Foraging patterns and home-ranges of breeding razorbills (*Alca torda*) from two colonies in North Wales, UK, as revealed by GPS-tracking in the seasons of 2011 and 2012

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DECLARATION AND STATEMENTS

This work has not previously been accepted in substance for any degree and is not being concurrently submitted for any degree.

This dissertation is being submitted in partial fulfillment of the requirement of M.Sc. Marine Environmental Protection.

This dissertation is the result of my own independent work / investigation, except where otherwise stated.

Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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Date 18. September 2012

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ABSTRACT

Razorbills *Alca torda* have experienced recent localised population declines with repeated breeding failure due to food shortage. An improved understanding of foraging behaviour would facilitate the implementation of appropriate at-sea protection measures. Using miniature GPS loggers, this study aimed to describe the foraging behaviour of breeding razorbills from two North Welsh colonies: Bardsey Island (2011) and Puffin Island (2011 and 2012). The study tested for inter-colony and inter-annual differences in maximum and total foraging trip distance and trip duration (using a GLM) and trip timing (using χ^2-tests), and applied a fixed-kernel analysis to determine the 95% home-range and 50% core foraging areas, relating the latter to environmental parameters. Birds from Bardsey and Puffin Island travelled up to c. 40 and 60km from the colony, respectively. Overall, both colonies/years showed similar patterns with mean values of c. 13km maximum distance, 37km total distance and 6h trip duration. However, when diurnal and nocturnal trips were analysed separately, a significant colony difference was found, with birds from Bardsey having longer distance diurnal trips, and shorter nocturnal trips. In both years/colonies, diurnal trips occurred between sunrise and sunset, whilst nocturnal trips revealed a significant diel pattern, probably representing crepuscular foraging. At Bardsey, the home-range extended in a south-western direction, with core foraging areas located c. 10-20km SW of the colony. At Puffin Island, the overall home-range extended NW of the colony, with core foraging areas located around Puffin Island and along the E/NE Anglesey coast. However, diurnal and nocturnal home-ranges and foraging areas differed substantially at both colonies, with diurnal foraging areas mainly over sandy substrates. In both years at Puffin Island, the diurnal foraging areas occurred in much shallower waters (<20m) than in nocturnal foraging areas (≤80m depth), whereas at Bardsey, both diurnal and nocturnal foraging areas occurred in waters of 50-100m deep.

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ABBREVIATIONS

ANOVA	Analysis of Variation
EEC	European Economic Community
EIA	Environmental Impact Assessment
EU	European Union
FAME	Future of the Atlantic Marine Environment
FKD	Fixed Kernel Density
GIS	Geographic Information System
GLM	Generalised Linear Model
GPS	Global Positioning System
MPA	Marine Protected Areas
NNR	National Nature Reserve
RSPB	Royal Society for the Protection of Birds
SSSI	Special Site of Scientific Interest
SPA	Special Protection Area
TDR	Time-Depth Recorder

1. INTRODUCTION

Seabirds are one of the ocean's top predators, and as such, play a key role in the marine ecosystem, influencing the structuring of marine communities through top-down ecological processes (Hindell *et al.,* 2011). Equally, they are themselves influenced by lower trophic processes and unpredictable food resources for survival and reproduction (Hindell *et al.,* 2011). As central-place foragers during the breeding season, seabirds are required to return frequently to their colony for incubation duty or chick provisioning, making them particularly sensitive to variation in food supply when breeding (Piatt *et al.,* 2007). Indeed, the recent population crashes and successive years of breeding failures, as experienced by many seabird species in the UK (Grémillet *et al.,* 2006; Heath *et al.,* 2009), have been extensively linked to poorer feeding conditions, likely as a result of interacting pressures from climate change and anthropogenic activities (Tasker *et al.,* 2000; Montevecchi, 2002; Mitchell and Daunt, 2010).

Although most seabirds in the UK are well protected on land via a network of breeding colony Special Protection Areas (SPAs) under the EU Birds Directive (79/409/EEC), they currently receive comparatively little protection at sea (Thaxter *et al.*¸ in press.). With declining fish stocks and increasing pressure from offshore developments, the protection of seabird foraging areas, particularly during the breeding season, is becoming increasingly recognised by conservation bodies as being fundamental to the continued health and survival of these apex predators (Thaxter *et al.,* in press.). This has become particularly relevant with the recently introduced legislation of the Marine And Coastal Area Access Act 2009, which obliges the UK to designate Marine Protected Areas (MPAs) as from 2012. The adequate protection of seabirds at sea, however, demands detailed knowledge of their foraging behaviour to allow us to understand how these animals are using the marine environment, and the constraints acting upon them when foraging (Kotzerka *et al.,* 2010).

Until recently, there have been no satisfactory methods of studying seabird feeding at sea, and, given they are difficult to observe when away from the nest, our knowledge and understanding of species and colony-specific seabird foraging patterns have remained limited (Kotzerka *et al.,* 2010). Past studies have relied on land or boat-based approaches, including transect methods (Webb *et al.,* 1985, Poot, 2003), which provided only very limited data in time and space (Weimerskirch *et al.,* 2005). It was not until the early 1990s that the use of radio telemetry gave rise to the first seabird tracking studies (e.g. Wanless *et al.*, 1991; Wanless, 1992; Croxall, 1994; Freeman *et al.*, 1997). Since then, the study of seabird foraging ecology has benefited from an increasing focus on at-sea behaviour. Recent technological advances of satellite devices (e.g. Hamer *et al.*, 2001, 2007; Weimerskirch *et al.*, 2005) and a variety of activity recorders have enabled and facilitated collection of positional data, as well as of bird's at-sea activities, flight duration, dive depth, and responses to environmental variables such as temperature (Benvenuti *et al.*, 2001; Dall'Antonia *et al.*, 2001; Daunt *et al.*, 2003; Thaxter *et al.*, 2010). The latest tracking devices to have become available are miniature Global Positioning System (GPS) loggers, which directly store positional data at set intervals (Grémillet *et al.*, 2004; Garthe *et al.*, 2007; Guilford *et al.*, 2008; McLeay *et al.*, 2010; Kotzerka *et al.*, 2010; Chivers *et al.*, 2012). GPS devices benefit from unlimited range, and compared to telemetry and satellite, provide a much higher resolution and accuracy (Hulbert and French, 2001; von Hünerbein *et al*., 2000).

The provision of such detailed information over a short time-frame makes this technique particularly attractive from a management point of view, as the data can quickly be used as a basis for management strategies (Grémillet *et al.*, 2006; Burger and Schaffer, 2008; Louzao *et al.*, 2009; Wilson *et al.*, 2009; Thaxter *et al.*, in press.). Globally, seabird tracking studies have already provided insights to aid the designation of Marine Protected Areas (Garte and Skove, 2006; Guilford *et al.*, 2008; Grémillet and Boulinier, 2009; Louzao *et al.*, 2009; Wakefield *et al.*, 2009; Wilson *et al.*, 2009). As with most new technologies, the earliest GPS loggers were too big and heavy to be used on all but the largest-bodied seabirds, such as albatrosses (Weimerskirch *et al.*, 2002) and gannets (Grémillet *et al.*, 2004). In the past few years, however, increasingly smaller GPS loggers have enabled even medium- and small-sized (approximately ≥300 g) birds to be tracked and studied by this means. This includes members of the auk family such as guillemots and razorbills, the latter of which is the focus of the present GPS-based study.

The razorbill (*Alca torda*, L. 1758) (Figure 1.1) is a stocky, medium sized (ca. 350-390 g) seabird with an extensive range across the North Atlantic and Arctic Ocean (Figure 1.2) (del Hoyo *et al.*, 1992). Over 20% of its global population resides in the UK (Mitchell *et al.*, 2004). The razorbill is one of the species that has faced local declines in numbers and productivity in the UK since 2000 (Mitchell *et al.*, 2004; Heath *et al.*, 2009), probably due to a shortage of sandeels, a key prey species of the razorbill which they capture during pursuit diving using their wings to propel them through the water column (Mitchell *et al.*, 2004; Davis *et al.*, 2005; Wanless *et al.*, 2005; Heath *et al.*, 2009). As a result, the razorbill has recently been given Amber status in the list of the UK's Birds of Conservation Concern (Eaton *et al.*, 2009), which calls for improved protection of that species during the breeding season.

Figure 1.1 Illustrations of the razorbill *Alca torda*. Source: www.rspb.org.uk.

The foraging ecology of breeding razorbills has been investigated by numerous authors using various methods. These range from direct observations, used to identify the foraging ranges and key feeding areas (e.g. Webb *et al.*, 1985) and their relationship to environmental variables such as depth (Stone *et al.*, 1995) and primary productivity (Begg and Reid, 1997; Durazo *et al.*, 1998), to remote-sensing studies based on activity loggers that allowed the study of the horizontal and vertical movement at sea, locations and depth of dives, and time allocation of specific activities such as flying, diving and post/inter-dive surface intervals (e.g. Benvenuti *et al.*, 2001; Dall'Antonia *et al.*, 2001; Thaxter *et al.*, 2010). In the UK, however, despite various razorbill colonies having been studied, including those from Lundy (Perry, 1940), Skomer (Lloyd, 1976), Skokholm (Corkhill, 1973) and Isle of May (e.g. Harris and Wanless, 1989; Wanless *et al.*, 1990; Thaxter *et al.*, 2010), the study by Thaxter *et al.* (2010) was the first to determine foraging ranges and duration on the basis of bird-borne loggers, and was the first study to ever calculate the home range and core foraging area of breeding razorbills. As a consequence, detailed knowledge of colony-specific razorbill foraging patterns and important foraging areas in the British Isles has remained sparse, and there are currently few studies that directly address inter-colony and inter-annual variation (see Stone *et al.*, 1992).

