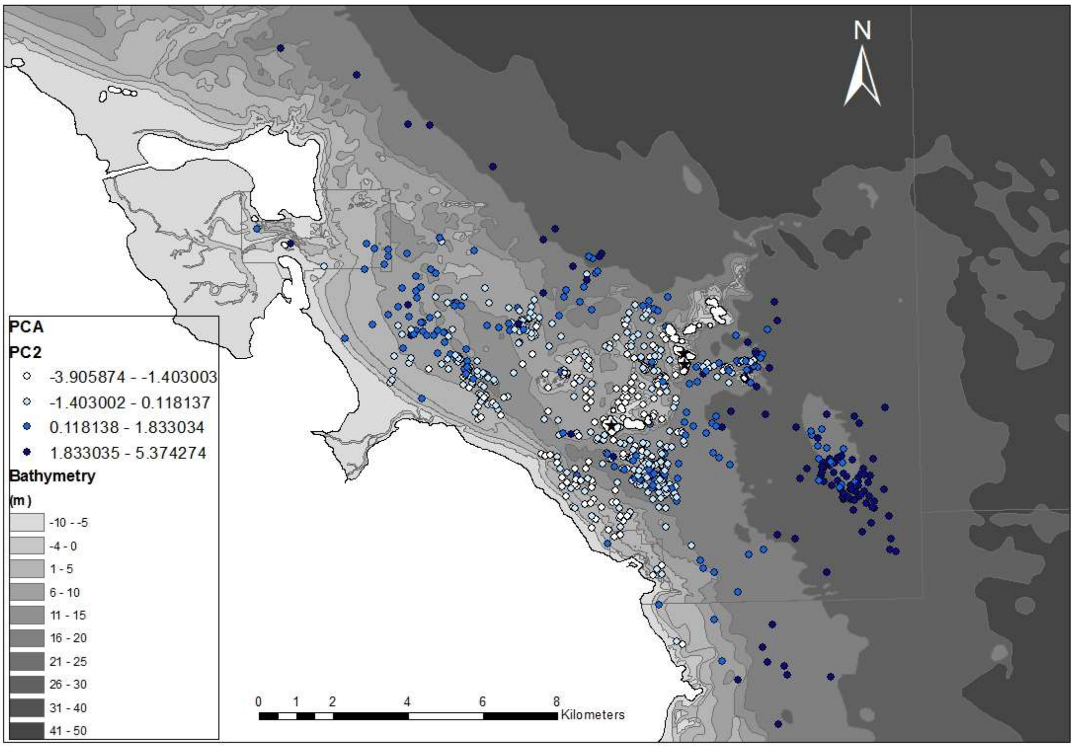


Figure 5-4 . Terminal point of each foraging trip graded by its PC value. (A) PC1, shown in red;

B.



C.

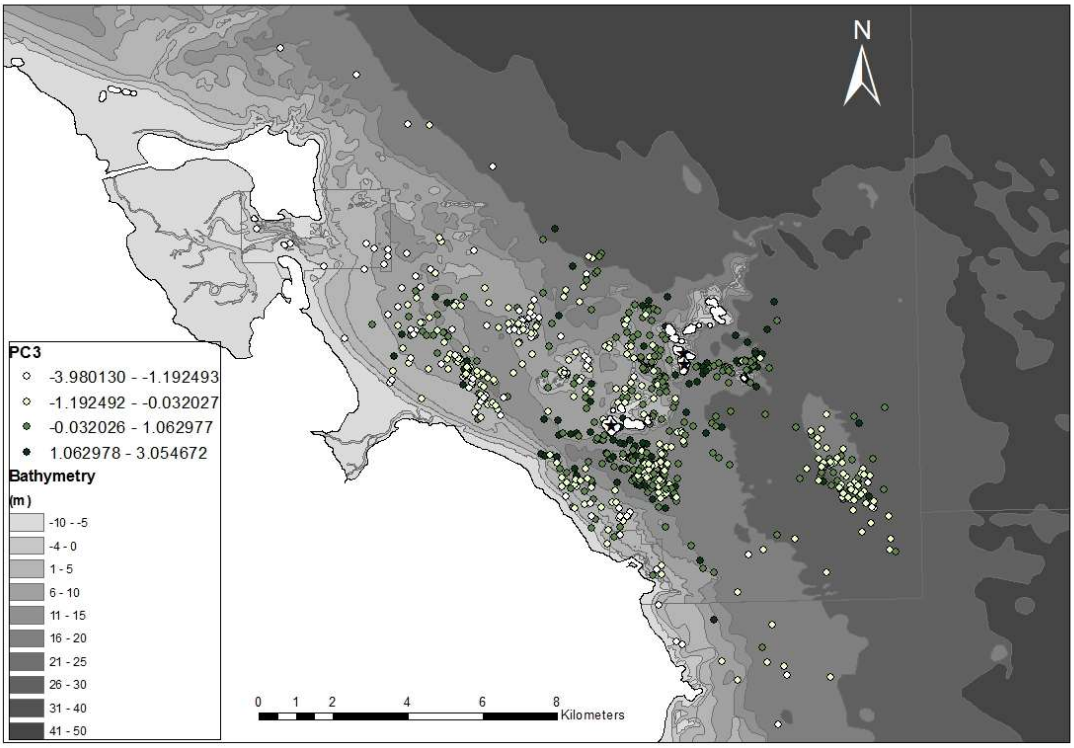


Figure 5-4. Terminal point of each foraging trip graded by its PC value. (A) PC1, shown in red; (B) PC3, in green; (C) PC2, in blue. Points with higher scores for each PC are shown in deeper colours. Bathymetry of the surrounding area is also shown.

Principal Components scores for individual birds showed significant repeatability but at only low-moderate levels (Table 5-5), presumably due to the low repeatability in trip duration and total distance travelled (see Chapter 4). Repeatability of PC1 and PC2 scores did not change between years whereas PC3 was significantly less repeatable in 2016 compared to both other years (Table 5-6). Birds tracked over multiple years did not all respond in the same way; rather, individuals differed in both the magnitude and direction of changes in PC scores across years (Figure 5-5).

Table 5-5. Annual variation in repeatability scores for each principal component of variation in foraging behaviour (see text for explanation). Mean values for each year are shown with SDs. Repeatability scores (r) are shown with 95% confidence intervals (significance of r at p<0.01 is marked with an asterisk).

	PC1		***PC2***		***PC3***	
year	**Mean score (±SD)**	***r (C.I.)***	**mean score (±SD)**	***r (C.I.)***	**mean score (±SD)**	***r (C.I.)***
2014	-0.45 (±1.52)	0.43 (0.25-0.57)*	-0.36 (±1.46)	0.36 (0.21-0.52)*	0.08 (±1.04)	0.38 (0.27-0.53)*
2015	-0.05 (±1.45)	0.25 (0.01-0.39)*	-0.06 (±1.57)	0.48 (0.29-0.63)*	-0.35 (±1.04)	0.44 (0.21-0.59)*
2016	1.26 (±2.38)	0.60 (0.18-0.81)*	1.04 (±1.89)	0.53 (0.07-0.74)*	0.42 (±1.15)	0.27 (0.00-0.55)*
3yr mean	0.01 (±1.80)	0.45 (0.34-0.57)*	0.01 (±1.66)	0.45 (0.34-0.53)*	-0.01 (±0.04)	0.39 (0.28-0.50)*

Table 5-6. Differences in repeatability of principal component scores between years. Z-Scores and confidence intervals between pairwise combinations of years for each PC. Values which do not cross zero are significant at the p=0.05 level and are shown in bold.

	PC1			**PC2**			**PC3**		
	z-scores	C.I.		**z-scores**	C.I.		**z-scores**	C.I.	
2014/15	0.304	-0.129	0.737	0.263	-0.170	0.696	0.153	-0.280	0.586
2015/16	**0.632**	**0.059**	**1.205**	0.06	-0.513	0.633	0.353	-0.220	0.926
2014/16	0.328	-0.203	0.859	0.323	-0.208	0.854	0.200	-0.331	0.731

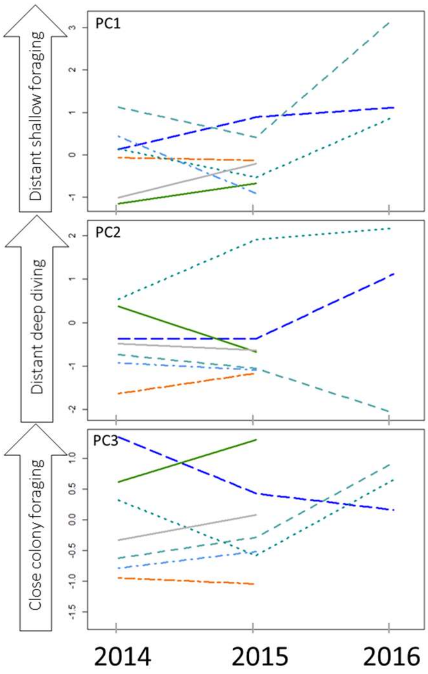


Figure 5-5. Interaction plots showing annual variation in mean scores of individual birds for three principal components of variation in foraging behaviour (PC1 – 3). Data are all for the first six trips each year, for individual birds tracked in more than one year.

5.4 Discussion

This study provides an insight into how birds' three-dimensional movement patterns differed with regards to intrinsic and extrinsic variables. The three principal components indicated different behavioural characteristics. PC2 was strongly influenced by dive depth and time spent resting, presumably due to the positive relationships between dive depth, duration and subsequent surface interval (Wanless et al. 1993, This study, Wanless et al. 1997, Wilson & Quintana 2004), as birds making deeper dives require longer surface intervals to replenish oxygen stores (e.g. Cook et al. 2008). Birds making deeper dives also spent less time at the bottom phase of dives, presumably due to the limits of their breath-holding capacity, and made fewer dives per trip. Previous work has shown diving efficiency decreases with increasing dive depth in this species (Wanless et al. 1997). Birds diving to shallower depths are able to spend longer at the bottom phase of each dive, presumably probing for prey at the seabed, and do not need to spend as long resting at the surface between dives, thus they can make more dives and spend more time foraging; these variables were strongly associated with PC1.

PC3 was heavily influenced by time spent resting, trip duration and distance travelled. High values of PC3 indicated birds were spending a large amount of time resting during foraging trips close to the colony. This could be due to a slight increase in dive depth associated with this factor (as in PC2 above), or due to birds resting on land during foraging trips. Due to their lack of plumage insulation, shags are required to dry their feathers on land after foraging (Grémillet et al. 1998b). Rocky outcrops are numerous around the islands and along the coast, and if birds are foraging in areas close to these potential resting sites they may be more likely to stop and dry their plumage before returning to the nest.

PCA results indicated that birds' three-dimensional behaviour at sea was largely driven by the location and bathymetry of their foraging areas. Similar geographical variation in foraging areas between colonies has been highlighted using PCA in other seabird species (e.g. Tremblay & Cherel 2003, Elliott et al. 2008, Paiva et al. 2010, Sala et al. 2014). Colony location has also been found to drive differences in foraging behaviour between conspecifics of other species (Angel et al. 2016, Mott et al. 2016) and between colonies of shags in NW Spain, largely due to differences between locations in habitat and prey availability (Velando & Freire 1999). However, density-dependent and social factors could also influence foraging distributions between adjacent colonies (Wakefield et al. 2013, Corman et al. 2016, Chapter 3). In this study, birds from the islands which lie further offshore (Outer Farnes) had higher PC2 values than those nesting at the Inner Farnes, indicating they were more likely to perform trips with deep dives. This could be driven by the fact that the average bathymetry surrounding these islands is deeper than that around the inshore islands. In keeping with these findings, birds from the inner group of islands were more likely to make trips with high PC1 values (behaviours associated with shallow dives).

Extrinsic factors such as year, sub-colony location and time of day had a larger effect on trip characteristics than intrinsic factors such as sex and brood size, in keeping with previous studies of individual variables such as time spent foraging and horizontal distance travelled per trip (Daunt et al. 2006, Daunt et al. 2014, Soanes et al. 2014, Lewis et al. 2015). Year, sub-colony and time of day were included in every model within the candidate model set for the first two PCs. Both PC1 and PC2 were significantly higher in 2016 compared to the two preceding years, probably due in large part to birds extending their foraging ranges in this year, as well as making more dives per trip (Chapter 2). Similar responses have been widely documented in shags at other colonies (Wanless et al. 1991, Bogdanova et al. 2014) and other seabirds (Hamer et al. 2007, Robertson et al. 2014), largely driven by changing environmental conditions (Davies et al. 2013, Lewis et al. 2015) and/or prey availability (Hamer et al. 1993, Croxall et al. 1999, Litzow & Piatt 2003).

The diving behaviour of shags is affected by the species' visual threshold, with birds making shallower dives when light intensity is lower (Wanless et al. 1999). My findings support this relationship, with birds showing similar diel patterns, making trips with shallower dives (resulting in lower values for PC2) around dawn and dusk. At my study site, as in other North Sea sites, distances from the colony to core foraging areas were multi-modal (Wanless et al.

1991), suggesting birds were using a number of foraging areas at varying distances from the colony. If some of these more distant areas have deeper bathymetry than others, this could mean certain places would effectively be inaccessible (i.e. too deep for prey to be visible) until light levels increased.

Birds also made trips with deeper dives during high and rising tides possibly due to water levels increasing and birds remaining in specific areas regardless of tidal state (the effect size of tide on dive depth was only around 1m - see Chapter 3). These results fit with those of Daunt et al. (2006) who found no evidence that shags adjusted their foraging activity in response to the tidal cycle, with dive depths closely matching tidal height. However, there is also evidence that adults may forage less at high tide than other tidal states during the post-fledging period (Velando 2001), and Waggitt et al. (2016) recently recorded higher densities of shags foraging around times of slack water (both at high and low tide) during the breeding season, which they suggested was due to low horizontal current speeds enhancing dive performance.

Due to shags' physiological limitations and short foraging ranges (Gremillet et al. 2005, Thaxter et al. 2012), small scale changes in environmental conditions could alter the accessibility of specific foraging locations without affecting the abundance of prey (Matthiopoulos 2003). In particular, wind speed and direction could potentially alter the accessibility of foraging sites to birds (Daunt et al. 2006, Lewis et al. 2015, Saraux et al. 2016). This also appears to be the case around the Farne Islands, as indicated by the fact that wind speed or direction affected scores for two of the three principal components (namely PC3). Hence birds altered their foraging trip characteristics in response to the weather conditions experienced as they left the colony. Prolonged periods of onshore (in this case easterly) winds increase the turbidity of the water column, resulting in increased foraging costs to at least some diving birds and potentially making prey more difficult to capture (Finney et al. 1999, Dehnhard et al. 2013), which might explain why PC3 (which was strongly influenced by increased time spent resting) was higher during easterly winds.

Intrinsic factors had less influence on trip characteristics but sex was included in some of the best model sets. Females have been reported to spend longer foraging and travel further from the colony than males at other sites (Bogdanova et al. 2014, Soanes et al. 2014, Lewis et al. 2015) but this was not the case at the Farne Islands (Chapter 3). However, interactions between sex and wind were important factors retained in models for PC1 and PC3. Females' PC3 scores were more affected by wind speed than males. Females are known to be more susceptible to the effects of adverse weather, spending more time foraging in poor weather than males (Lewis et al. 2015). These effects may be more pronounced in females due to their smaller body size and more demanding role during the breeding season (Daunt et al. 2006, Lewis et al. 2015). The capacity of females to reach more exposed feeding sites may be hindered due to flight constraints or their diving efficiency may be more constrained by increased turbidity in the water column compared to males (Lewis et al. 2015). This could explain why females generally increased time spent resting and/or decreased horizontal distances travelled from the colony more than males during strong winds, potentially using shelter from the islands to buffer these effects or spending more time resting on land between diving bouts.

Principal Components scores for individual birds showed significant repeatability but birds differed in both the magnitude and direction of changes in PC repeatability scores between years, indicating that individuals responded differently to annual fluctuations in environmental conditions. The sample size of individuals tracked in more than one year was small and so this result should be viewed with caution. Nonetheless, shags have been found to show individual variation in the time they spend foraging, especially during the spring and summer (Daunt et al. 2006) and in their foraging behaviour during the breeding season (Chapter 4), so variation in their response to changing prey availability may also be expected.

5.4.1 Conclusions

This study has shown that fine-scale environmental variables affect foraging trip characteristics of shags and can have important interactive effects with intrinsic factors such as sex. To better understand the nature of behavioural responses, it is important to establish patterns of variation in different foraging traits that are related to one another. Here I used PCA as a more integrative method to examine variability in foraging behaviour, extracting uncorrelated orthogonal factors that could explain the underlying patterns from multiple trip variables. This method provides an informative way of identifying how different axes of variation in three-dimensional foraging behaviour respond to environmental variation and should be used more widely in the field of animal movement ecology (e.g. Pettex et al. 2012, Patrick & Weimerskirch 2014). The finding that individuals responded differently to annual variation in conditions has potential demographic implications, for instance if individuals with particular traits had greater flexibility in their foraging behaviour, and this requires further study.

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Chapter 6 - General Discussion

6.1 Introduction

Foraging behaviour is a key component in the daily routines of many species and the acquisition of food is closely linked with population processes such as survival and reproduction (Kacelnik 1984, Hamer et al. 1991, White 2008, Kitaysky et al. 2010, Arlettaz et al. 2017). Resource partitioning to reduce competition is a widespread phenomenon in ecology (Begon et al. 2006). Foraging behaviour and diet often differ between the same species in different locations due to variations in resource availability (Garthe et al. 2007, Zhou et al. 2011, Chivers et al. 2012, Paredes et al. 2012, Clare et al. 2014, Tsuji et al. 2015). However intraspecific variations in foraging behaviours can also occur due to different nutritional requirements or physiological constraints (e.g. size dimorphism) between sexes (Lewis et al. 2002, Phillips et al. 2004, Page et al. 2005, Quintana et al. 2011, Wilson et al. 2015, Beerman et al. 2016, Matsumoto et al. 2017). Individuals may also change foraging behaviours with respect to age or breeding status (Gonzalez-Solis et al. 2007, Pelletier et al. 2014, Weimerskirch et al. 2014, Fayet et al. 2015, Campioni et al. 2016, Cunningham et al. 2017).

Individual foraging specializations have also been widely documented irrespective of factors such as age or sex both in dietary preferences and in foraging locations (Irons 1998, Bolnick et al. 2003, Araujo et al. 2011, Ceia & Ramos 2015, Wakefield et al. 2015, Patrick & Weimerskirch 2017). Understanding the causes and consequences of variation in foraging behaviour at varying scales could allow conservation management decisions to be tailored to an appropriate level, and enable more comprehensive assessments of species conservation statuses. Intra-individual or intra-population level heterogeneity may mean certain members of a population respond differently to extrinsic factors e.g. weather (Lewis et al. 2015), understanding how these factors interact is therefore also crucial to assess population dynamics in a changing environment (Lewis et al. 2009). Consequently, there is a need to better understand the causes and consequences of variation in foraging behaviour at species, population and individual level.

So far few studies have comprehensively assessed variation in behaviour across multiple scales within a species (e.g. Potier et al. 2015, Wakefield et al. 2015). I aimed to achieve this in a short-ranging seabid – the European shag. This thesis examines the levels of consistency in shag foraging behaviour and explores factors which may impose constraints on foraging distributions across varying spatial and temporal scales. In this chapter, I summarise the key findings from my research and discuss their relevance with regards to the biology of the species and their wider applications within the field of animal movement ecology. I also discuss the implications of my results for population management and conservation, and identify priorities for further research.

6.2 Flexibility, consistency and constraint in the foraging behaviour of European shags

From a species specific perspective, this research has increased our knowledge on the factors which constrain the foraging behaviour of shags from an individual level up to a population level. My findings have increased our understanding of behavioural consistency in this species and how this changes across spatial and temporal scales.

The results presented within this thesis support and build upon previous studies into the foraging ecology of the species. Prior to this research, shags' diet and foraging ranges were known to vary between locations (Velando & Freire 1999, Al-Ismail et al. 2013, Soanes et al. 2016) and there were indications that population size could influence foraging ranges within a single site (Bogdanova et al. 2014). By compiling existing data with data collected for this study, I show foraging ranges can differ substantially between sites (**Chapter 2**). I also show that habitat availability plays a role in driving these differences (**Chapter 2**). My findings support those of Wanless et al. (1998) in that the distribution of resources has a strong influence in shaping foraging distributions. My results show that proximity to preferred habitats is an important factor in determining foraging locations over both large and small scales (**Chapter 2, 3 and 5**). On a broader scale, distance to areas with large coastlines (a proxy for habitat availability) was found to be a strong predictor of colony foraging range; I suggest this could be a useful parameter to use (alongside population size and bathymetry) to establish important foraging areas of un-tracked populations.

As the data collected during this study come from a population (of shags) which has been relatively understudied in recent decades, this thesis provides information about the species foraging ecology from an additional geographic location. So far the majority of research on the species has primarily been carried out on birds nesting in the Firth of Forth (see Daunt et al. 2015). This information can now be used in conjunction with recently published tracking studies (Fortin et al. 2013, Soanes et al. 2014, Evans et al. 2015) to better inform the identification of important areas for shags at sea across a broader scale (Daunt et al. 2015).

Akin to many other seabird species (e.g. Pinaud et al. 2005, Ballance et al. 2006, Hamer et al. 2007, Pettex et al. 2012), my results (**Chapters 3, 4 and 5**) provide additional evidence that shags modify their foraging trips in response to annual fluctuations in environmental conditions (Wanless et al. 1998, Daunt et al. 2007, Bogdanova et al. 2014, Soanes et al. 2014). However, findings from **Chapter 3** suggest birds may be constrained in how they respond to these fluctuations based on their nesting location. On the Farne islands, in productive years birds showed sub-colony specific foraging locations between islands, similar findings have been documented elsewhere between different sub-colonies on the same island (Bogdanova et al. 2014). My results also indicate that these spatial constrains could be driving differences in foraging behaviours such as, dive depth and trip duration between sub-colonies. Proximity to suitable foraging habitat is likely to be driving differences in these behaviours on a small scale (**Chapter 3**) and is also likely to be contributing to differences in foraging ranges across larger spatial scales (**Chapter 2**). On the other hand, I also show these behavioural responses may be modified by environmental conditions. Most notably I found spatial segregation between colonies was more pronounced in years where conditions were more favourable (**Chapter 3**). Context dependent responses in foraging behaviour have been found in this species at other sites; on the Isle of May a relationship between population size and foraging range was apparent only in years with poor breeding success (Bogdanova et al. 2014). Davies et al. (2013) found the influence of population size on trip durations in northern gannets was much weaker when prey was more abundant. I used productivity to assess environmental conditions (akin to Bogdanova et al. 2014) suggesting lower productivity in certain years could be due to reduced food availability. However, weather could also have had an impact on foraging success and nestling survival (Elkins 1988, Finney et al. 1999, Elliott et al. 2005, Newell et al. 2015, **Chapters 3 and 5**).

Previous studies have found shags show consistent individual variation in the amount of time spent foraging during the winter and show consistent migratory behaviour (Daunt et al. 2014, Grist et al. 2014), In addition to this, I discovered shags show repeatability in their fine scale foraging behaviours across the breeding season (**Chapter 4**). This repeatability seems to be associated with the fact individuals' show foraging site fidelity (IFSF). Furthermore, I show that individuals vary in the levels of IFSF they express and this IFSF is largely retained across years (**Chapter 4**). **Chapter 4** is one of only a handful of studies which has been able to link IFSF to increased individual fitness, and is (to the best of my knowledge) the only study to do so over a short timescale in a short-ranging marine predator (c.f. Patrick and Weimerskirch (2017) who found short term fitness consequences of IFSF in a long-ranging pelagic seabird). The fitness benefits I documented were only evident in females and could potentially be linked to age. Variability in IFSF has been found to be independent of age in albatross (Patrick & Weimerskirch 2017), but appears to be higher in adult gannets than in immature birds (Votier et al. In Press). My findings are consistent with previous work that indicates a stronger relationship between time spent foraging and breeding phenology in females (Daunt et al. 2006), here early breeders spent less time foraging during pre-laying than late breeders. Early breeders are likely to be older more established birds (Potts et al. 1980, Daunt et al. 1999) and it has been shown that more experienced parents are more efficient foragers (Daunt et al. 2007). IFSF provides a potential mechanism that could contribute to these patterns; birds may spend less time foraging if they are able to travel directly to a known prey patch, which would decrease searching time and could also increase foraging success due to familiarity with the site.

The findings from **Chapter 4** indicate that individual variation exists within certain sub-sections of a population, which has the potential to create an age/sex skew within populations. IFSF only seems to have a noticeable impact on female fitness which might be linked to sexual size dimorphism in this species, i.e. females are generally are around 15–20% smaller than males (Daunt et al. 2001). Foraging appears to be more exacting for females, though the exact mechanisms behind this are unclear (Lewis et al. 2015). Foraging effort between sexes becomes more marked in poor weather conditions, while males may avoid foraging in extremely poor conditions females are less likely to 'sit it out' (Lewis et al. 2015). Lewis et al. (2015) suggest these differences may be due to reduced foraging and / or flight efficiency in females which makes them more vulnerable to the effects of adverse weather. The effect of consistency on body condition may also be more pronounced in females due to the importance of resource allocation to egg production and laying early in the breeding season. As the smaller and lighter sex they might also have less body reserves to rely on if conditions deteriorate. If IFSF becomes canalised, then birds may be less capable of moving to different areas if (or when) conditions deteriorate; this has the potential to decrease survival or reproductive output of older (more successful breeders) and could have detrimental effects on the species demographic trends. On the other hand, Daunt et al. (2007) showed that experienced individuals were better able to adjust their foraging effort when environmental conditions changed. At a population level, I show that birds seem to adjust their foraging effort (increased time spent foraging and time on the seabed) in a year with comparatively lower productivity than the previous seasons.