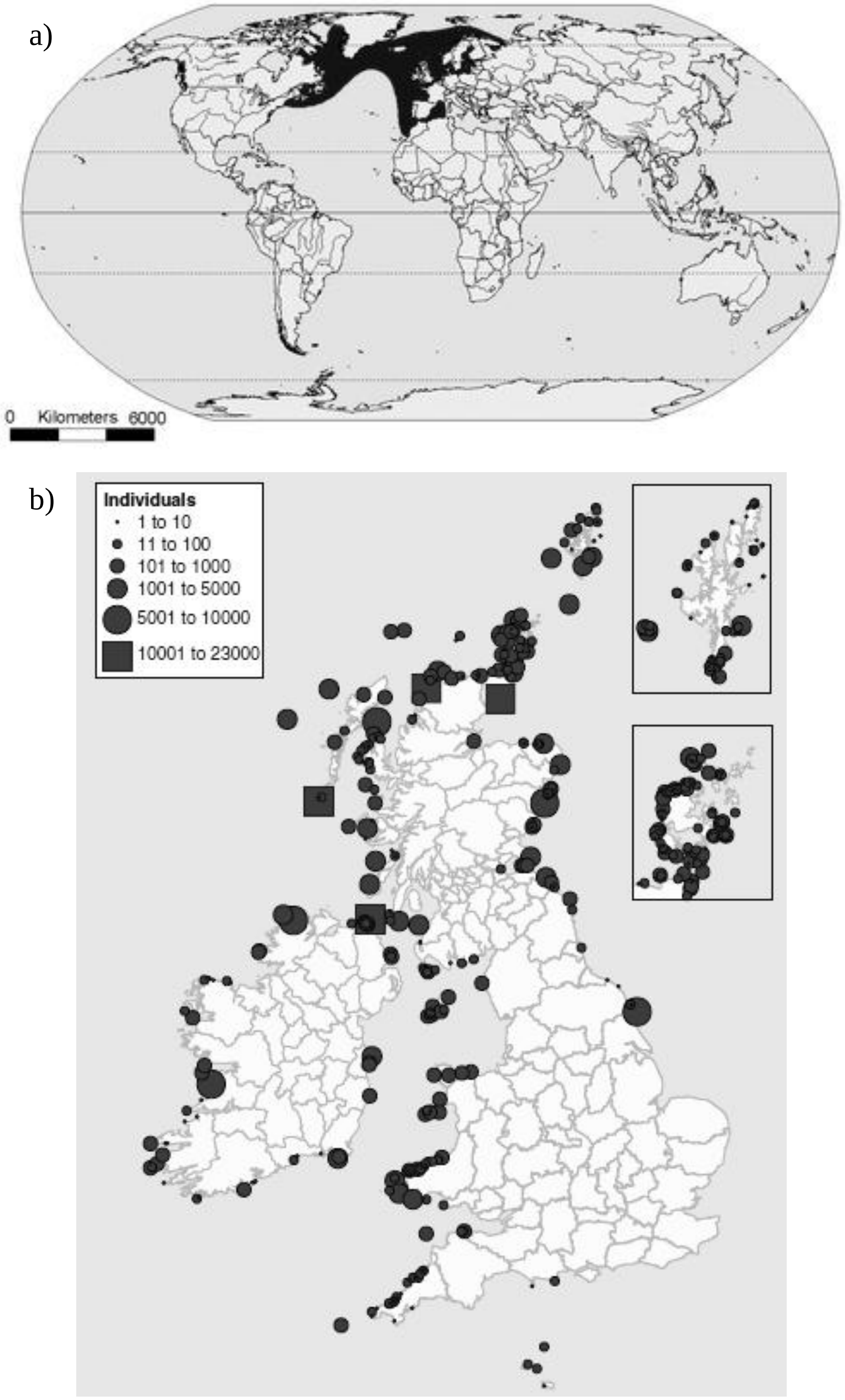

Figure 1.2 Razorbill distribution a) across the globe (1990 – 1999); b) in the British Isles (1998 – 2002). Source: a) www.groms.de; b) Mitchell et al. (2004).

A strategic transnational project called the Future of the Atlantic Marine Environment (FAME), led and coordinated by the Royal Society for the Protection of Birds (RSPB) is currently addressing this deficiency by GPS-tracking razorbills, as well as other key indicator species[1] from a range of colonies around the British Isles, with the aim of identifying key marine feeding areas and their associated habitats. By matching the habitat such as depth and substrate type to foraging areas, it is possible to identify which at-sea habitats constitute important feeding grounds for breeding seabirds.

Based on data collected as part of FAME, the present study reports the first use of miniature GPS data loggers to characterize the foraging patterns and home-ranges of breeding razorbills from two colonies in North Wales. The data were collected from Bardsey Island during the breeding seasons of 2011, and from Puffin Island during the breeding seasons of 2011 and 2012. The objectives of this study were to use this spatial data to:

(1) determine foraging trip parameters (maximum and total foraging trip distance, and foraging trip duration) of breeding razorbills at Bardsey Island and Puffin Island, and investigate whether these differed between colonies (Bardsey Island 2011 and Puffin Island 2011) and between years (Puffin Island 2011 and 2012);

(2) determine foraging trip departure and return times in relation to time of day, and compare patterns between colonies (Bardsey Island 2011 and Puffin Island 2011) and between years (Puffin Island 2011 and 2012);

(3) calculate the home-ranges and core foraging areas of razorbills from Bardsey Island and Puffin Island and make descriptive comparisons between colonies (Bardsey Island 2011 and Puffin Island 2011) and between years (Puffin Island 2011 and 2012) in terms of size and geographical distribution;

(4) relate the core foraging areas calculated for the razorbill colonies at Bardsey Island (2011) and Puffin Island (2011 and 2012) to environmental variables including depth and substrate type.

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[1] In the UK, FAME is GPS-tracking five key species that reflect a variety of foraging styles and ranges, in an attempt to identify crucial marine feeding locations. Tracked species include the Common guillemot *Uria aalge*, European shag *Phalacrocorax aristotelis*, Black-legged kittiwake *Rissa tridactyla*, Northern fulmar *Fulmarus glacialis*, Northern gannet *Morus bassanus*, and razorbill *Alca torda*.

2. METHODS

2.1. STUDY AREA

The two colonies used for this study are located on Bardsey Island (52° 45′ 41″ N, 4° 47′ 2″ W) and Puffin Island (53° 19′ 5″ N, 4° 1′ 40″ W) in the eastern Irish Sea, off the coast of North Wales, UK (Figure 2.1, 2.2). Bardsey Island, covering about 2 km^2 (200 ha), is situated approximately 3.1 km (1.9 miles) off the Lleyn Peninsula and is protected under various conservation designations, including National Nature Reserve (NNR), Special Site of Scientific Interest (SSSI), and Special Protected Area (SPA). The island lies in waters of up to 35 m deep, although water depths within 5 km from Bardsey extend up to 50 m to the south and up to 100 m to the east. The bottom type surrounding Bardsey Island is dominated by coarse sediment (gravel), with an extensive sandbank extending southeast of Bardsey. The razorbill colony at Bardsey has been increasing steadily, with approximately 300 individuals in 1970 (Cramp *et al*., 1974), c. 500 individuals in mid 1980s (Barnes, 1997), and approximately 2000 individuals in 2002-2003 (Barton and Pollock, 2005) and in 2008 (S.G. Dodd. *pers. comm.*).

Puffin Island, covering an area of 0.28 km^2 (28 ha) is situated approximately 750 m off Penmon Point on the south-eastern coast of Anglesey, marking the northeastern end of the Menai Strait. Like Bardsey, Puffin Island is a designated SSSI and SPA. Puffin Island is surrounded by extensive sandbanks and shallow waters of up to 17 m deep, and once held one of the major razorbill colonies in the UK, with approximately 600 individuals in the mid-1980s (Barnes, 1997; Mitchell *et al.*, 2004). The razorbill colony has recovered from approximately 113 individuals from the late 1990s to 416 individuals in 2010, following a successful rat eradication programme in 1998 (Arnold, 2001; CCW, unpubl. data).

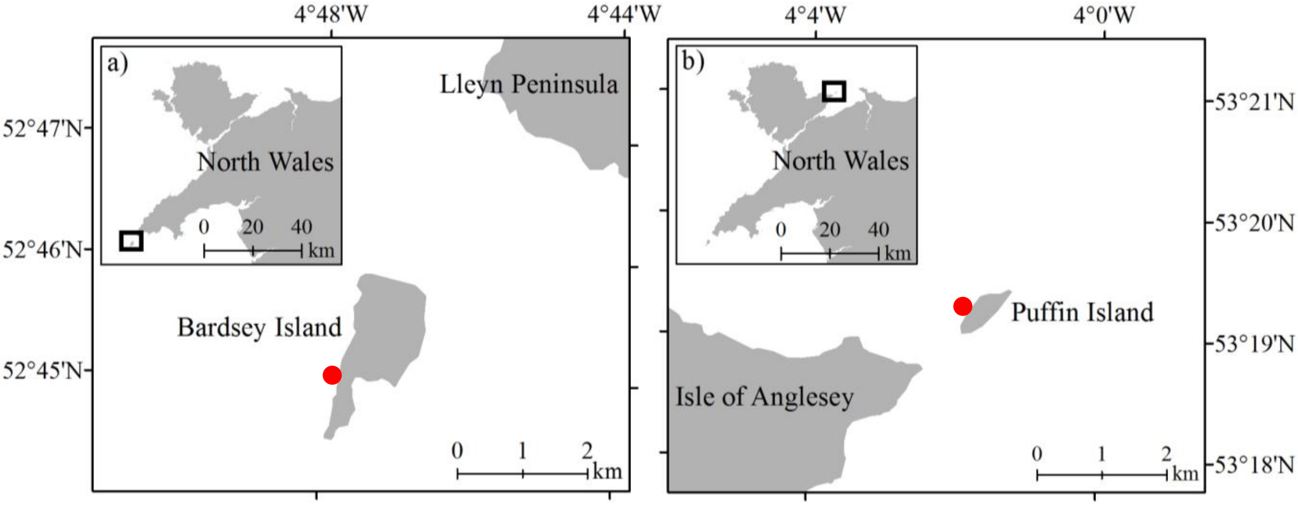

Figure 2.1 Maps showing the location of a) Bardsey Island and b) Puffin Island in relation to North Wales, UK. ● = Location of study colonies.