In **Chapter 5**, I investigated how individual differences in foraging trip characteristics interact with environmental variation, focusing on establishing which intrinsic and extrinsic factors shape individual foraging behaviours. The methods used in this chapter highlight a feature which is often overlooked in telemetry studies; that different aspects of foraging behaviour are often highly correlated with one another. To better understand the nature of behavioural responses, it is important to establish how variation in different foraging traits are related to one another. I use PCA to accomplish this and show, similar to previous findings (which analysed singular trip response variables), factors such as year, sex, sub-colony and weather influence foraging behaviours (Bogdanova et al. 2014, Soanes et al. 2014, Lewis et al. 2015). This method provides an informative way of identifying how different axes of variation in foraging behaviour respond to environmental variation and could be used more widely in this field to do so (e.g. Pettex et al. 2012, Patrick & Weimerskirch 2014b).

Soanes et al. (2014) examined factors which affect the fine scale foraging behaviour of shags breeding off the Welsh coast. I build upon this research by also considering how birds foraging decisions are influenced by short term changes in environmental conditions (i.e. weather). Using data from devices with lower spatial resolution (i.e. saltwater immersion devices), wind was found to affect shag foraging behaviour (Daunt et al. 2014, Lewis et al. 2015), and the current study provides information on how birds' respond to weather across a finer spatial and temporal scale in both their two and three-dimensional movements (**Chapters 3 and 5**). In **Chapter 5**, I tested birds' fine scale responses to prevailing weather conditions, my findings were consistent with those of Lewis et al. (2015), showing female birds seem more vulnerable to adverse weather conditions (**Chapter 5**). Females are known to increase their daily foraging times during periods of strong onshore winds (Lewis et al. 2015). I found they were more likely to respond to immediate unfavourable wind conditions by staying closer to the colony (**Chapter 5**). In addition, they could not or did not increase their dive depths in response to wind speed in the same way as males (**Chapter 3**), perhaps lending support to Lewis et al. (2015)'s theory that females may have reduced breath-hold capacity (reducing their maximum dive depth capacity) due to their smaller body mass. However, the deepest dive recorded during this study (c.50m) was from a female bird, and there were no overall sex differences apparent in mean maximum dive depths (**Chapter 3 and 5**). **Chapter 5** also highlights that individual birds did not all respond in the same way to fluctuating environmental conditions. The finding that individuals responded differently to annual variation in conditions has potential demographic implications, for instance if individuals with particular traits had greater flexibility in their foraging behaviour, and this requires further study.

6.3 Wider perspectives

The findings reported here add to the growing body of work which indicates the foraging behaviour of short-ranging species are constrained by similar mechanisms and respond in a comparable manor to mid- to long-ranging pelagic species (Irons 1998, Ainley et al. 2003, Potier et al. 2015, Corman et al. 2016, Wakefield et al. 2017). Therefore, these conclusions should be applicable across a broad range of seabird species and may also be relevant to other colonial central place foragers e.g. other bird species, certain species of bat, breeding seals and eusocial bees.

A positive relationship between population size and energy expenditure has been documented in other short range foragers (Jodice et al. 2006, Ballance et al. 2009). There was a slight trend between population size and foraging range in shags (**Chapter 2**), and similar relationships have been recorded in many other seabird species (Lewis et al. 2001, Oppel et al. 2015, Wakefield et al. 2017). However, environmental conditions can modify these relationships (Davies et al. 2013, Bogdanova et al. 2014), which may be why I found environmental conditions (e.g. habitat accessibility) had a stronger effect on foraging range than colony size. Density dependent effects on foraging distances/durations may not be apparent in smaller colonies (Davies et al. 2013, Jovani et al. 2016), as only six colonies were included in my analysis, data from additional colonies is required in order to verify this relationship in shags. A recent analysis using data from 13 different colonies, also found a positive relationship between colony size and foraging range in shags (Wakefield et al. 2017). If birds derive an advantage from foraging in large groups then this relationship could potentially be disrupted (i.e. larger colonies would experience increased foraging success and there would be little association between range and population size). Social foraging has been documented in European shags (Velando 2001, Evans et al. 2015) and in other *Phalacrocorax* species (Weimerskirch et al. 2010, Cook et al. 2017), however this does not appear to be the case at all breeding sites (**Chapter 3**).

When environmental conditions are favourable, shags respond to density dependent competition and show similar spatial resource partitioning as seen in other seabird species (Ainley et al. 2003, Wakefield et al. 2013, Corman et al. 2016, Wakefield et al. 2017). My results show spatial segregation patterns can vary annually, it is likely that other species could show variation in these patterns under differing conditions (as seems to be the case in Adelie penguins, Ainley et al. (2004)). How these species might respond is unclear, shags may be more strongly tied to static foraging habitats i.e. benthic sediments, whereas surface or pelagic feeders respond to more dynamic features such as oceanographic fronts (Hamer et al. 2009, Scales et al. 2014, Cox et al. 2016) or chlorophyll and SST (sea surface temperatures) (Robertson et al. 2014, Wakefield et al. 2017).

Differences in species foraging ecology between sites could mean their responses to changing prey availability could differ. For example, Angel et al. (2015) found gannets from two colonies in close proximity increased their foraging effort within restricted ranges during times of poor prey availability, whereas, Warwick-Evans et al. (2016) found individuals from the same colony all responded to declines in inter-annual conditions by visiting larger areas. Our findings fit with the theory that repeatability is likely to reflect the stability of a particular marine habitat and persistence of prey patches over time (Ceia & Ramos 2015, Sommerfeld et al. 2015). In gannets, the strength of the relationship between foraging trip durations and population size weakens under favourable environmental conditions (Davies et al. 2013). Context dependent variations in the repeatability of behavioural traits have been widely documented in other taxa e.g. fish (see review by Killen et al. 2016). It would be advisable for more studies examining spatial segregation and individual consistency to consider the extrinsic conditions under which they occur. Individual animals may differ in their responsiveness to environmental variation (i.e. plasticity) (reviewed in Dingemanse et al. 2010), with repeat measures from individuals across a range of conditions these 'behavioural reaction norms' can be measured (Dingemanse et al. 2010).

Individual variation and repeatability in foraging behaviour seem widespread in seabirds irrespective of their foraging range (Ceia & Ramos 2015). For example, consistency has been found in; long ranging oceanic surface feeders e.g. *Diomedeidae* and *Procellariidae* (Jaeger et al. 2010, Ceia et al. 2012, Patrick & Weimerskirch 2014a, Ramirez et al. 2016), members of the *Sulidae* family which tend to be mid ranging plunge diving predators (Hamer et al. 2007, Votier et al. 2010, Sommerfeld et al. 2013, Patrick et al. 2014, Wakefield et al. 2015), *Phalacrocorax* species which are generally short ranging pursuit diving predators (Wanless et al. 1992, Kato et al. 2000, Tremblay & Cherel 2005, Daunt et al. 2006, Ratcliffe et al. 2013, Harris et al. 2014, Potier et al. 2015, This study), various gull species (Irons 1998, Masello et al. 2013) and in flightless long and short ranging members of the *Spheniscidae* (Mattern et al. 2007, Baylis et al. 2015). Few studies report little to no individual specialisations in foraging behaviours (Ceia & Ramos 2015). However, most of these studies were conducted at high latitudes where prey resources are likely to be more predictable (Weimerskirch 2007) and there is still a lack of knowledge on whether these traits persist in tropical seabird populations (Ceia & Ramos 2015). Recently, Sommerfeld et al. (2015) examined foraging patterns in a pan-tropical seabird, the Masked booby, *Sula dactylatra*, and found birds showed strong foraging site fidelity close to the colony but showed less fidelity to more distant foraging sites. The authors attribute these differences to prey patch size and predictability of resources (Sommerfeld et al. 2015), which supports the theory that IFSF is modified by the spatio-temporal predictability of prey resources (Weimerskirch 2007).

Repeatable individual variation has been reported in many other taxa (Hayes & Jenkins 1997, Bell et al. 2009, Patrick et al. 2014, Killen et al. 2016). The results presented here add to this and highlight the fact that individual reactions to annual fluctuations in environmental conditions could differ. In addition to a potential sex skew in flexibility (as previously discussed), I also found individual trip characteristics changed between years, with some birds differing in the direction and magnitude of these responses (**see Chapter 5**). Conversely, Warwick-Evans et al. (2016) found individual northern gannets responded to inter-annual variation by visiting larger areas in all of their trips rather than individuals diversifying to visit different locations (but this study did not include annual repeat measures from the same individuals). A longer term dataset with higher sample size of repeat individuals would allow this to be analysed more comprehensively e.g. to quantify individual variation in plasticity (Reed et al. 2006, Nussey et al. 2007, Brommer et al. 2008, Dingemanse et al. 2010). However, if the fitness consequences linked with foraging consistency are context dependent, this could allow maintenance of multiple foraging ‘personalities’.

Individual variation in plasticity has been investigated primarily in the phenology of behaviours, for example, Reed et al. (2009) found significant among-individual variation and plasticity in laying dates of female guillemots, with individuals exhibiting variable responses to environmental conditions (though population-level trends were directionally similar to individual level trends). However, in the same species at a different site no individual variation in phenology was detected (Reed et al. 2006), this also supports the theory that repeatability in behaviour may be context dependent (Killen et al. 2016). Variability in behaviours may have important fitness consequences, I show levels of IFSF were associated with female body condition and laying dates within a breeding season. Few other studies have documented fitness advantages associated with consistency in foraging behaviour, of those which have, most indicate these benefits are only apparent across longer timescales (Bradshaw et al. 2004, Patrick & Weimerskirch 2014a). Recently, short term fitness consequences of IFSF were found in a long-ranging pelagic forager (Patrick & Weimerskirch 2017), however, this study is the first to document similar findings in a short-ranging diving seabird.

6.4 Relevance of findings to conservation

The majority of the conclusions from this thesis follow a similar vein; that it is important to consider that populations are made up of individuals (or groups of individuals) which could respond differently under changing environmental conditions. Examining these findings at an appropriate scale (i.e. at an individual, sub-colony, colony, regional or metapopulation level) could improve conservation management decisions and should be considered when modelling demographic trends. Some threats to seabirds may be widespread (e.g. climate change) whereas other threats may be more localised (e.g. marine renewable energy instalments or fisheries bycatch), so targeting conservation measures at an appropriate scale is vital. For instance, **Chapter 2** highlights that applying an average foraging radius (BirdLife-International. 2010, Thaxter et al. 2012) for the species across a broad scale may not be sufficient to identify important at sea areas for the species. However, the number of individuals tracked, the duration of tag deployments and the number of year's data can affect perceived foraging distributions (Soanes et al. 2013, Bogdanova et al. 2014).

Differences in the levels of IFSF (**Chapter 4**) indicates that consistent individuals (especially females), who are in better condition and breed earlier, could potentially have an increased reproductive output and higher survival rates than less consistent individuals. The extent of this variation within and between populations could alter demographic trends between colonies, though further work is needed to establish whether this variation is due to measurable intrinsic factors (e.g. age or health) or due to individual 'personalities' (which may be more difficult to model).

This study adds to the growing body of work which indicates consistency is dependent upon the temporal or spatial scale over which it is examined. For example, in **Chapter 4** this effect is highlighted showing individuals with low levels of consistency within a season can be highly consistent between years. Frederiksen et al. (2004) showed that the onset of breeding (i.e. phenology) reflects the scale at which seabirds perceive their environment. Species which disperse widely outside the breeding season were affected by large scale climatic drivers (North Atlantic Oscillation) whereas shags (which do not migrate too far from their colony in winter i.e. <500km (Grist et al. 2014)) were more affected by local scale effects (Frederiksen et al. 2004).

Therefore, choosing an appropriate scale when examining consistency is important, e.g. northern gannets are known to search over seasonally persistent fronts at scales of around 10Km but focus foraging effort in at smaller scales within these areas (Hamer et al. 2009, Scales et al. 2014). To ascertain an appropriate scale to examine IFSF over for shags, I calculated birds' mean area of active use within single foraging trips and used this value to establish kernel overlap statistics (**see Chapter 4**). Due to the fact surface intervals between dives were often less than the sampling resolution used in this study (60 seconds) relocations between dives were often infrequent; it would be useful to validate the average size of foraging areas birds use within a foraging bout with another method, e.g. visual observations with rangefinders or higher resolution telemetry data.

I found habitat availability was important in determining the foraging behaviour of breeding birds both within and between colonies (**Chapters 2 and 3**). In addition birds altered their foraging behaviours in response to immediate weather conditions at a local scale (**Chapter 3 and 5**). Environmental conditions are likely to be correlated over regional scales (Frederiksen et al. 2007, Lewis et al. 2015) and birds' diets and habitat associations also appear similar at this scale (see **Chapter 2**). Yet, in short ranging species like shags with low dispersal rates between breeding sites (Barlow et al. 2013), colonies could effectively become independent at small scales (though not to the extent that they differ genetically (Barlow et al. 2011)). I document how this can result in differences in the foraging patterns of birds breeding on two islands in close proximity (**Chapter 3**). In this case the distribution and availability of prey could drive differences in productivity even between close colonies. For example, in 2016, productivity of shags on the Farne islands was lower than the previous two years (Tooth et al. 2016) whereas the Isle of May had the most successful breeding season on record (Newell et al. 2016). As weather can affect the foraging capabilities of this species, it is difficult to disentangle whether this was due to prolonged periods of adverse weather preventing adults from providing adequate resources, or if prey availability was low around the Farnes in this year.

With an increased knowledge of how and why behavioural traits vary, predictions of species-level responses to environmental change and our ability to identify and protect important areas for this species can be improved. Recently tracking data from multiple seabird colonies has become available (Wakefield et al. 2017); this has enabled a more in depth analyses of the factors which are shaping colony specific at-sea distributions for certain seabird species (including European shags). These findings were then used to predict important areas for species at a colony level for sites tracking data are not available (Wakefield et al. 2017), incorporating tracking data from additional colonies (i.e. those not included in initial models) could help to validate such predictions. Akin to findings presented in this thesis, Wakefield et al. (2017) found habitat availability, accessibility and sympatric density-dependent competition were important in determining the at sea distribution of shags. Our results suggested that distance to the shore might be an important parameter influencing shag foraging distributions, this is supported by Wakefield et al. (2017)'s finding that shags showed a preference for mixed waters close to the coast.

Wakefield et al. (2017) found density dependent competition did not have a strong effect on shag distributions between neighbouring colonies. However, by looking at this across multiple islands in close proximity with higher shag breeding densities I show spatial segregation in foraging areas does occur in this species (**Chapter 3**). Yet these segregation patterns were not maintained in all years of my study, this highlights the scale at which birds operate as functional units (e.g. separate colonies) may have a dynamic nature. With an improved knowledge of colony-specific foraging distributions (e.g. **Chapter 3**, Wakefield et al. 2017), the potential impacts of anthropogenic developments and climatic changes could be assigned to specific colonies, which means marine spatial planning decisions could be made at appropriate scales. Understanding how environmental conditions can alter these distributions would make colony-specific management decisions and demographic predictions more robust especially in light of future climate change.

The changing patterns of spatial usage with environmental conditions observed during this study (**Chapter 3**) could provide a useful study system on which to test how resource availability and distribution relate to species foraging distribution patterns (e.g. Warwick-Evans et al. 2016). A study of this nature would however require prey availability within patches to be assessed (e.g. as per Grémillet et al. 2004). The main prey patches likely to be used by shags around the Farnes are within a confined accessible area (i.e. close to the islands) and are at depths which could be reached by SCUBA divers, so a study of this nature could be feasible.

The presence of consistent individual variability in shag populations (**Chapter 4**), might affect the accuracy of models used to predict species at sea distributions (Wakefield et al. 2017). As spatial modelling techniques advance an understanding of the extent of IFSF within populations and the mechanisms behind it will be crucial in order to develop accurate hierarchical modelling frameworks. The level of IFSF in a population could have important implications for managing interactions between birds and fisheries, especially in the Mediterranean region where shags are particularly vulnerable to entanglement gill-net fisheries (Velando & Freire 2002). A knowledge of which members of a population could be subject to bycatch induced mortality and the location of at risk areas could help predict survival estimates and demographic trends for these populations. Similar applications would also be relevant to understanding the population dynamics of these species under a period environmental change.

6.5 Priorities for future research

Although this study highlights that consistency varies between individuals and that individuals may differ in their responses to environmental change, we cannot fully ascertain what is driving some individuals to be fixed and others more flexible. Ongoing work has found parasite burdens can impact the time allocated to foraging behaviours in shags. Birds with higher parasite loads spend less time travelling to foraging areas; i.e. they may spend less time in flight (Hicks et al. 2016). Intrinsic personality traits, such as boldness, can also impact foraging behaviours (Patrick & Weimerskirch 2014a). Shags showed varying degrees of aggressiveness in response to capture and handling procedures during this study; quantifying these traits and measuring their relationships with foraging parameters and reproductive success could be an interesting avenue for future studies.

In this study I suggest that age could explain individual variance in IFSF (Chapter 4), however, I could not establish how fixed these behaviours were over longer timescales. Older individuals may be better able to adjust behaviours to match environmental conditions (Daunt et al. 2007), however, without longer term datasets or experimental manipulations understanding how flexible individuals are will be difficult to establish. Birds responses to environmental perturbations could provide an insight into the species ability to respond to changing conditions; For example, after the Prestige oil spill in 2002, shags breeding around the Spanish coast were able to alter their foraging behaviour, switching from sandeel to more pelagic species of fish (Moreno et al. 2013). At other colonies birds appear robust to annual changes in the abundance of sandeel in their diet (Swann et al. 2008, Newell et al. 2016). However, the proportion of sandeel in seabirds' diets is generally linked with higher breeding success (Rindorf et al. 2000) and shags breeding at other locations e.g. Shetland isles have experienced high rates of breeding failure and near colony collapse due to declines in sandeel availability (Huebeck 2015). Recent trends suggest sandeel are becoming less frequent in diet at other UK colonies (Howells et al. 2016, Newell et al. 2016). Norwegian shag populations, which are less reliant on sandeel, seemed to be faring better than the rest of the North Atlantic population (Bustnes et al. 2013), but the latest population trends now suggest shags are declining across Europe (BirdLife-International 2017).

The species' ability to adapt will ultimately depend on the presence of alternate food sources, and perhaps individuals' ability to maintain adequate foraging success if they deviate from their consistent foraging areas (see **Chapter 4**). Shags' physiological constraints mean they are particularly vulnerable during poor weather conditions (Frederiksen et al. 2008, Daunt et al. 2014, Lewis et al. 2015, **Chapter 5**), so even when prey are present birds may be unable to access (or forage efficiently in) certain areas due to adverse weather conditions. Recent evidence suggests females may be particularly at risk from the effects of increased wind speeds (Lewis et al. 2015, **Chapter 5**). Birds are likely to respond to weather conditions in similar ways (i.e. as a species they have similar physiological constraints), however, certain locations (i.e. colonies) may be differentially affected due to regional differences in prevailing wind conditions and projected changes to weather conditions. With predicted changes to global climates likely to increase wind speeds across the European region (McInnes et al. 2011) and effects of climate induced changes already reported (Frederiksen et al. 2013), this species may be particularly at risk (Burthe et al. 2014, Russell et al. 2015).

My study was undertaken over a relatively short timescale (three breeding seasons) which makes it difficult to capture a full range of environmental conditions. The results presented within this thesis suggest foraging patterns differ in poor years, but without multiple good/bad years to compare these results must be interpreted with caution.

Device attachment did not appear to have any direct adverse effects on birds (see **Chapter 2**). However, while I obtained a high return rate from telemetry deployments (see **Chapter 2**), obtaining tracking data from the same individuals across multiple years was more challenging. Most of my study birds returned to breed in subsequent years (between 2014 and 2015, 92% of adults tagged in the previous season were seen in at the breeding colony, and between 2015 and 2016, 89% were re-sighted), but some changed nesting locations between years - moving into sites which were inaccessible. This, coupled with technology failures on some repeat birds resulted in relatively small sample sizes of repeat individuals, especially across all three years. In addition, certain individuals proved easier to catch (and re-catch) than others. Personality traits such as boldness have been shown to be repeatable and can result in spatial variations in foraging areas in other species (Patrick et al. 2013, Patrick & Weimerskirch 2014a). If 'catchability' is a consequence of individual differences in stress tolerance levels or 'personality' traits (Grace & Anderson 2014, Patrick & Weimerskirch 2014b) this could introduce a potential source of bias in my dataset. Nest site locations are less likely to change in older well established pairs, particularly in males (Aebischer et al. 1995). Therefore, these repeat birds could potentially be bolder, more established individuals, and this requires further study.

Results from my research indicate that birds may show differences in where they forage based on time of day (particularly at dawn/dusk) (**Chapter 3 and 5**). It would thus be useful to examine the level of repeatability in these diurnal patterns. These findings could indicate how capable birds are of adapting their behaviour to prevailing environmental conditions. Temporal patterns could mask high levels of individual repeatability, but studies looking at the spatial consistency in relation to factors such as time/tide are scarce.

Previous work has shown birds may switch foraging areas and habitats within a single trip (Watanuki et al. 2008). The IFSF I report might seem contradictory to these findings, however, I did not examine individual habitat associations. It would be informative to examine whether the most consistent birds are repeatable in their associations with particular benthic habitats. Shags have been reported to switch between benthic and pelagic foraging in the English Channel (Grémillet et al. 1998) but have mostly been recorded as primarily benthic foragers elsewhere (Wanless et al. 1991, Watanuki et al. 2008). It could be revealing to examine diving tactics in relation to bathymetry at this site; In the year with the highest productivity (2014), bait balls and mixed feeding flocks (including shags) could be seen from the islands (pers. obs.). I predict there would be a higher percentage of mid-water dives recorded in this year due to birds making use of these opportunistic foraging prospects, which could potentially have weakened individual site foraging fidelity.

Additional investigations are required to understand why some individuals are more repeatable than others. A longer term dataset where individual ages and life histories are known would enable a more in depth examination of the causes and consequences of individual consistency. This could also provide a deeper insight into how consistency changes with regards to environmental conditions. Northern gannets were found to show consistency beyond a win–stay, lose–shift foraging strategy, largely due to the temporal persistence of IFSF (Wakefield et al. 2015). To ensure the repeatability observed within and between years in this study is not just a consequence of long-term environmental predictability (e.g. Davoren et al. 2003) this could be investigated further for shags. If a measure of foraging success within specific patches could be established e.g. catch per unit effort (Grémillet et al. 1996) or prey capture events (Chimienti et al. 2016), these questions could be answered without collecting data over many more years. It may be possible to examine this within existing data; dive bottom time or tortuosity in the dive profile could be used as a proxy for prey capture attempts (Wanless et al. 1993, Simeone & Wilson 2003, Sala et al. 2012). However, this approach would be more robust if ‘prey capture attempts’ could be validated e.g. using accelerometer data, stomach temperature loggers or nest balances to establish prey capture success from each patch.

6.6 Concluding remarks

In conclusion, this study has revealed that certain members of a population may be more susceptible to risk than others, and that these effects can differ depending on environmental conditions. These environmental influences could be fixed, i.e. distance of suitable foraging habitat from the colony, or variable, i.e. effects of weather or annual fluctuations in prey availability and distributions. I reiterate the notion that has emerged from the recent rise in individual based studies; that population level behaviour may mask individual specialisations and this could result in unequal responses of subsections of the population to anthropogenic and environmental stressors. As shags are constrained to specific areas (Potts 1969, Aebischer & Wanless 1992, Aebischer 1995, Barlow et al. 2013), how resilient each population will be to change will ultimately depend on individual plasticity in birds' ability to change their foraging locations, tactics or main prey sources. However, these factors may be influenced by colony specific effects such as population size and proximity to suitable foraging habitats. To effectively conserve any species, individual variations in behavioural responses and the context under which they occur must be established. This information will be vital in order to predict demographic trends and species distributions in light of future environmental change.

6.7 Literature cited

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Appendix A (Chapter 2)

A.1 Tracking data collected from shags breeding on the Farnes prior to 2014

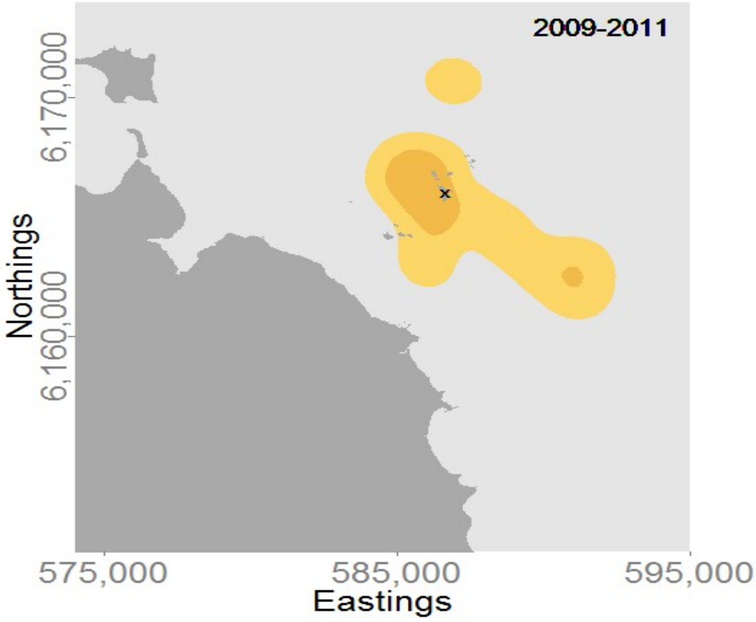


Figure A1: Foraging areas of chick-rearing shags tracked on the Farne Islands between 2009 and 2011. Kernels represent core (50%UD dark yellow) and areas of active use (95%UD light yellow) for all potential foraging locations (i.e. birds resting on water away from the colony). All birds n=4 were nesting on Brownsman Island. Colony location is marked with an X.

Table A6-1: Dive data from 2002-2009 showing mean and maximum depths recorded for each individual tracked. The duration of the device deployments are shown as n days.