Figure 2.2 Aerial photographs of a) Bardsey Island and b) Puffin Island.
Sources: a) www.education.gtj.co.uk; b) Adrian Warren

2.2. DATA COLLECTION

Data collection was undertaken by the RSPB as part of the Future of the Atlantic Marine Environment (FAME) initiative during the breeding season of 2011 from both Bardsey Island (14th May – 10th June) (hereafter referred to as BAR11) and Puffin Island (17th May – 6th June) (hereafter referred to as PUF11), and in 2012 only from Puffin Island, (17th May – 2nd June) (hereafter referred to as PUF12). In 2012, data collection was assisted by the author of this report. Ninety breeding adult razorbills (43 from BAR11, 26 from PUF11, and 21 from PUF12) were captured using a wired hook or a noose-pole and fitted with an IgotU-120 GPS logger (Mobile Action Technology, UK). The loggers were attached dorsally using three thin strips of black waterproof tape (TESA®, Extra Power) (see Wilson *et al.,* 1997), each anchored beneath a small amount of back feathers and closed over the top of the device (Figure 2.3). Tape attachments are suggested to have less impact than harnesses (Philips *et al*., 2003), and the seawater eventually causes the tape to fail after two to three weeks, providing a welfare failsafe in case an individual could not be recaptured. Birds used for tagging were selected at random, and included both incubating and brooding individuals; however, none of the birds were known to be paired with any of the other study birds. Sample number was mainly determined by economic and temporal factors, which dictated the number of GPS loggers deployable. Birds were recaptured 2 to 17 days later using a noose matt, noose pole or hooked pole (Figure 2.4), and the loggers were retrieved by carefully peeling the tape away from the feathers.

Figure 2.3 Modified I-got-U 120 GPS logger attached to the back feathers of a razorbill *Alca torda*. Photographs by Steve Dodd.

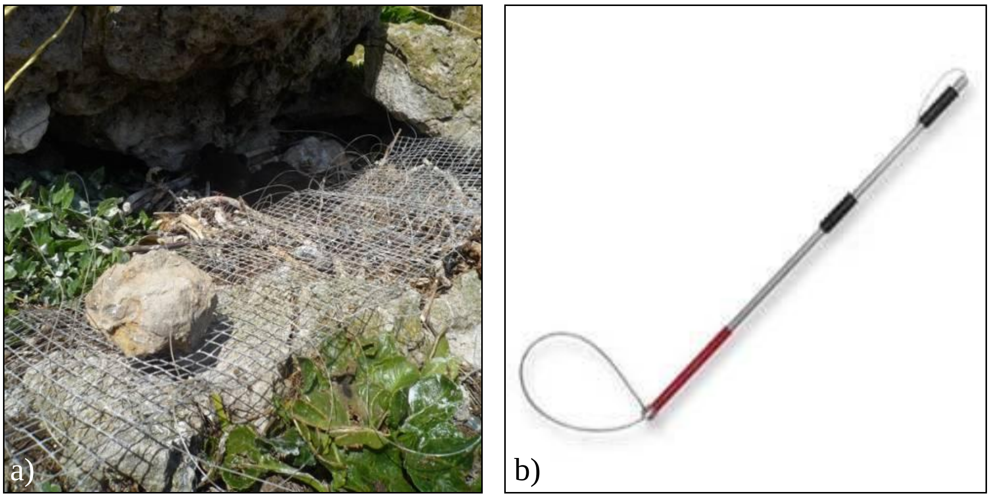

Figure 2.4 a) A noose matt fitted at the entrance of a razorbill nest – dozens of fishing wire nooses are attached to the metal grid; b) An extendible noose pole.

For each tagged bird, time of capture and release were noted, and where possible, nest status (i.e. whether bird was on an egg or a chick (small, medium or large)) was noted both at capture and at recapture. Nest status could not always be obtained accurately at Puffin Island, as it was not always clear which nest the birds belonged to in cases where several pairs were nesting under the same boulder, for example. Before deployment, morphometric measurements were taken of body weight (g), wing span (mm) and head-bill size (mm). The sex was not determined, since it can only accurately be determined through a range of behavioural methods (Insley, 2003), which were beyond our logistical capabilities. Birds without a BTO ring were ringed for future identification purposes. Individuals were weighed again upon recapture and removal of the tag to assess weight loss over the deployment period. However, this was not always possible, as some tags were found to have been dislodged in the nest.

Every effort was taken to minimise the stress caused to the birds, with the bird’s head mostly covered by a fabric bag during handling. Handling time (capture to release) during deployment and removal of loggers never exceeded 15 minutes. Twelve individuals from Bardsey Island were returned to their nest crevice after deployment, where they stayed. The remainder were released at the deployment site and observed to fly out to sea. In order to avoid excessive disturbance to the birds, we limited our visits to the colonies to the time necessary to recapture the tagged birds, and never spent more than one hour at any given location, keeping a safe distance so as not to prevent the target bird from returning to its nest. Therefore, we refrained from collecting observational data on prey type delivered to the chicks, or any other aspects of the bird's breeding biology.

2.2.1. *THE DATA LOGGERS*

The data loggers used for this study were IgotU-120 GPS loggers (Mobile Action Technology, UK). The loggers were stripped of their original casing and waterproofed in heat-sealed plastic tubing to produce a streamlined device of 75 x 25 x 7 mm (Figure 2.3). The whole instrument, including the built-in 230mAh Lithium-ion battery, the built-in GPS patch antenna and the waterproof container, weighed < 18 g, representing between 2.6 and 3.4 % of the bird's body mass. The memory capacity of the device was 16 Mb, and loggers were set to record a fix every 140 seconds during deployment. This timing was chosen as a compromise between accuracy of the birds' trajectories and the devices' battery life (see Ryan *et al.*, 2004). With every fix, the loggers recorded date, time, latitude, longitude, speed and altitude. Speed and altitude data were discarded due to inaccuracies (M. Bolton, *pers. comm.*), whilst the remaining data were used for analysis. Due to the very small positional error of the GPS loggers (advertised as having an accuracy of <20 m), it was possible to assess fine-scale habitat use patterns by following the bird's trajectories.

2.2.2. *WEATHER CONDITION DURING STUDY PERIOD*

Although spring 2011 was exceptionally warm and dry, and overall much warmer than spring 2012, the month of March was relatively warm in both seasons, and hence the breeding seasons have been similarly advanced during time of data collection in 2011 and 2012. Furthermore, weather conditions during data collection were reasonably good in both seasons and at both colonies. Hence, any differences observed are unlikely to have been caused by meteorological effects.

2.3. DATA PROCESSING AND FILTERING

Upon retrieval of the data loggers, data were downloaded using associated @trip PC software (Mobile Action Technology, UK). Due to occasional signal failure, GPS units did not consistently record fixes as programmed. In order to avoid temporal and spatial bias caused by this defect, fixes were interpolated to every 10 seconds using the package "Trip" (Sumner, 2012) within R statistical software (v. 2.15.0®, R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) according to the method used by McLeay et *al*., 2010). Individual interpolated tracks were then imported into ArcMap 9.3® (ESRI, California) where fixes on the islands, including a 20 m buffer (in line with GPS accuracy), were removed as these were not representative of foraging trips but represented the time spent at the colony. This allowed the tracks to be categorised into individual trips; an individual trip being defined by the GPS-fixes between a nest departure and subsequent return. Incomplete trips, usually caused by battery depletion, were discarded (n = 8). Short trips of less than 10 min and/or of less than 300 m maximum distance from the colony were also discarded from analysis, in an attempt to only use data representative of actual foraging trips. This assumption may have resulted in the discarding of some trips of short duration, but direct observations at Puffin Island indicated that the razorbills used the waters immediately surrounding the islands (ca. 300m range, as seen through binoculars) almost exclusively for resting and preening activities (*pers. observ*.).

2.4. DATA ANALYSIS

SPSS (v.19) and Minitab (v.15) were used to perform univariate statistics. For all statistical tests, an alpha value of 0.05 was used. Wherever a general linear model was applied, the data were tested for homogeneity of variance using the Levene's test (Dytham, 2011). In cases where residuals were not normally distributed and the Levene's test was significant, data were transformed appropriately. The data were not tested for normality as, according to Underwood (1996), a general linear model is sufficiently robust to deal with non-normalised data. In order to allow the use of more robust tests and avoid replication in figures and tables, BAR11, PUF11 and PUF12 were always considered together, unless stated otherwise, even though direct comparisons were only ever made between BAR11 and PUF11 to test for an inter-colony effect, and between PUF11 and PUF12 to test for an inter-annual effect. Values are presented as mean ± standard error (SE), unless stated otherwise.

2.4.1. EFFECTIVENESS OF THE TRACKING TECHNIQUE

To assess the effectiveness of the tracking technique, a series of descriptive statistics were performed with regard to the number of birds tracked and foraging trips obtained. Using weight as the independent variable, and capturing occasion (capture or recapture) and colony/year as factors, a two-way ANOVA was performed to assess the trend in adult body mass over the deployment period. Potential negative impacts of the GPS devices on the study birds were assessed using a Pearson's rank correlation to analyse the relationship between changes in body mass and hours of device deployment on individual birds.

2.4.2. FORAGING TRIP PARAMETERS

In order to gain an insight into the foraging behaviour of the razorbills from Bardsey and Puffin Island, GPS data were used to determine the following foraging trip parameters: (1) Maximum foraging trip distance from the colony (hereafter referred to as maximum distance), which was defined as the most distant point of a trip from the colony (Kotzerka *et al.*, 2010), and was measured as a straight line from the colony using the measuring tool in ArcMap on Transverse-Mercator projected data (projected coordinate system: WGS 1984); (2) total foraging trip distance (hereafter referred to as total distance), which corresponded to the summed distance between consecutive fixes between departure from and return to the colony (Kotzerka *et al.*, 2010); (3) trip duration, which corresponded to the total elapsed time between departure from and return to the colony; (4) Trip times, representing the time of day when the birds left and returned from foraging trips. The latter, although also a type of foraging trip parameter, will hereafter be referred to separately.

To test whether birds on eggs and birds on chicks showed significant differences in their foraging trip parameters (maximum distance, total distance and duration), two-tailed t-tests were carried out on pooled data from BAR11, PUF11 and PUF12. Data were pooled due to the small sample size of nest status obtained at PUF11 and PUF12, particularly as the analysis was based only on birds with the same nest status (egg or chick) at capture and recapture (BAR11: n(egg) = 9, n(chick) = 7; PUF11: n(egg) = 3, n(chick) = 2, PUF12: n(egg) = 1, n(chick) = 3).