Year	ID	mean depth at bottom phase of dives (m)	±SD (m)	max depth (m)	n dives recorded	n days
2002	1364090	34.0	8.5	44.0	50	1
2003	1323174	57.4	8.3	71.6	256	3
	1345308	26.9	17.3	72.8	507	3
	1364087	30.7	17.3	62.8	202	3
	1364088	23.4	5.6	44.0	90	2
2004	1343009	29.3	4.8	37.0	129	1
	1345457	32.7	5.4	41.4	129	3
2009	1364476	17.9	3.5	23.4	229	4
	1407246	17.4	2.9	23.8	95	4

Appendix B (Chapter 3)

B.1 Supplementary model results

Table B1. Model-averaging results.

Response variable	**rank**	**Top models (ΔAICc < 2)**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Trip duration	1	sub-colony + time of day^2 + year + time of day	9	-378.17	774.58	0	0.15
	2	sub-colony + time of day^2 + year	8	-379.37	774.92	0.34	0.12
	3	sub-colony + time of day^2 + year + date + time of day	10	-377.39	775.07	0.49	0.12
	4	sub-colony + time of day^2 + year + date	9	-378.51	775.26	0.68	0.11
	5	sub-colony + time of day^2 + year + time of day + wind speed	10	-377.77	775.83	1.24	0.08
	6	sub-colony + wind direction + time of day^2 + year	9	-378.94	776.11	1.53	0.07
	7	sub-colony + time of day^2 + year + date + time of day + wind speed	11	-376.99	776.32	1.74	0.06
	8	sub-colony + sex + time of day^2 + year + time of day	10	-378.03	776.35	1.77	0.06
	9	sub-colony + wind direction + time of day^2 + year + time of day	10	-378.03	776.35	1.77	0.06
	10	sub-colony + wind direction + time of day^2 + year + date	10	-378.05	776.39	1.81	0.06
	11	sub-colony + time of day^2 + year + wind speed	9	-379.09	776.42	1.84	0.06
	12	sub-colony + time of day^2 + year + brood size + time of day	10	-378.09	776.46	1.88	0.06
Foraging range	1	sub-colony + sex + time of day^2 + year + sub-colony*sex + sub-colony*year + sex*year	14	-695.05	1418.66	0	0.07
	2	sub-colony + sex + time of day^2 + year + date + sub-colony*sex + sub-colony*year + sex*year	15	-694.03	1418.7	0.04	0.06
	3	sub-colony + sex + time of day^2 + year + date + sub-colony*year + sex*year	14	-695.21	1418.97	0.31	0.06
	4	sub-colony + sex + time of day^2 + year + sub-colony*year + sex*year	13	-696.4	1419.27	0.61	0.05
	5	sub-colony + sex + time of day^2 + year + wind speed + sub-colony*sex + sub-colony*year + sex*year + sex*sub-colony*sex	16	-693.33	1419.37	0.71	0.05
	6	sub-colony + sex + time of day^2 + year + date + wind speed + sub-colony*sex + sub-colony*year + sex*year + sex*sub-colony*sex	17	-692.45	1419.7	1.04	0.04
	7	sub-colony + sex + time of day^2 + year + date + time of day + sub-colony*sex + sub-colony*year + sex*year	16	-693.5	1419.71	1.05	0.04
	8	sub-colony + sex + time of day^2 + year + time of day + sub-colony*sex + sub-colony*year + sex*year	15	-694.57	1419.78	1.11	0.04
	9	sub-colony + wind direction + sex + time of day^2 + year + date + sub-colony*sex + sub-colony*year + sex*year	16	-693.53	1419.78	1.12	0.04
	10	sub-colony + wind direction + sex + time of day^2 + year + sub-colony*sex + sub-colony*year + sex*year	15	-694.6	1419.82	1.16	0.04
	11	sub-colony + sex + time of day^2 + year + wind speed + sub-colony*year + sex*year + sex*sub-colony*sex	15	-694.63	1419.89	1.23	0.04
	12	sub-colony + sex + time of day^2 + year + date + wind speed + sub-colony*year + sex*year + sex*sub-colony*sex	16	-693.6	1419.91	1.25	0.04
	13	sub-colony + sex + time of day^2 + year + date + time of day + sub-colony*year + sex*year	15	-694.65	1419.93	1.27	0.03
	14	sub-colony + wind direction + sex + time of day^2 + year + date + sub-colony*year + sex*year	15	-694.66	1419.96	1.29	0.03
	15	sub-colony + wind direction + sex + time of day^2 + year + date + time of day + sub-colony*sex + sub-colony*year + sex*year	17	-692.61	1420.03	1.37	0.03
	16	sub-colony + wind direction + sex + time of day^2 + year + date + time of day + sub-colony*year + sex*year	16	-693.7	1420.11	1.45	0.03
	17	sub-colony + sex + time of day^2 + year + time of day + wind speed + sub-colony*sex + sub-colony*year + sex*year + sex*sub-colony*sex	17	-692.71	1420.24	1.58	0.03
	18	sub-colony + wind direction + sex + time of day^2 + year + time of day + sub-colony*sex + sub-colony*year + sex*year	16	-693.77	1420.25	1.59	0.03
	19	sub-colony + wind direction + sex + time of day^2 + year + sub-colony*year + sex*year	14	-695.89	1420.34	1.68	0.03
	20	sub-colony + sex + time of day^2 + year + time of day + sub-colony*year + sex*year	14	-695.89	1420.34	1.68	0.03
	21	sub-colony + wind direction + sex + time of day^2 + year + time of day + wind speed + sub-colony*sex + sub-colony*year + sex*year + sex*sub-colony*sex	18	-691.75	1420.4	1.74	0.03
	22	sub-colony + sex + time of day^2 + year + wind speed + sub-colony*sex + sub-colony*year + sex*year	15	-694.91	1420.46	1.79	0.03

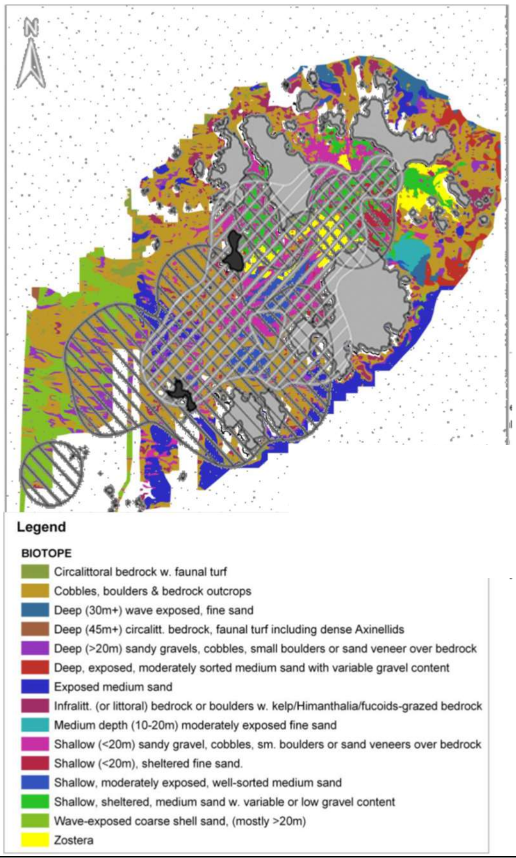
	23	sub-colony + wind direction + sex + time of day^2 + year + wind speed + sub-colony*sex + sub-colony*year + sex*year + sex*sub-colony*sex	17	-692.83	1420.47	1.81	0.03
	24	sub-colony + sex + time of day^2 + year + date + time of day + wind speed + sub-colony*sex + sub-colony*year + sex*year + sex*sub-colony*sex	18	-691.79	1420.48	1.82	0.03
	25	sub-colony + wind direction + sex + time of day^2 + year + date + time of day + wind speed + sub-colony*sex + sub-colony*year + sex*year + sex*sub-colony*sex	19	-690.75	1420.5	1.83	0.03
	26	sub-colony + wind direction + sex + time of day^2 + year + date + time of day + wind speed + sub-colony*year + sex*year + sex*sub-colony*sex	18	-691.82	1420.54	1.88	0.03
	27	sub-colony + sex + time of day^2 + year + date + wind speed + sub-colony*sex + sub-colony*year + sex*year	16	-693.91	1420.55	1.88	0.03
	28	sub-colony + sex + time of day^2 + year + date + time of day + wind speed + sub-colony*year + sex*year + sex*sub-colony*sex	17	-692.92	1420.64	1.98	0.02
Max dive depth	1	sub-colony + wind direction + sex + tidal state + year + brood size + wind speed + sex*year	16	-171.1	374.98	0	0.15
	2	sub-colony + wind direction + sex + time of day^2 + tidal state + year + brood size + wind speed + sex*year	17	-170.24	375.37	0.39	0.12
	3	sub-colony + wind direction + sex + tidal state + year + date + brood size + wind speed + sex*year	17	-170.4	375.69	0.71	0.1
	4	sub-colony + wind direction + sex + tidal state + year + brood size + wind speed + sex*year + sex*wind speed	17	-170.5	375.89	0.91	0.09
	5	sub-colony + wind direction + sex + tidal state + year + brood size + wind speed + sex*wind direction + sex*year	17	-170.51	375.92	0.93	0.09
	6	sub-colony + wind direction + sex + time of day^2 + tidal state + year + date + brood size + wind speed + sex*year	18	-169.59	376.17	1.19	0.08
	7	sub-colony + wind direction + sex + time of day^2 + tidal state + year + brood size + wind speed + sex*wind direction + sex*year	18	-169.68	376.36	1.38	0.07
	8	sub-colony + wind direction + sex + tidal state + year + date + brood size + wind speed + sex*year + sex*wind speed	18	-169.69	376.38	1.39	0.07
	9	sub-colony + wind direction + sex + time of day^2 + tidal state + year + brood size + wind speed + sex*year + sex*wind speed	18	-169.71	376.41	1.43	0.07
	10	sub-colony + wind direction + sex + tidal state + year + brood size + wind speed + sex*wind direction + sex*year + sex*wind speed	18	-169.71	376.42	1.44	0.07
	11	sub-colony + wind direction + sex + tidal state + year + date + brood size + wind speed + sex*wind direction + sex*year	18	-169.87	376.73	1.75	0.06
Time at seabed	1	sub-colony + sex + time of day^2 + year + time of day + sub-colony*year + sex*year	14	-489.37	1007.35	0	0.17
	2	sub-colony + time of day^2 + year + time of day	9	-494.83	1007.92	0.57	0.13
	3	sub-colony + time of day^2 + year + date + time of day	10	-494.03	1008.38	1.02	0.1
	4	sub-colony + sex + time of day^2 + year + time of day + sub-colony*sex + sub-colony*year + sex*year	15	-488.88	1008.44	1.09	0.1
	5	sub-colony + sex + time of day^2 + year + time of day + wind speed + sub-colony*year + sex*year	15	-488.96	1008.62	1.27	0.09
	6	sub-colony + sex + time of day^2 + year + date + time of day + sub-colony*year + sex*year	15	-489.01	1008.72	1.37	0.09
	7	sub-colony + sex + time of day^2 + year + brood size + time of day + sub-colony*year + sex*year	15	-489.02	1008.73	1.38	0.09
	8	sub-colony + time of day^2 + year + time of day + wind speed	10	-494.27	1008.85	1.5	0.08
	9	sub-colony + wind direction + sex + time of day^2 + year + time of day + sub-colony*year + sex*year	15	-489.25	1009.19	1.84	0.07
	10	sub-colony + sex + time of day^2 + year + time of day + sex*year	12	-492.41	1009.28	1.92	0.07

Response variable	rank	Top models (ΔAICc < 2)	df	logLik	AICc	ΔAICc	weight
Trip duration (mins) [log]	1	colony + time of day^2 + year + time of day	9	-371.95	762.13	0	0.17
	2	colony + time of day^2 + year	8	-373.09	762.36	0.23	0.15
	3	colony + time of day^2 + year + time of day + wind speed	10	-371.45	763.19	1.06	0.1
	4	colony + time of day^2 + year + date + time of day	10	-371.58	763.45	1.32	0.09
	5	colony + time of day^2 + year + date	9	-372.66	763.55	1.42	0.08
	6	colony + time of day^2 + year + wind speed	9	-372.75	763.73	1.59	0.07
	7	colony + time of day^2 + year + brood size + time of day	10	-371.73	763.74	1.61	0.07

	8	colony + wind direction + time of day^2 + year	9	-372.75	763.74	1.61	0.07
	9	colony + time of day^2 + year + brood size	9	-372.85	763.94	1.81	0.07
	10	colony + sex + time of day^2 + year + time of day	10	-371.84	763.97	1.84	0.07
	11	colony + wind direction + time of day^2 + year + time of day	10	-371.86	764	1.87	0.07
Foraging range (km distance to TP) [log]	1	colony + sex + time of day^2 + year + date + colony*sex + colony*year + sex*year	15	-685.73	1402.09	0	0.09
	2	colony + sex + time of day^2 + year + date + colony*year + sex*year	14	-686.78	1402.11	0.02	0.09
	3	colony + sex + time of day^2 + year + colony*sex + colony*year + sex*year	14	-686.98	1402.51	0.42	0.07
	4	colony + sex + time of day^2 + year + colony*year + sex*year	13	-688.18	1402.83	0.74	0.06
	5	colony + sex + time of day^2 + year + date + wind speed + colony*sex + colony*year + sex*year + sex*wind speed	17	-684.07	1402.95	0.86	0.06
	6	colony + sex + time of day^2 + year + date + wind speed + colony*year + sex*year + sex*wind speed	16	-685.14	1403	0.91	0.06
	7	colony + sex + time of day^2 + year + wind speed + colony*sex + colony*year + sex*year + sex*wind speed	16	-685.18	1403.07	0.98	0.05
	8	colony + sex + time of day^2 + year + date + time of day + colony*year + sex*year	15	-686.24	1403.11	1.02	0.05
	9	colony + sex + time of day^2 + year + date + time of day + colony*sex + colony*year + sex*year	16	-685.21	1403.14	1.05	0.05
	10	colony + sex + time of day^2 + year + wind speed + colony*year + sex*year + sex*wind speed	15	-686.39	1403.41	1.32	0.05
	11	colony + sex + time of day^2 + year + date + wind speed + colony*sex + colony*year + sex*year	16	-685.42	1403.55	1.46	0.04
	12	colony + sex + time of day^2 + year + date + wind speed + colony*year + sex*year	15	-686.48	1403.58	1.49	0.04
	13	colony + sex + time of day^2 + year + date + time of day + wind speed + colony*year + sex*year + sex*wind speed	17	-684.42	1403.65	1.56	0.04
	14	colony + sex + time of day^2 + year + date + time of day + wind speed + colony*sex + colony*year + sex*year + sex*wind speed	18	-683.38	1403.66	1.57	0.04
	15	colony + wind direction + sex + time of day^2 + year + date + colony*year + sex*year	15	-686.53	1403.68	1.59	0.04
	16	colony + wind direction + sex + time of day^2 + year + date + colony*sex + colony*year + sex*year	16	-685.49	1403.69	1.6	0.04
	17	colony + sex + time of day^2 + year + time of day + colony*sex + colony*year + sex*year	15	-686.54	1403.72	1.63	0.04
	18	colony + sex + time of day^2 + year + wind speed + colony*sex + colony*year + sex*year	15	-686.63	1403.89	1.8	0.04
	19	colony + sex + time of day^2 + year + time of day + wind speed + colony*sex + colony*year + sex*year + sex*wind speed	17	-684.57	1403.94	1.85	0.03
		colony + sex + time of day^2 + year + time of day + colony*year + sex*year	14	-687.73	1404.01	1.92	0.03
Max dive depths [log]	1	colony + wind direction + sex + tidal state + year + date + brood size + wind speed + sex*year	17	-169.66	374.21	0	0.08
	2	colony + wind direction + sex + time of day^2 + tidal state + year + date + brood size + wind speed + sex*year	18	-168.75	374.5	0.29	0.07
	3	colony + wind direction + sex + tidal state + year + brood size + wind speed + sex*year	16	-170.86	374.5	0.29	0.07
	4	colony + wind direction + sex + time of day^2 + tidal state + year + brood size + wind speed + sex*year	17	-169.92	374.73	0.52	0.06
	5	colony + wind direction + sex + tidal state + year + date + brood size + wind speed + sex*wind direction + sex*year	18	-169.06	375.11	0.89	0.05
	6	colony + wind direction + sex + tidal state + year + date + brood size + wind speed + sex*year + sex*wind speed	18	-169.08	375.15	0.94	0.05

	7	colony + wind direction + sex + tidal state + year + brood size + wind speed + sex*wind direction + sex*year	17	-170.2	375.3	1.08	0.05
	8	colony + wind direction + sex + time of day^2 + tidal state + year + date + brood size + wind speed + sex*wind direction + sex*year	19	-168.17	375.44	1.23	0.04
	9	colony + wind direction + sex + time of day^2 + tidal state + year + brood size + wind speed + sex*wind direction + sex*year	18	-169.29	375.57	1.36	0.04
	10	colony + wind direction + sex + tidal state + year + brood size + wind speed + sex*year + sex*wind speed	17	-170.34	375.57	1.36	0.04
	11	colony + wind direction + sex + time of day^2 + tidal state + year + date + brood size + wind speed + sex*year + sex*wind speed	19	-168.25	375.6	1.38	0.04
	12	colony + sex + time of day^2 + tidal state + year + date + brood size + wind speed + sex*year	17	-170.39	375.68	1.46	0.04
	13	colony + wind direction + sex + tidal state + year + date + brood size + wind speed + sex*wind direction + sex*year + sex*wind speed	19	-168.29	375.68	1.46	0.04
	14	colony + wind direction + sex + tidal state + year + wind speed + sex*year	15	-172.54	375.77	1.56	0.04
	15	colony + wind direction + sex + tidal state + year + date + wind speed + sex*year	16	-171.54	375.87	1.66	0.04
	16	colony + wind direction + sex + time of day^2 + tidal state + year + wind speed + sex*year	16	-171.55	375.9	1.68	0.04
	17	colony + wind direction + sex + time of day^2 + tidal state + year + brood size + wind speed + sex*year + sex*wind speed	18	-169.48	375.95	1.74	0.03
	18	colony + wind direction + sex + tidal state + year + brood size + wind speed + sex*wind direction + sex*year + sex*wind speed	18	-169.5	376	1.79	0.03
	19	colony + wind direction + sex + time of day^2 + tidal state + year + date + wind speed + sex*year	17	-170.59	376.06	1.84	0.03
	20	colony + wind direction + tidal state + year + date + brood size + wind speed	14	-173.77	376.15	1.94	0.03
	21	colony + wind direction + sex + time of day^2 + tidal state + year + date + brood size + wind speed + sex*wind direction + sex*year + sex*wind speed	20	-167.49	376.2	1.98	0.03
	22	colony + wind direction + time of day^2 + tidal state + year + date + brood size + wind speed	15	-172.76	376.21	2	0.03
Total time spent on seabed (secs) [log]	1	colony + time of day^2 + year + time of day	9	-479.43	977.12	0	0.36
	2	colony + time of day^2 + year + date + time of day	10	-479.07	978.45	1.33	0.18
	3	colony + time of day^2 + year + time of day + wind speed	10	-479.07	978.46	1.35	0.18
	4	colony + time of day^2 + year + brood size+ time of day	10	-479.34	978.99	1.88	0.14
	5	colony + wind direction + time of day^2 + year + time of day	10	-479.38	979.08	1.97	0.13

B.2 Habitat comparisons between sites



Foraging areas of shags breeding on the Scilly isles overlaid onto a benthic habitat map. Figures adapted from Evans et al. 2015 and Scilly Isles management plan, Natural England 2005.

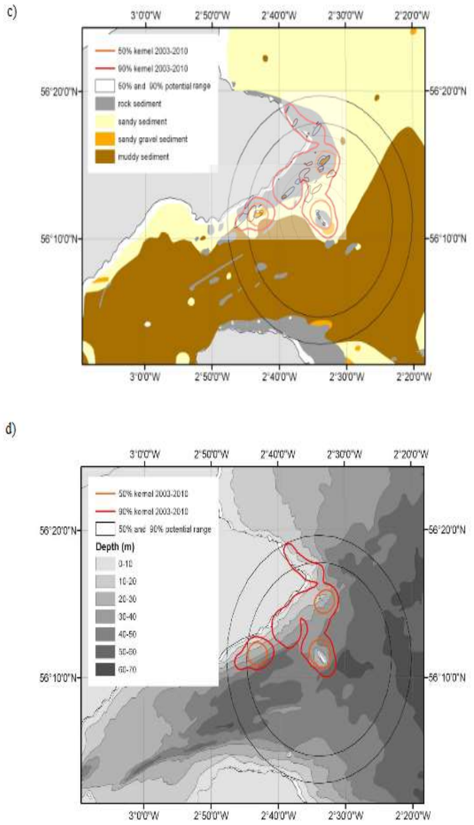
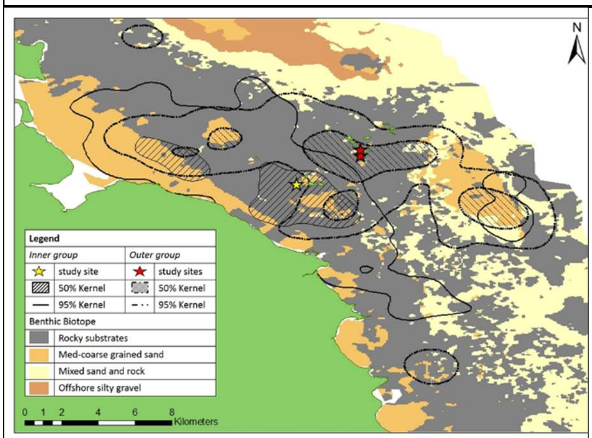
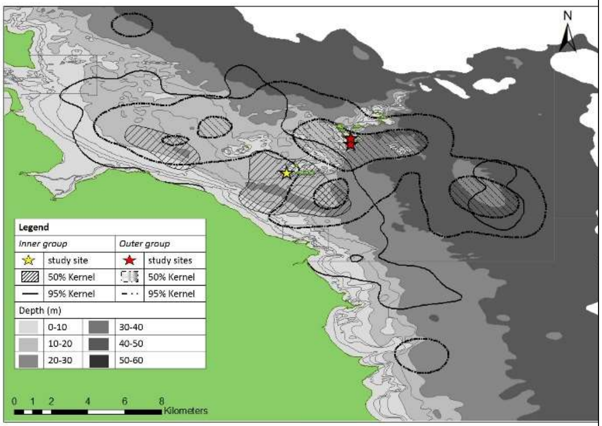


Figure12 (cont). Kernel density distributions (50% and 90% for 2003-2010) in relation to c) seabed sediment and d) bathymetry. Potential foraging ranges as set by the 50% and 90% kernels and used in the habitat preference analysis also shown.



Farnes benthic and bathymetry data with overlap results from this study.

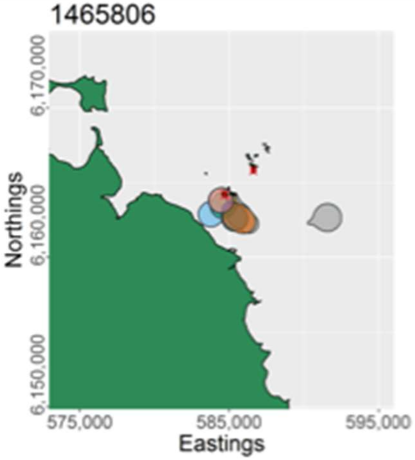
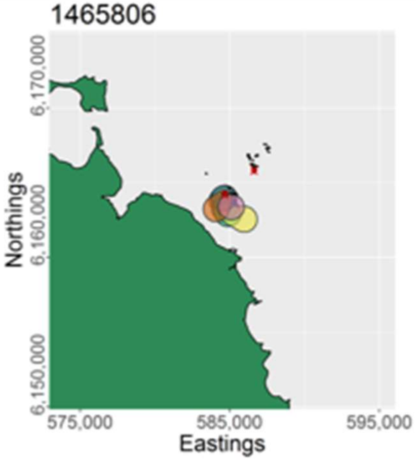
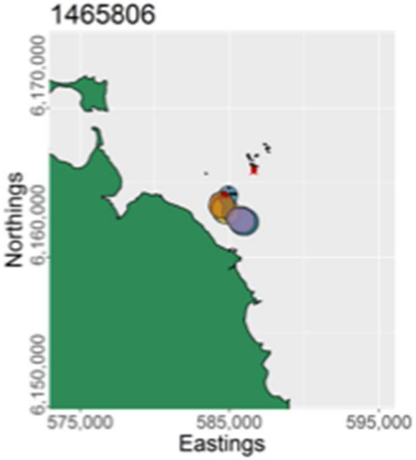
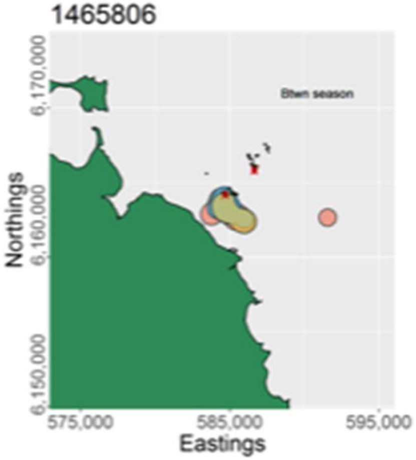