The relationship between maximum distance, total distance and trip duration was determined using a Pearson's rank correlation. A generalised linear model (GLM) was carried out to determine inter-colony (BAR11 vs. PUF11) and inter-annual (PUF11 vs. PUF12) differences in maximum distance, total distance and trip duration, using colony/year as a fixed factor, and individual birds as random factors nested within colony/year. This approach, also carried out by e.g. Hamer *et al.* (2007), was preferred over separate t-tests on mean values, due to a GLM providing the advantage of acknowledging within-bird variation when individuals performed more than one trip, whilst accounting for pseudo-replication of data points (Hamer *et al.*, 2007; Paredes *et al.,* 2008).

2.4.3. TRIP TIMING

In order to determine patterns of foraging trip departure and return times in relation to the time of day, both departure and return times were split into three-hour categories for BAR11, PUF11, and PUF12 individually. Chi-square goodness-of-fit tests were carried out only on categories that included observed values, in order to determine if departure and return times were evenly distributed across the period of day during which they occurred. This approach was preferred to analysing departure and return times across the entire day as the high number of zeros made the chi-squared tests invalid (C. Hughes, *pers. comm.*). Patterns of trip departures and return times were compared, where sample number allowed, between colonies (BAR11 and PUF11) and between year (PUF11 and PUF12) using a chi-square test of independence. Time of day in this report is stated as British Summer Time (UTC +1).

2.4.4. HOME-RANGE ANALYSIS

In order to determine density estimates and potential foraging areas from the point distribution provided by the GPS data, a home-range analysis was carried out. For the purpose of this study, the term "home-range" is defined as "a minimum area in which an animal has some specified probability of being located" (Worton, 1989). Following previous studies (Weimerskirch *et al.,* 2005; Hamer *et al.*, 2007; Calenge, 2007; Thaxter *et al.,* 2010; Kokobun *et al.,* 2010, L.M. Soanes *et al.*, unpubl.), home-range estimates were derived from tracking data via the bivariate normal kernel analysis (the *ad hoc* method, Worton, 1995; also known as the fixed kernel method) to calculate the 95% and 50% fixed kernel density (FKD) distribution contours for BAR11, PUF11 and PUF12, using the R package "AdehabitatHR" (Calenge, 2007). As described previously by e.g. Hamer *et al.* (2007), the 95% and 50% FKD were taken to represent the active-use area and core-use area, respectively.

Kernel estimators are popular home-range analysis tools because they are robust to autocorrelation, they are non-parametric, allow multiple centres of activity, and have the ability to provide an utilisation distribution that separates transitional points from potential foraging points (Wood *et al*., 2000). The latter is particularly true for the fixed-kernel method, which has the advantage over other kernels, such as the harmonic mean, in being of enhanced spatial resolution, allowing it to determine more accurately the range of different activities (Wood *et al*., 2000). This provides a much clearer indication of where the largest concentration of activities occur, and hence where foraging is most likely to occur based on the rational that razorbills would spend more time in an area where they actively exploit a prey patch, than when commuting between feeding patches (see Benvenuti *et al.*, 2001; Dall'Antonia *et al.*, 2001). It was therefore assumed that the 50% core-use area was primarily associated with feeding activities, whilst the 95% active-use area was also associated with inbound and outbound journeys.

Some studies only use a subsample of their trips for home-range estimates, as not to bias the analysis on birds that provided more trips (e.g. Gremillet *et al.,* 2008; McLeay *et al.,* 2010; Yorio *et al.,* 2010; Quintana *et al.,* 2011). However, following preliminary analyses of home-ranges based on equal trip numbers per individual versus all trips per individuals, it was decided that home-range estimates were more likely to be representative when all data were used, given considerable within- and between-individual variation in trip parameters (see Appendix 6.1). Hence, the 95% and 50% FKD estimates were calculated from pooled data from all trips from all individuals sampled at a particular colony/ in a particular year. However, the 50% FKD was calculated with hours of darkness fixes (22:00h-04:00h) removed. This was to provide a more accurate estimate of actual foraging areas, as it has been suggested by previous authors that, whilst razorbills may spend the night at sea, they are unlikely to be foraging during hours of complete darkness (Benvenuti *et al.*, 2001; Dall'Antonia *et al.*, 2001; Paredes *et al.*, 2008; Thaxter *et al.*, 2010 - See Discussion (Section 4.3) for more detailed information).

The 95% and 50% home-range contours were then plotted on geographical maps in ArcGIS. The 50% core-use areas (hereafter referred to as core foraging area), were further plotted on bathymetric and substrate maps, to allow the identification of potentially important habitat types by calculating percentage overlap of foraging areas with specific depths and substrate categories. Broad inter-colony and inter-annual comparisons were made in terms of home-range sizes (for BAR11 vs. PUF11 and PUF11 vs. PUF12), as well as distribution and percentage overlap (for PUF11 vs. PUF12, only), using the measuring and intersect tools in ArcMap on Transverse-Mercator projected data (projected coordinate system: WGS 1984).

Finally, in order to investigate the representativeness of the data in terms of the entire colonies of BAR11, PUF11 and PUF12, a series of saturation curves were plotted of the predicted active-use and core foraging areas calculated from all trips made by an increasing number of randomly chosen razorbills included in the sample. In each case, the plotted data points represented an average value from repeated calculations, the number of repeats being equivalent to the number of birds in the individual colonies/years. These calculations were performed in R, using the R packages 'Adehabitat' (Calenge, 2007). The rationale of this quality check was based on a study by Soanes *et al.* (in review.), who showed that the relationship between number of seabirds and their home-range area is a non-linear asymptotic one, where individuals have broadly different home-ranges, but with some overlap, until a sufficient number of birds have been sampled for all available habitat to be used.

3. RESULTS

3.1. EFFECTIVENESS OF THE TRACKING TECHNIQUE

Usable GPS data were collected from 41 out of 90 birds (BAR11: n = 19, PUF11: n = 12, PUF12: n = 10), constituting a roughly 50% success rate per colony/year. This is in line with success rates from other studies (e.g. Guilford *et al.,* 2008). GPS tracks confirmed that most birds returned to the colony in less than 30 minutes after deployment, and only two out of 41 birds returned to the colony more than one hour after release. Although deployment periods varied from 2 to 17 days, data from any individual were only recorded over a maximum of 3.5 days, before battery depletion of the devices (Table 3.1). Furthermore, although study periods spanned over similar dates at BAR11, PUF11 and PUF12, the actual period over which data was obtained varied between colonies and years, and entailed an extra 6 days in June at BAR11 compared to PUF11 and an extra 10 days at PUF11 compared to PUF12 (Table 3.1).

The loggers provided data from a total of 211 trips (BAR11: n = 82, PUF11: n = 82, PUF12: n = 47) (Figure 3.1 a-c). With the exception of a single bird (in PUF12), data from more than one trip per bird was obtained, and for the majority of birds, data included both diurnal and nocturnal trips (Table 3.2; Figure 3.1 d-f). Following Benvenuti *et al.* (2001), diurnal trips are referred to as trips that occurred between sunrise and sunset, ending on the same day as they started. Nocturnal trips are referred to as trips that include hours of darkness (here, approximately 22:00h to 04:00h). Despite having similar sample sizes for PUF11 and PUF12, the number of trips recorded in 2011 was almost twice as high as the number of trips recorded in 2012, even though the tags were attached to individual birds for similar periods (Table 3.1).

Based on data where an entire day was sampled (i.e. excluding tag deployment/retrieval days and days where the battery became depleted), individual birds were calculated to daily perform up to 4 diurnal trips (1.16 ± 0.201) at BAR11 and up to 6 diurnal trips at PUF11 (1.538 ± 0.324) and PUF12 (1.235 ± 0.433), and no more than one nocturnal trip (BAR: 0.69 ± 0.083, PUF11: 0.069 ± 0.092, PUF12: 0.59 ± 0.123). Visual inspection of the tracks (Figure 3.1a) revealed that individual birds visited various areas within any given day, similar areas in successive days, with some evidence that particular areas were favoured by different birds over the short term. Nocturnal trips revealed extensive straight, low-speed tracks running in a south/north direction at Bardsey Island, and in an east-west direction at Puffin Island (Figure 3.1b).