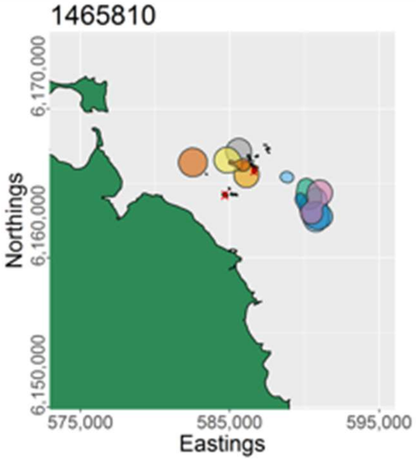
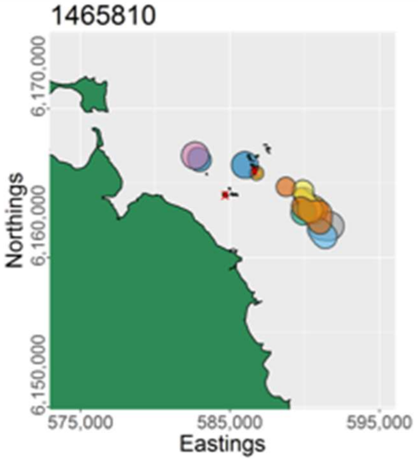
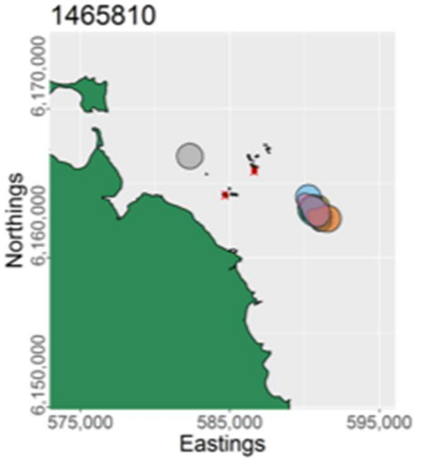
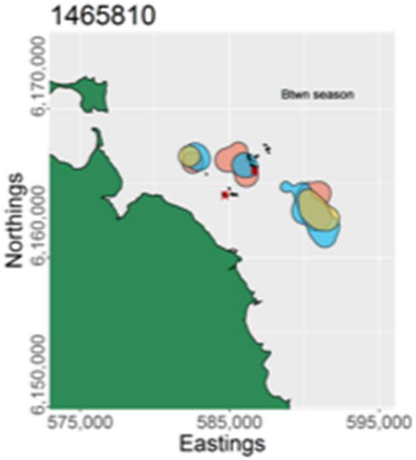
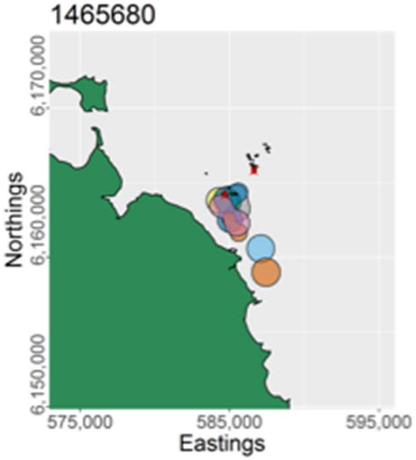
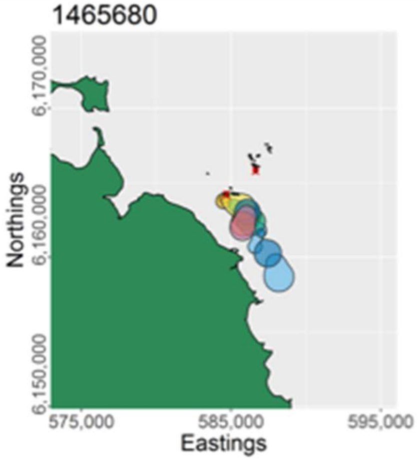
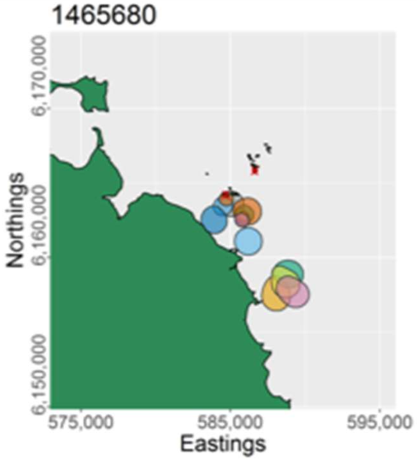
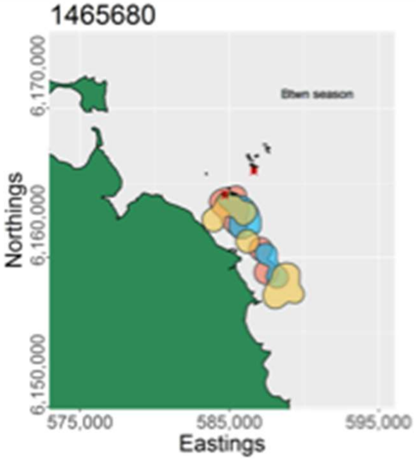
Farnes benthic and bathymetry data with overlap results from this study.

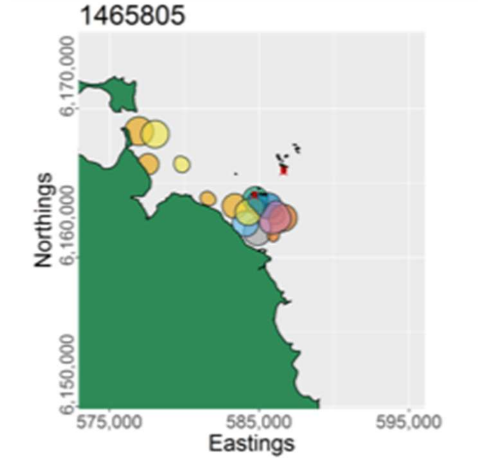
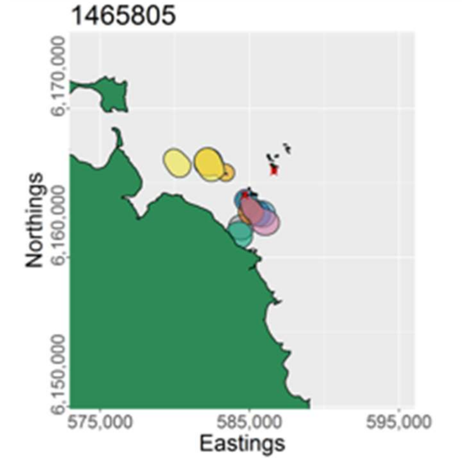
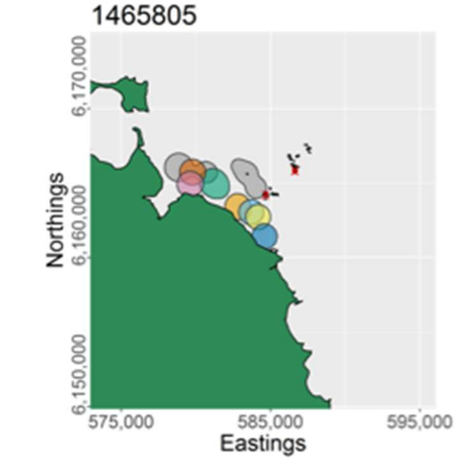
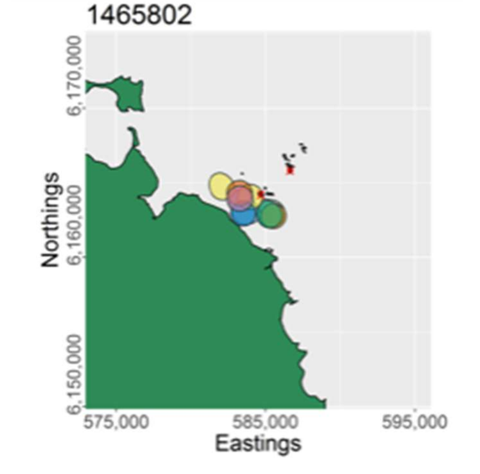
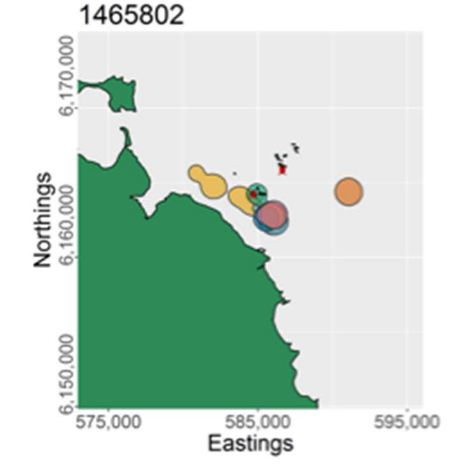
Figure B1: Habitats associated with shag foraging areas at other UK colonies

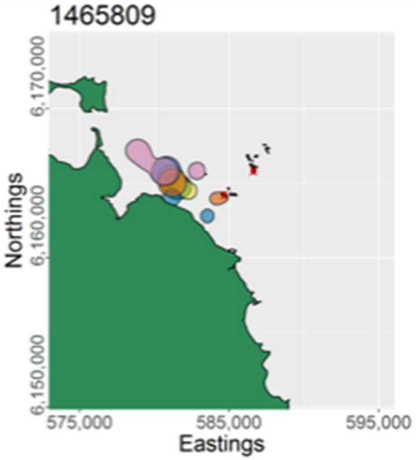
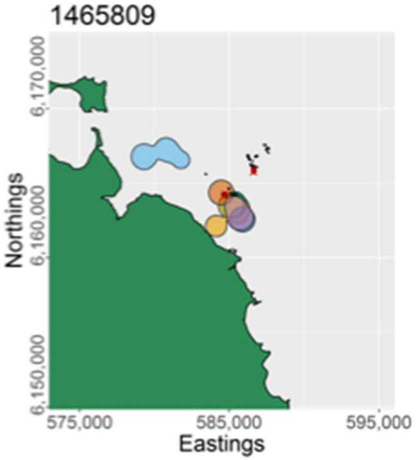
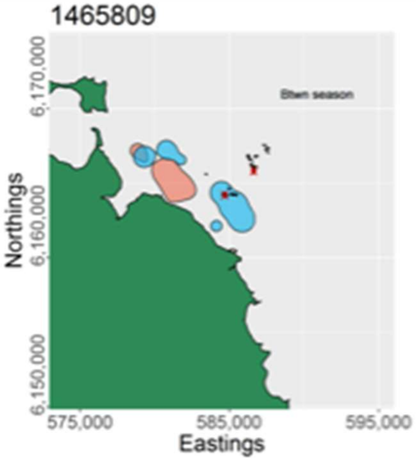
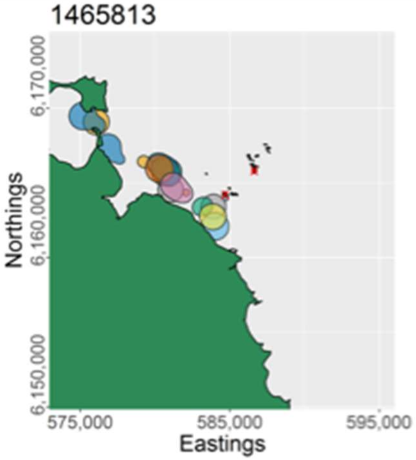
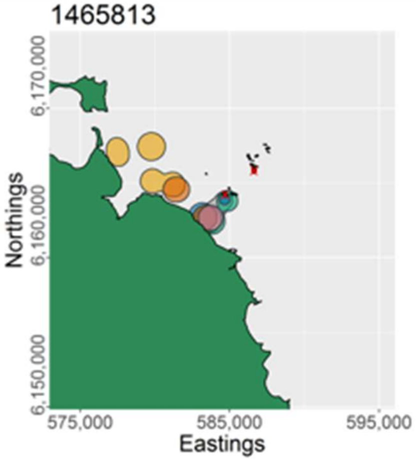
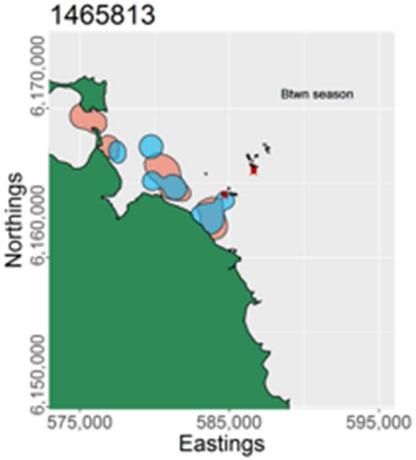
Appendix C (Chapter 4)