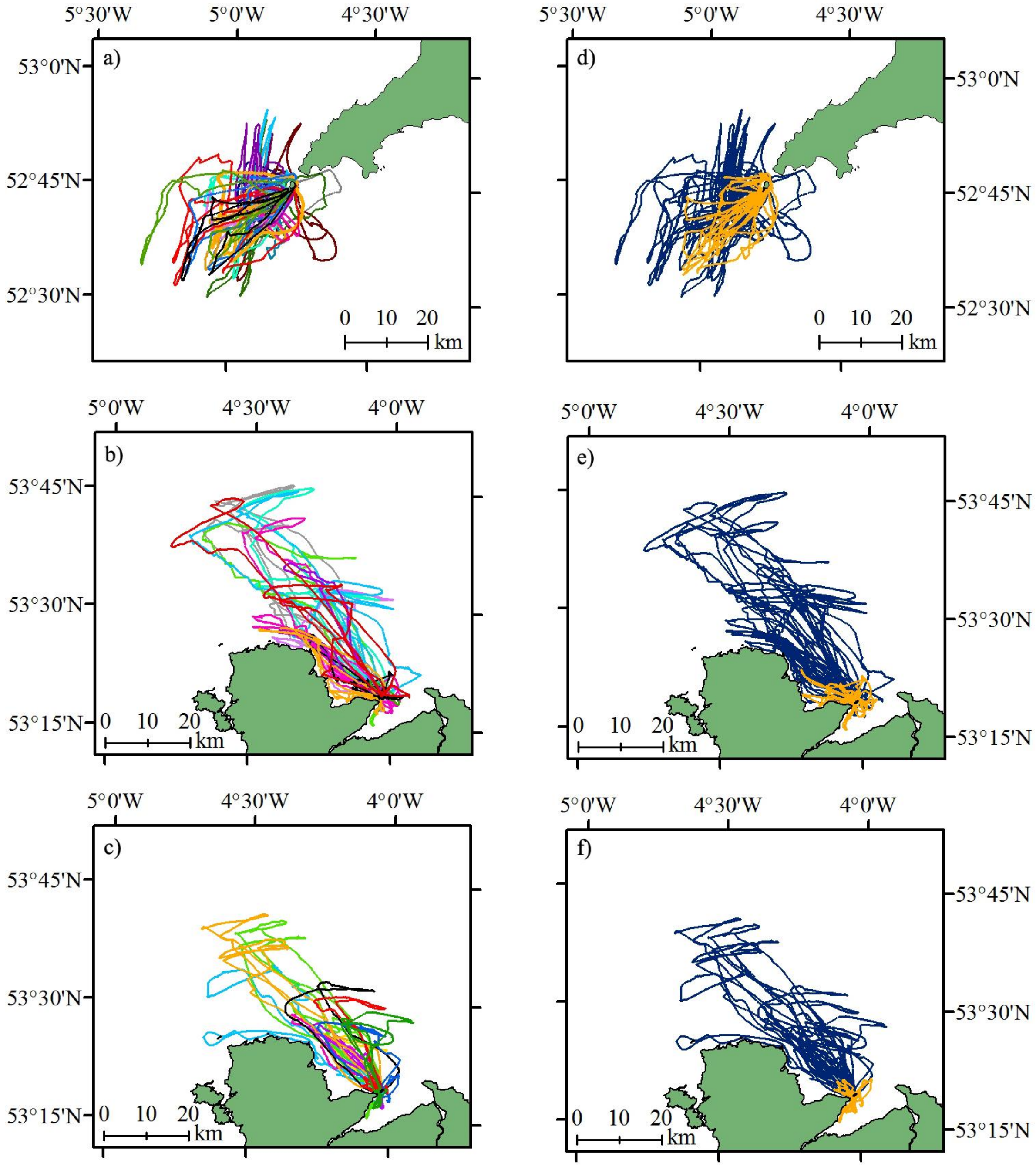

Figure 3.1 All foraging tracks of individual razorbills (a-c) tagged at Bardsey Island 2011 (a), and Puffin Island 2011 (b) and 2012 (c). Different colours in individual maps (a-c) represent all the tracks recorded for individual birds, although the same colours in different maps do not represent the same individuals. Figures d-f show diurnal (orange lines) and nocturnal (dark blue lines) foraging tracks of tagged razorbills at Bardsey 2011 (d) and Puffin Island 2011 (e) and 2012 (f).

Table 3.1 Summary of deployment and actual data collection periods (in days) from razorbill colonies at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11) and Puffin Island 2012 (PUF12).

Colony	Study period (1st tag deployed to last tag removed)	Actual period obtained data for	Period of tag deployment on individual birds (d, mean ± SE)	Actual period of data collection per individual bird (d, mean ± SE)
BAR11	14 May - 10 June 2011	15 May – 10 June 2011	3-8 (4.26 ± 0.35)	0.5-3.5 (2.05 ± 0.16)
PUF11	17 May - 6 June 2011	17 May – 4 June 2011	2-17 (5.41 ± 1.26)	1.5-3.5 (2.50 ± 0.20)
PUF12	17 May - 2 June 2012	17 May – 25 May 2011	2-16 (6.50 ± 1.49)	1-3 (2.25 ± 0.29)

Table 3.2 Overview of number of birds caught and trip numbers obtained from razorbill colonies at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11) and Puffin Island 2012 (PUF12) over their respective data collection periods (see Table **3.1**). DN = diurnal and nocturnal trips together, D = diurnal trips, N = nocturnal trips).

Colony	No. of birds tagged	Total no. of trips recorded	Min. no. of trips per bird	Max. no. of trips per bird	Mean no. of trips per bird ± SE
BAR11	41	DN = 82 D = 52 N = 30	DN = 2 D = 0 N = 0	DN = 8 D = 7 N = 3	DN = 4.32 ± 0.37 D = 3.06 ± 0.37 N = 1.76 ± 0.16
PUF11	12	DN = 82 D = 56 N = 26	DN = 2 D = 0 N = 0	DN = 14 D = 11 N = 4	DN = 6.83 ± 1.0 D = 5.6 ± 1.0 N = 2.36 ± 0.33
PUF12	10	DN = 47 D = 31 N = 16	DN = 1 D = 0 N = 1	DN = 11 D = 9 N = 3	DN = 4.7 ± 0.84 D = 3.44 ± 0.80 N = 1.66 ± 0.22

Out of the 41 successful study birds, weight at recapture was obtained for a total of 36 birds (BAR11: n = 19, PUF11: n = 9, PUF12: n = 6). Weight of birds at capture and recapture did not significantly differ between colonies/ years (ANOVA, $F_{2,67} = 0.347$, p = 0.708). However, apart from three birds who had gained weight (BAR11: n = 1, PUF12: n = 2), birds from both colonies/ years showed a significant decline in body mass over the tracking period (Two-way ANOVA, $F_{1, 67} = 10.141$, p = 0.002; Table 3.3), with daily average weight loss during the deployment period in birds from BAR11, PUF11 and PUF12 having been 9.1g (1.5%), 11.51g (1.8%) and 6.7g (1.1%), respectively. Percentage change in weight of individuals showed no relationship with hours of tag deployment (Pearson’s rank correlation: n = 34, r = 0.027, p = 0.880).

Table 3.3 Weight (g) at capture and recapture, and % weight changes of tracked birds during deployment period at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11) and Puffin Island 2012 (PUF12). BAR11: n = 19, PUF11: n = 9, PUF12: n = 6.

Colony/ year	Weight at capture (g)			Weight at recapture (g)			Weight change (%)		
	Min	Max	Mean ± SE	Min	Max	Mean ± SE	Min	Max	Mean ± SE
BAR11	573	680	631.74 ± 7.61	541	658	598.47 ± 7.92	+0.18	-0.02	5.24 ± 0.71
PUF11	550	700	628.89 ± 17.18	530	650	583.89 ± 13.64	-2.73	-11.01	7.02 ± 1.14
PUF12	585	635	622.21 ± 11.45	560	605	605.0 ± 12.65	+1.59	-6.34	2.79 ± 1.31

3.2. FORAGING TRIP PARAMETERS

Two-tailed t-tests on mean parameter values of pooled data from BAR11, PUF11 and PUF12 revealed that birds on eggs and birds on chicks did not significantly differ in foraging trip parameters (maximum distance: $t_{23} = 0.106$, $p = 0.916$; total distance: $t_{23} = 0.604$, $p = 0.551$; duration: $t_{23} = 1.059$, $p = 0.301$). This is in agreement with findings at other razorbill colonies (e.g. at Orkney: RSPB, unpublished data), and hence, data from all birds were combined for each colony/year for all subsequent analyses.

Foraging parameter values for birds from BAR11, PUF11 and PUF12 are summarised in Table 3.4. Pearson’s rank correlations revealed a highly significant positive relationship between (1) maximum distance and trip duration (Figure 3.2; Table **3.5**), (2) total distance and trip duration, and (3) total distance and maximum distance in both colonies/years (Table **3.5**), although the relationships were much weaker for the colony at BAR11 compared to PUF11. Hence, patterns of distributions and frequencies of these three variables will show close correlation throughout the rest of this study in both colonies/years, although with slightly more variation for the BAR11 colony.

Table 3.4. Summary of a) maximum distance (km), b) total distance (km), and c) duration (h) of diurnal (D) and nocturnal (N) trips, as well as for all trips combined (DN) for tracked razorbill from colonies at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11) and Puffin Island 2012 (PUF12).

a) Maximum distance (km)

Colony/year	D			N			DN
	Min	Max	mean ± SE	Min	Max	mean ± SE	mean ± SE
BAR11	0.33	30.15	6.98 ± 1.29	11.05	42.03	22.65 ± 1.62	12.54 ± 1.29
PUF11	0.43	14.93	2.76 ± 0.39	4.8	60.1	35.20 ± 3.19	13.05 ± 1.97
PUF12	0.33	7.02	2.53 ± 0.34	18.39	57.2	33.41 ± 3.41	13.08 ± 2.44

b) Total distance (km)

Colony/year	D			N			DN
	Min	Max	mean ± SE	Min	Max	mean ± SE	mean ± SE
BAR11	0.69	63.9	16.04 ± 2.82	33.17	142.76	75.67 ± 4.36	37.86 ± 3.98
PUF11	0.81	31.24	7.20 ± 0.99	15.71	180.95	98.88 ± 9.32	36.27 ± 5.61
PUF12	0.89	19.26	6.56 ± 0.90	53.71	166.61	94.71 ± 8.46	37.82 ± 7.03

c) Duration (h)

Colony/year	D			N			DN
	Min	Max	mean ± SE	Min	Max	mean ± SE	mean ± SE
BAR11	0.20	8.88	1.36 ± 0.27	9.25	29.68	13.06 ± 0.74	5.63 ± 0.70
PUF11	0.19	9.65	1.32 ± 0.25	6.78	26.08	13.77 ± 0.77	5.27 ± 0.71
PUF12	0.23	3.88	1.21 ± 0.17	11.22	31.13	15.68 ± 1.33	6.14 ± 0.71

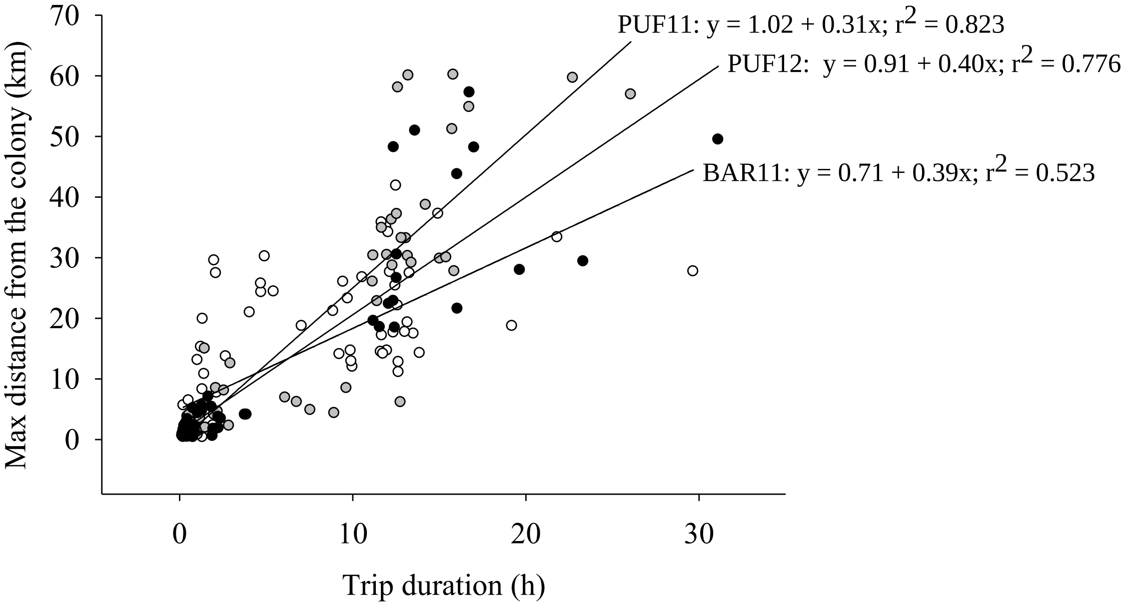

Figure 3.2 Scatter plot showing the relationship between maximum distance from the colony (km) and foraging trip duration (h) of the razorbill colonies at Bardsey Island 2011 (BAR11) (●), Puffin Island 2011(PUF11) (●) and Puffin Island 2012 (PUF12) (○).

Table 3.5 Summary of the Pearson's rank correlation results relating maximum distance (km), total distance (km) and duration (h) of razorbill foraging trips from colonies at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11) and Puffin Island 2012 (PUF12). * Correlation is significant at an alpha value of 0.05. r = Pearson's rank statistic.

Colony/year	Max. dist. vs duration	Total dist. vs duration	Max. dist. vs total dist.
BAR11	r = 0.759; p < 0.001*	r = 0.909; p < 0.001*	r = 0.914; p < 0.001*
PUF11	r = 0.907; p < 0.001*	r = 0.921; p < 0.001*	r = 0.986; p < 0.001*
PUF12	r = 0.881; p < 0.001*	r = 0.938; p < 0.001*	r = 0.982; p < 0.001*

The data were not normally distributed, showing a positive skew in foraging parameters due to a much higher number of short compared to long trips (e.g. Anderson-Darling test for maximum distance: BAR11: n = 82, AD = 18.84, p < 0.001, skewness = 0.58; PUF11: n = 82, AD = 10.07, p < 0.001, skewness = 1.11, PUF12: n = 47, AD = 4.99, p < 0.001, skewness = 1.36; Figure 3.3). Diurnal and nocturnal trip parameters showed very different trends. Over half of all diurnal trips from both colonies occurred within 2 km of the colony (BAR11: 56%, PUF11: 59%, PUF12: 52%) and in less than one hour (BAR11: 65%, PUF11: 59%, PUF12: 58%). By contrast, all but three nocturnal trips at

PUF11, occurred at distances greater than 10 km, with the vast majority of trips taking over ten hours (BAR11: 83%, PUF11: 92%, PUF12: 100%).

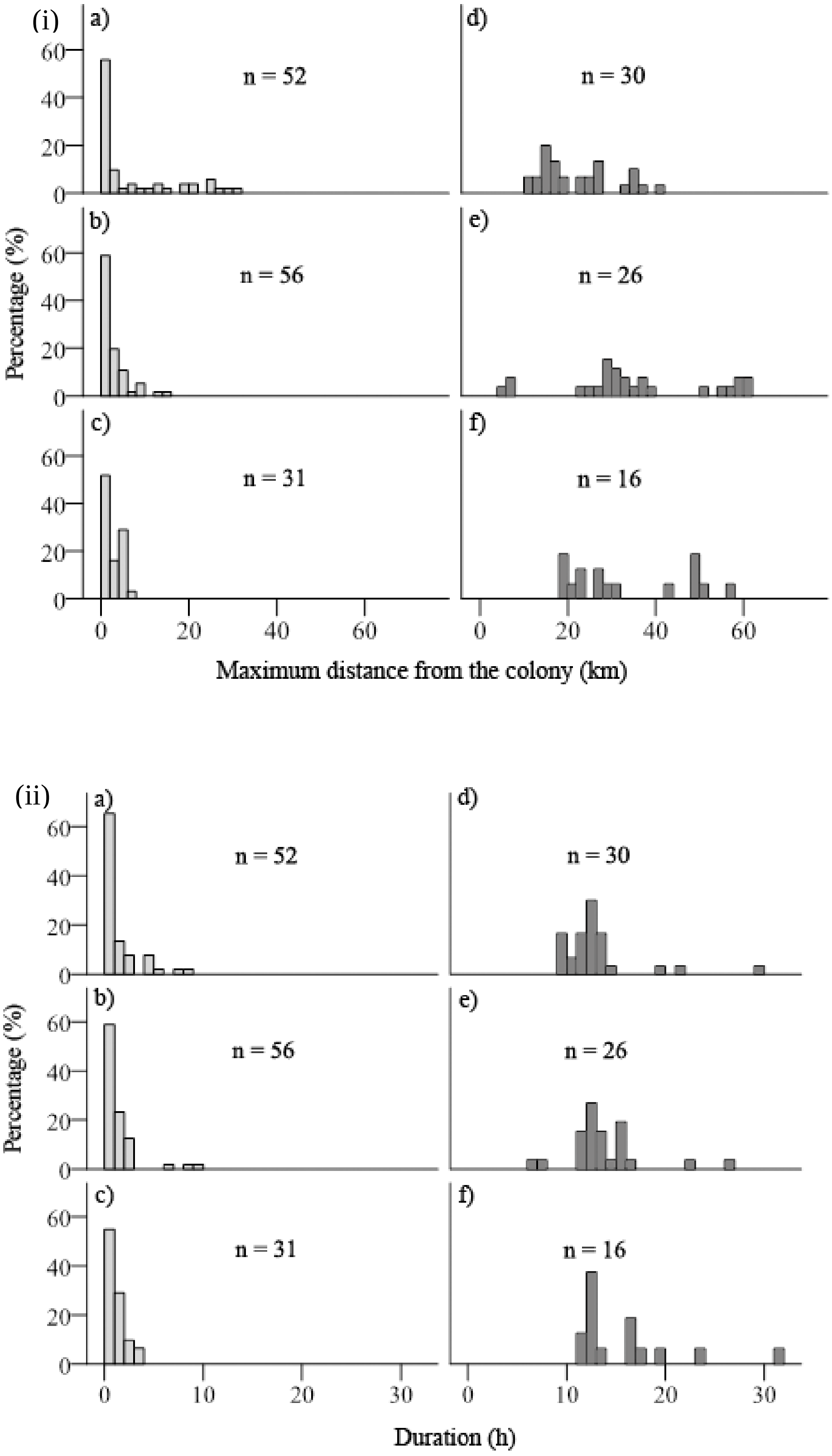

Figure 3.3 Percentage frequency histograms for (i) maximum distance (km) and (ii) trip duration of diurnal (a-c) and nocturnal (d-f) foraging trips of razorbills from colonies at Bardsey Island 2011 (a, d) and Puffin Island 2011 (b, e) and 2012 (c, f).

A one-tailed paired t-test using mean values of data of birds that produced both diurnal and nocturnal trips confirmed that maximum distance, total distance and trip duration were significantly greater for nocturnal trips, on average, compared to diurnal trips in both colonies/years (Table 3.6). Because we did not obtain equal numbers of diurnal and nocturnal trips per bird (Table 3.2), and in order to attain homogeneity of variance and to allow the use of more powerful statistical tests, the two types of trips were analysed separately in all subsequent analyses, unless stated otherwise.

Table 3.6 Summary of one-tailed paired t-test results comparing maximum distance from the colony (km), total trip distance (km) and trip duration (h) of diurnal and nocturnal foraging trips of tagged razorbills from the colonies at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11) and Puffin Island 2012 (PUF12). df = degrees of freedom**.**

Colony/ year	Maximum distance (km)			Total distance (km)			Duration (h)		
	t	df	p	t	df	p	t	df	p
BAR11	- 11.959	14	<0.001	-3.112	14	<0.001	-0.416	14	<0.001
PUF11	-6.372	8	<0.001	-5.415	8	<0.001	-7.423	8	<0.001
PUF12	-6.402	8	<0.001	-8.164	8	<0.001	-0.873	8	< 0.001

Equal variance of residuals, as shown by the Levene’s test, allowed foraging parameters of diurnal and nocturnal trips to be individually compared between colonies and years using a GLM. No significant inter-annual effects in foraging parameters were determined at the Puffin Island colony, with overall trip parameters found to be remarkably similar in both years, especially for diurnal trips, despite trips averaging marginally longer distances and durations in the season of 2011 (Figure 3.4; Table 3.7). However, diurnal and nocturnal maximum distance, as well as diurnal total trip distance showed a significant difference between colonies in 2011, with Bardsey’s diurnal trips averaging longer distances, whereas nocturnal trips were of shorter distances. Despite the differences in distance, however, the two colonies showed almost identical averages in trip duration. This inconsistency reflects the colony difference in the strength of correlation between maximum distance and trip duration, as shown in Figure 3.2.