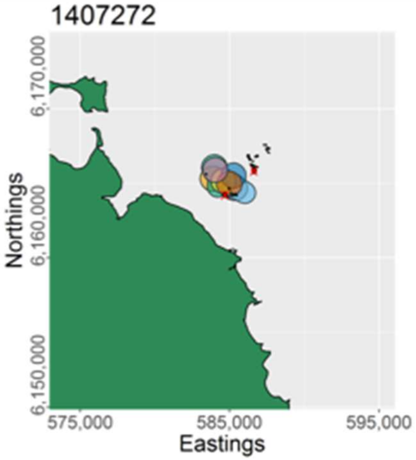
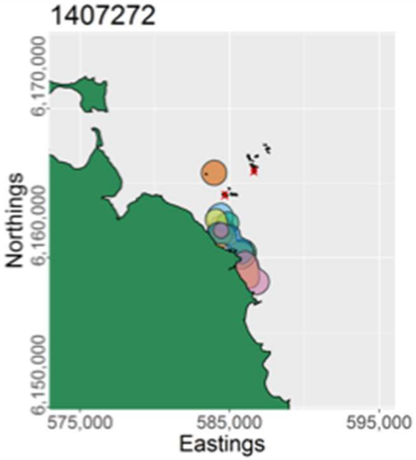
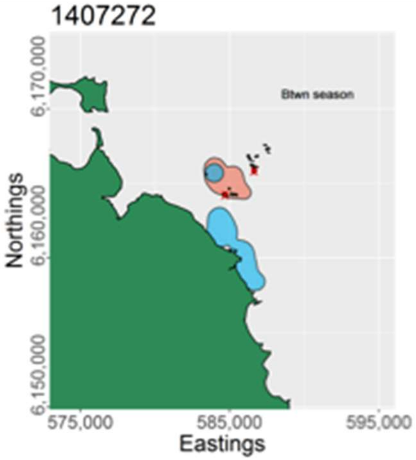
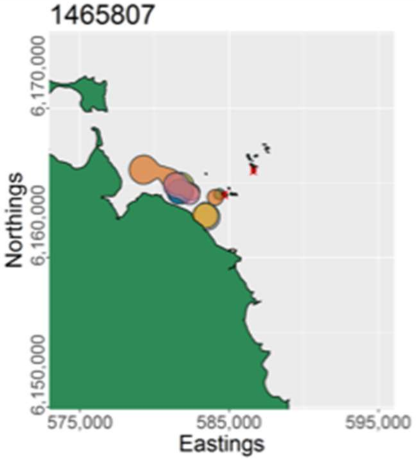
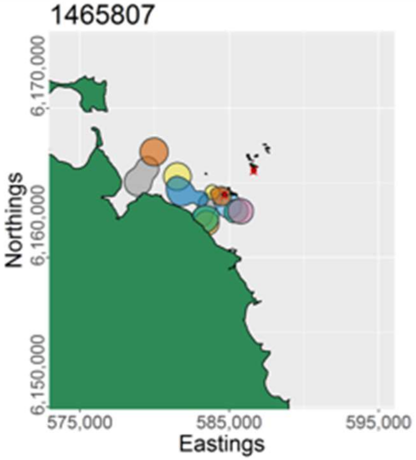
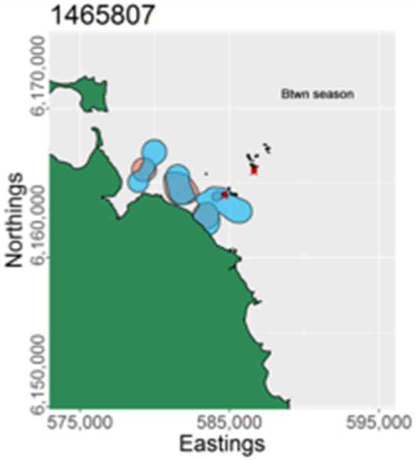
C.1 Figure C1: Individual trip-trip kernel maps : Within- and between-season overlap maps for each bird with multiple years of data. Kernels of differing colours represent different foraging trips. Colour of the ID column shows the sex of the individual pink=female blue=male. Birds with high within-season and low between-season scores are highlighted in red.

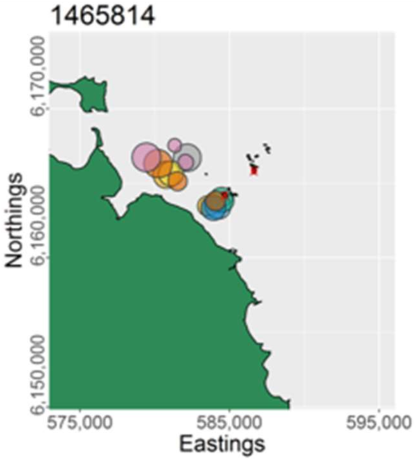
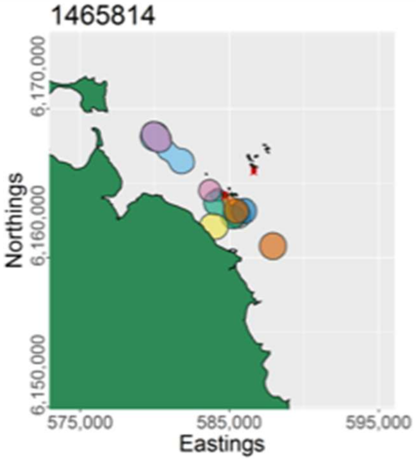
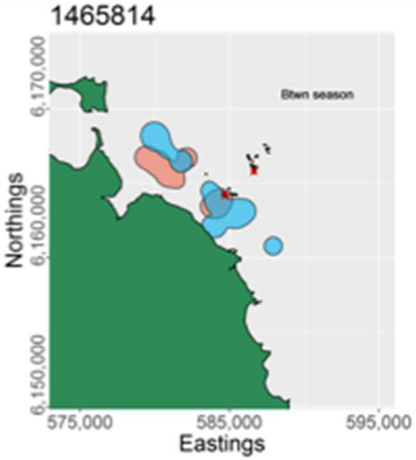
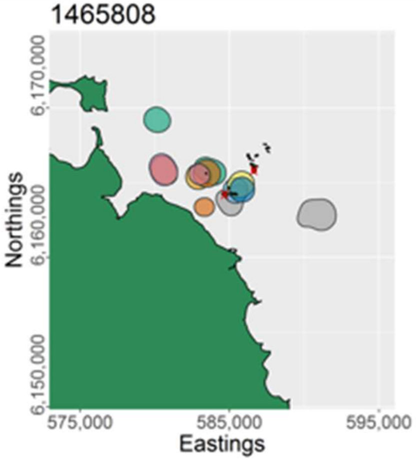
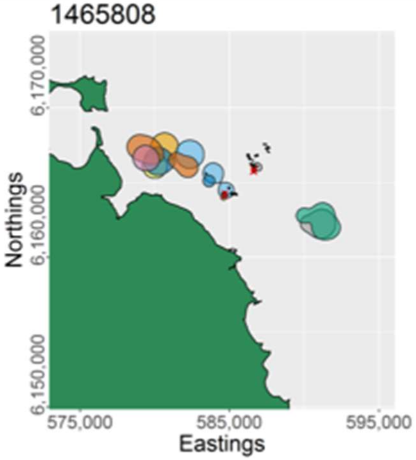
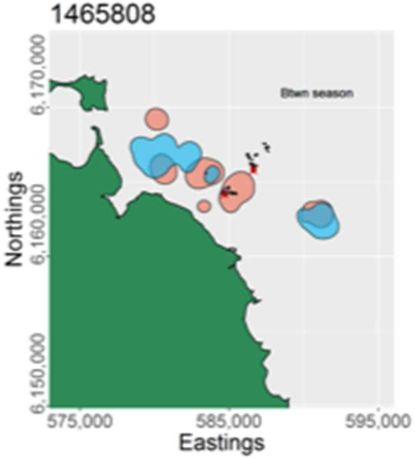
ID	Within BA 2014	Within BA 2015	Within BA 2016	Between Years BA
1465806-RWRU				
	0.311726	0.463952	0.47429	0.82

1465810-RWRP				
	0.112277	0.191617	0.523638	0.64
1465680-RRZF				
	0.275831	0.415299	0.093364	0.43

1465805-RWRW				
	0.114299	0.195406	0.060164	0.34
1465802-RWPZ				
	0.22728	N/A	0.68993	0.49

1465809-RWRR			NOTED AS SUB AD 2014….	
	0.511999	0.306755	N/A	0.02
1465813-GCBE				
	0.245953	0.52502	N/A	0.45

1407272-RCIR				
	0.302589	0.285172	N/A	0.09
1465807-exWRT				
	0.375908	0.093189	N/A	0.60

1465814-GCBR				
	0.178555	0.203375	N/A	0.23
1465808-RWRS				
	0.174064	0.130666	N/A	0.30

C.2 Appendix 2: Sensitivity Analyses

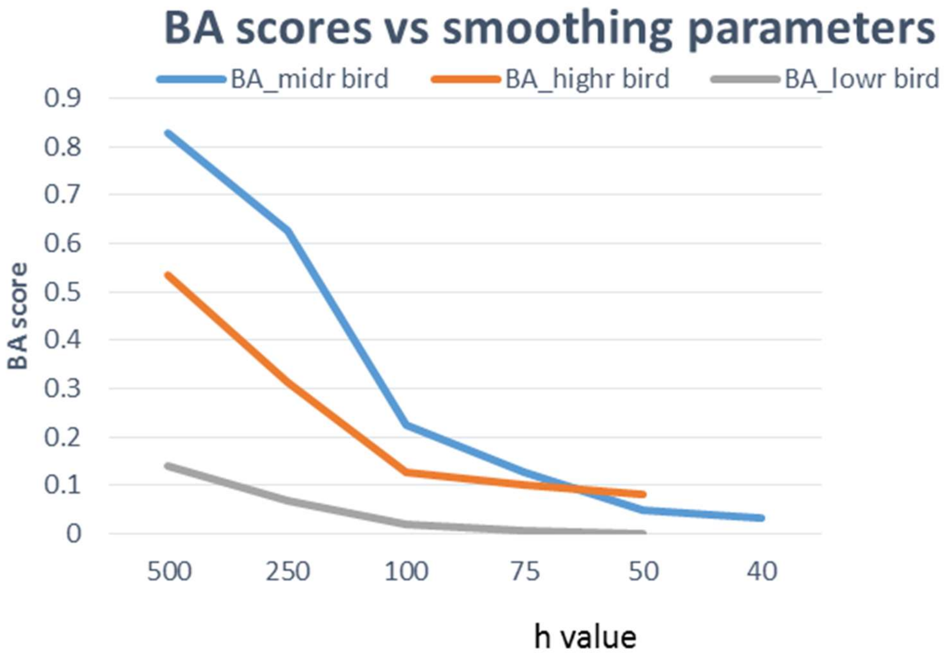


Figure C2: Sensitivity analyses showing how smoothing parameter (h value) affects BA overlap scores. Results are shown for a bird with a high repeatability (blue line), low repeatability (grey line) and a bird with middling levels of repeatability (orange line).

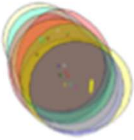
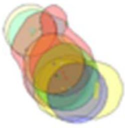
H values :	500 m	250 m	100 m	75 m	50 m
High r bird					
Mid r bird					
Low r bird					

Figure C3: Visual representation of how changing smoothing parameter (H value in meters) affects spatial overlap results. Results are shown for a bird with a high repeatability, low repeatability and a bird with middling levels of repeatability. Different coloured kernels represent different foraging trips.

Appendix D

D.1 Weather on the Farnes during the study period

Weather throughout the study period May-July.

Daily means were calculated from hourly wind and visibility variables. Rainfall and hours of sunshine which were summed to give daily totals. To see if weather was significantly different between years, Kruscall-Wallis tests were carried out on daily weather data. Post hoc Nemenyi tests were used to show which years varied significantly from each other.

Across all three years; wind speed and direction were correlated with Westerly (onshore) winds generally being stronger than Easterly (offshore). Westerly winds were also associated with warmer conditions, higher visibility and their prevalence decreased as the season progressed (see table 1). Date was highly correlated with air temperature, with conditions becoming warmer as the season progressed. Mean wind speed (X^2=26.3, df=2, p<0.01) and wind direction (X^2=8.25, df=2, p=0.02) differed between years. Conditions in 2014 (av speed: 7 knots ±0.24) were calmer than conditions in 2015(av speed: 9knots ±0.32, p<0.01) and 2016 (av speed: 8knots ±0.29 , p=0.02) (a percentage increase of 29% and 14%, respectively). Conditions in 2015 were also windier than both 2014 and 2016(p=0.04). There were more days with Easterly winds in 2014 compared to 2015 (p=0.02), whereas in 2015 and 2016 westerly winds predominated. There were annual differences in air temperature (X^2=19.22, df=2, p<0.01) and visibility (X^2=92.96, df=2, p<0.01) .Temperatures were slightly warmer in 2014 than 2015 (p<0.01) and 2016 (<0.01), but only by around 1^{o}C. Temperatures were similar across 2015 and 2016. On average, visibility was 1.2km less in 2016 than in 2014 (p<0.01) and 2015 (p<0.01) (a reduction of approximately 55% from the previous two years). There was no difference in the total hours of sunshine (X^2=4.89, df=2, p=0.09) or total daily rainfall (X^2=1.9, df=2, p=0.38) between years. There were significant interactions between months and years. In 2014 May and June were warmer than in other years. Wind speed was lower in June 2014 compared to June 2015 and 2016.

Table 2: correlation co-efficient matrix for daily weather variables throughout the study period. Correlations which were significant at the p<0.05 level are shown in bold. Weather data is from the chick rearing period May-July for all three years combined (n= 276).

n= 276	**wind dir (sine)**	**wind speed**	**air temp**	**visibility**
wind dir (sine)				
wind speed	**-0.5**			
air temperature	**-0.23**	**-0.18**		
visibility	**-0.51**	**0.22**	0.09	
date	**-0.13**	**-0.24**	**0.73**	0.05