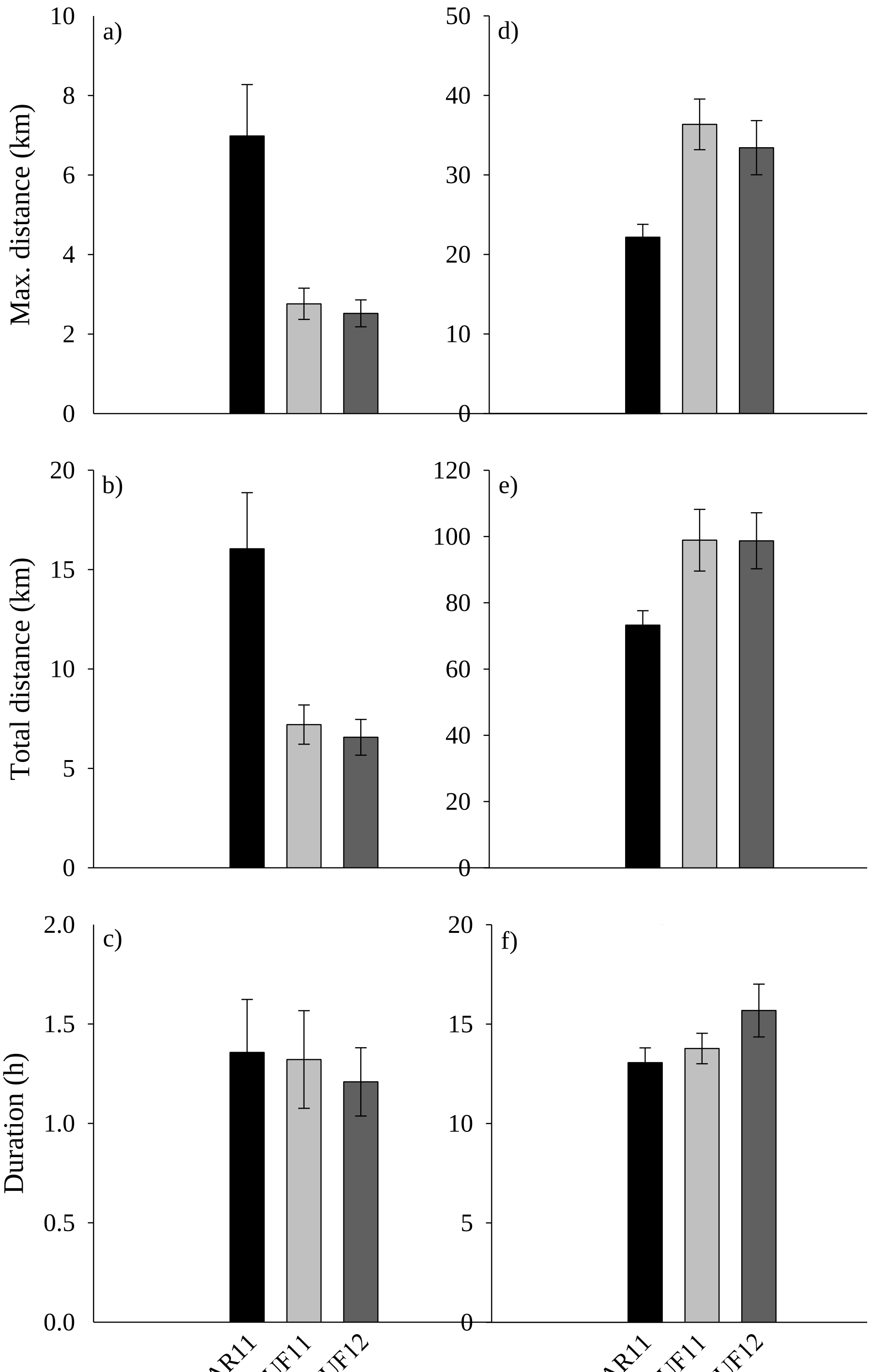

Figure 3.4 Means ± standard error of maximum distance (a, d), total distance (b, e), and trip duration (c, f) for diurnal (a-c) and nocturnal (d-f) razorbill foraging trips for the colonies at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11) and Puffin Island 2012 (PUF12). Note the difference in scale between diurnal (a-c) and nocturnal (d-f) trips.

Table 3.7 a) Summary of GLM results to determine an inter-colony (Bardsey Island vs. Puffin Island 2011) and inter-annual (Puffin Island 2011 vs. 2012) differences in razorbill foraging trip parameters: maximum distance (km), total distance (km), and duration (h). b) Bonferroni pair-wise comparisons with respect to the GLM results in (a). D = diurnal trips, N = nocturnal trips; $_1$ = log10 transformed; * = significant at an alpha value of 0.05 level. df = degrees of freedom.

a) GLM results

Independent variable	Fixed factor	Nested random factor	df	F	p
Max. distance (D)	Colony / year	Bird id	2	4.750	0.014*
Max. distance (N)	Colony / year	Bird id	2	3.432	0.042*
Total distance (D)	Colony / year	Bird id	2	4.614	0.016*
Total distance (N)	Colony / year	Bird id	2	1.918	0.159
Duration (D)	Colony / year	Bird id	2	0.199	0.852
Duration (N)$_1$	Colony / year	Bird id	2	2.401	0.103

b) Bonferroni multiple comparison between colonies/year using

Independent variable	Pair-wise comparisons		p
Max. distance (D)	PUF11	BAR11	<0.001*
		PUF12	0.925
Max. distance (N)	PUF11	BAR11	<0.001*
		PUF12	0.533
Total distance (D)	PUF11	BAR11	<0.001*
		PUF12	0.966
Total distance (N)	PUF11	BAR11	0.073
		PUF12	0.854
Duration (D)	PUF11	BAR11	0.939
		PUF12	0.862
Duration (N)$_1$	PUF11	BAR11	0.944
		PUF12	0.176

3.3. TRIP TIMING

At both colonies, and for Puffin Island, in both years, departures on diurnal trips occurred between sunrise and sunset (approximately 05:00h and 21:00h, respectively, during sampling dates), with only one departure having occurred before 05:00h (at PUF12; Figure 3.5; Table **3.8**). At BAR11 and PUF11, departure times were fairly evenly spread through the day, with no strong patterns emerging (χ^2-test of frequency data, BAR11: n = 52, χ^2 = 6.149, 5 df, p = 0.292; PUF11: n = 56, χ^2 = 6.361, 5 df, p = 0.273). By contrast, PUF12 showed significant clustering of diurnal departures in the morning between 06:00h and 09:00h (χ^2-test of frequency data, PUF12: n = 31, χ^2 = 17.234, 4 df, p = 0.241; Figure 3.5). Distributions of departure times showed no inter-colony difference (χ^2-test of frequency data, BAR11 vs PUF11: n(total) = 108, χ^2 = 4.803, 5 df, p = 0.441), but did differ significantly between years (χ^2-test of frequency data, PUF11 vs PUF12: n(total) = 87, 5 df, χ^2 = 15.413, 5 df, p = 0.009). It should be noted that the latter analysis produced 5 out of 12 expected values of less than five (see Dytham, 2011). Whilst the result should therefore be viewed with caution, the low p-value, as well as the significant clustering of PUF12 compared to PUF11, both suggest a true difference in pattern.

Departures on nocturnal trips occurred predominantly in the evening hours before sunset, although some also occurred at earlier times, especially at PUF12 (Figure 3.5; Table **3.8**). Goodness-of-fit tests revealed significant clustering over the period during which nocturnal trip departures occurred at BAR11 and PUF11 (χ^2-test of frequency data, BAR11: n = 30, χ^2 = 61.672, 4 df, $p < 0.001$; PUF11: n = 26, χ^2 = 7.919, 2 df, p = 0.019), with the majority of trips departing between 18:00h and 20:00h (Figure 3.5). At PUF12, however, clustering of nocturnal trip departure times was not significant (χ^2-test of frequency data, n = 16, χ^2 = 6.501, 4 df, p = 0.165), although departures still peaked between 18:00h and 20:00h (Figure 3.5). Tests of independence were not possible due to the small sample sizes and narrow spread of data. However, given the goodness-of-fit test results and the patterns illustrated in Figure 3.5, it appears that inter-colony patterns were more similar than inter-annual patterns, as was the case for diurnal departures times.

Table 3.8 Earliest and latest departure and return times of diurnal (D) and nocturnal (N) trips of razorbills at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11) and Puffin Island 2012 (PUF12).

Colony/year	Earliest and latest departure times		Earliest and latest return times	
	N	D	N	D
BAR11	09:49, 23:00	05:31, 19:32	04:41, 15:17	05:49, 19:46
PUF11	12:02, 22:02	04:25, 19:56	04:12, 18:08	04:45, 20:40
PUF12	11:11, 23:00	05:33, 16:36	04:42, 11:52	06:22, 17:12

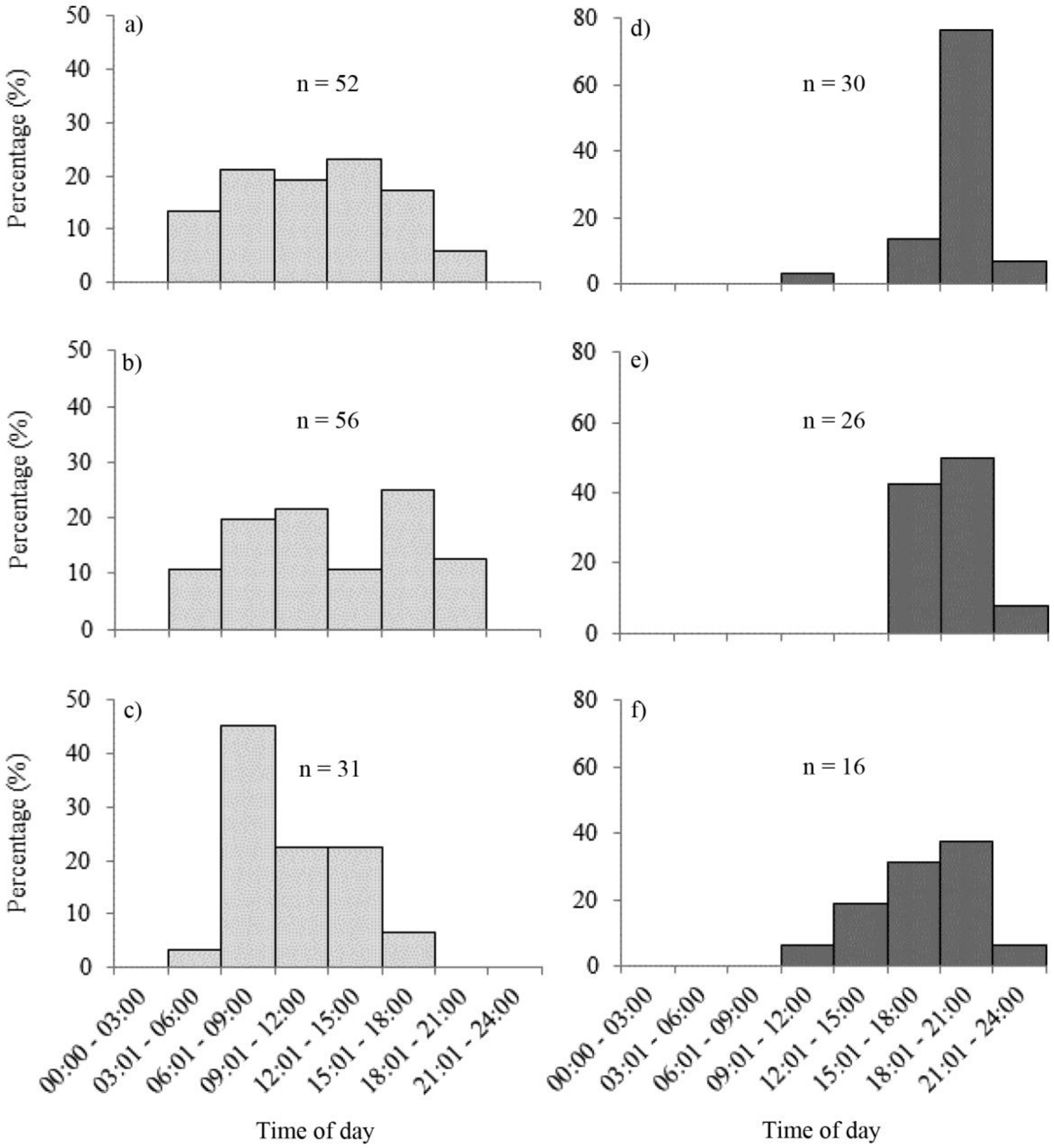

Figure 3.5 Histograms showing the percentage frequency of diurnal (a-c) and nocturnal (d-f) foraging trip departures made throughout the day by razorbills from Bardsey Island 2011 (a, d), Puffin Island 2011 (b, e) and Puffin Island 2012 (c, f). Figure illustrates percentage frequency, instead of actual counts, in order to facilitate inter-colony and inter-annual comparisons of patterns.

Given the relatively short duration of diurnal trips, their return times followed a broadly similar pattern to departure times, peaking during the day between sunrise and sunset in both colonies/years (Figure 3.6; Table **3.8**). Goodness-of-fit tests revealed significant clustering of diurnal return times during this period at BAR11 around noon/early afternoon and at PUF11 in the late afternoon from 15:00h to 18:00h (χ^2-test of frequency data, BAR11: n = 52, $\chi^2 = 18.153$, 5 df, p = 0.003; PUF11: n = 56, $\chi^2 = 17.069$, 5 df, p = 0.015; Figure 3.6). Despite this difference in peaks at PUF11 and BAR11, a test of independence revealed no significant difference in overall patterns of diurnal trip return times between these colonies (χ^2-test of frequency data, n(total) = 108, $\chi^2 = 8.911$, 5 df, p = 0.113). PUF12 diurnal return times showed no clustering across the period during which they occurred (χ^2-test of frequency data, PUF12: n = 31, $\chi^2 = 5.773$, 3 df, p = 0.123), although there was a marked peak in the morning between 06:00h and 09:00h (Figure 3.6). A test of independence revealed a weakly significant difference between PUF11 and PUF12 diurnal trip return patterns (χ^2-test of frequency data, n(total) = 87, $\chi^2 = 11.238$, 5 df, p = 0.047), although sample sizes were small, with 6 out of 12 expected values being less than 5.

Nocturnal return times occurred predominantly in the early morning hours at both colonies/years (Figure 3.6; Table **3.8**). Goodness-of-fit tests revealed significant clustering between 06:00h and 09:00h at BAR11 and PUF11 (χ^2-test of frequency data, BAR11: n = 30, $\chi^2 = 45.671$, 4 df, $p < 0.001$; PUF11: n = 26, $\chi^2 = 33.079$, $p < 0.001$; Figure 3.6). Although not significant, PUF12 also showed a peak in nocturnal return times between 06:00h and 09:00h (χ^2-test of frequency data, n = 16, $\chi^2 = 3.375$, 2 df, p = 0.144; Figure 3.6). Due to small sample sizes and narrow spread of data, tests of independence were not possible. However, the similarities in patterns, both between colonies and between years, are evident (Figure 3.6).

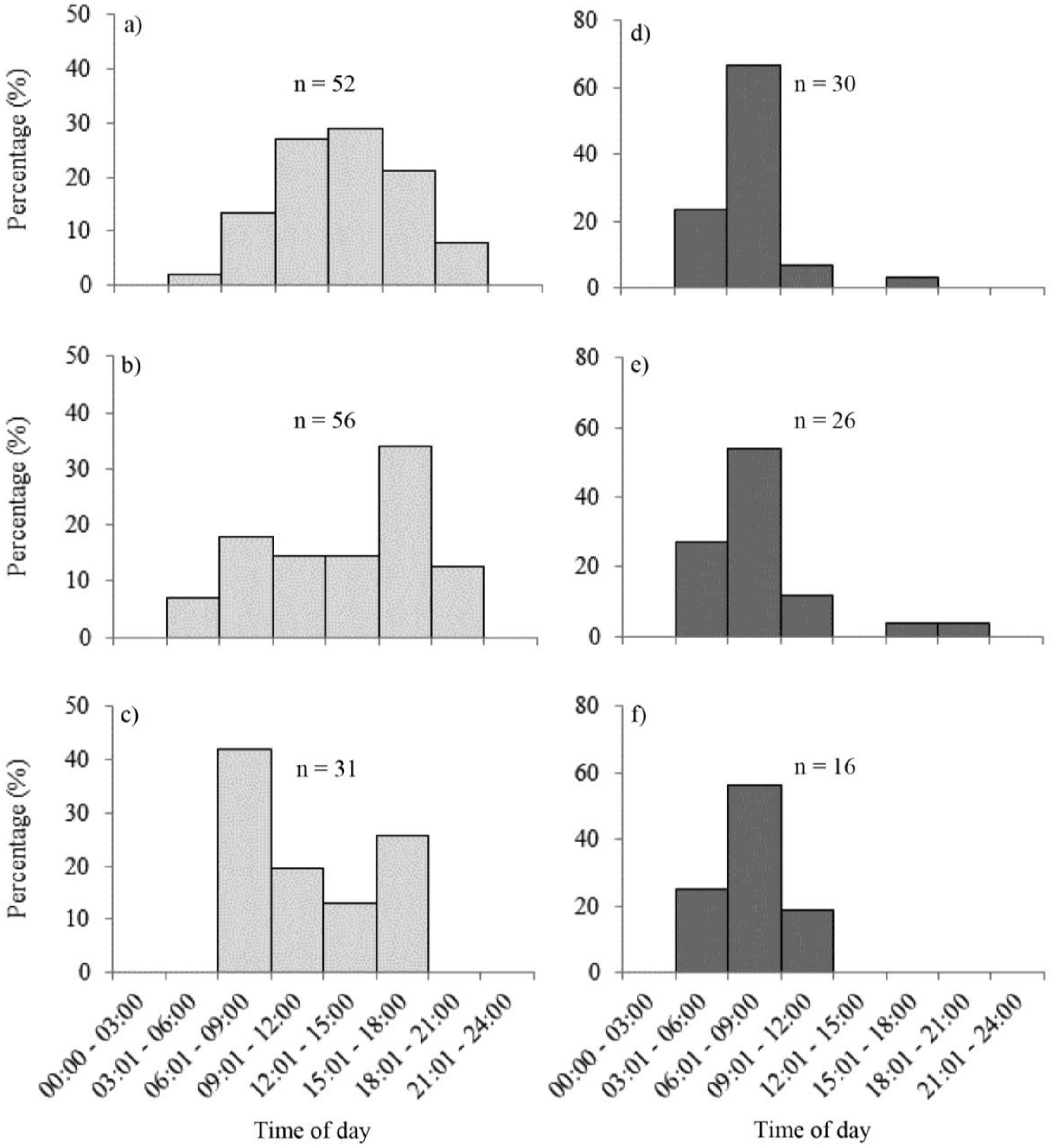

Figure 3.6 Histograms showing the percentage frequency of diurnal (a-c) and nocturnal (d-f) foraging trip returns made throughout the day by razorbills from Bardsey Island 2011 (a, d), Puffin Island 2011 (b, e) and Puffin Island 2012 (c, f). Figure illustrates frequency, instead of actual counts, in order to facilitate inter-colony and inter-annual comparisons of patterns.

3.4. HOME-RANGE

3.4.1. TOTAL HOME-RANGE: SIZE AND DISTRIBUTION

The saturation curves for BAR11, PUF11 and PUF12 home-range predictions, based on diurnal and nocturnal trips combined, all leveled off before the final samples were added to the analysis (Figure 3.7). This suggests that at both colonies, and for Puffin Island, in both years, enough individuals had been tracked, and enough data had been collected, for home-range estimates to be representative of their respective colonies with regards to the time period for which data had been obtained. Inter-colony and inter-annual comparisons could therefore still be made, despite home-range estimates of BAR11, PUF11 and PUF12 having been based on different sample sizes, although it should be kept in mind that data were not collected over identical time periods.

Total home-range estimates, based on diurnal and nocturnal trips combined, of BAR11, PUF11 and PUF12 are illustrated in Figure 3.8 (p.44), with according sizes summarised in Table 3.9 (p.45). Birds from both colonies did not access all areas available to them, given their maximum foraging trip distances, and did not access all accessed areas to the same extent. At Bardsey, the area of the razorbills' active-use (95% FKD) predominantly extended in a south-western direction from the colony, spanning approximately 45 km in a south-western direction, and 40 km in a south-east/north-western direction. Razorbills did not appear to be using the waters east of Bardsey within Cardigan Bay. Multiple core foraging areas (50% FKD) included the waters surrounding the colony, with the largest potential foraging area being located approximately 10-20 km southwest of the colony.

At Puffin Island, the total active-use areas were of comparable sizes in both seasons, roughly 1.5 times larger than at Bardsey, and extended approximately 60 km north/north-westwards from the colony along the eastern coast of Anglesey in a 10-35 km wide belt. The active-use area at Puffin Island also stretched southwards into the mouth of the Menai Strait, as far as the town of Beaumaris. In 2012, the Skerries located on the northwestern tip of Anglesey also formed part of the active-use area, although Figure 3.1 shows that the area was only visited by one bird on a single occasion. The razorbills did not use the coastal area eastwards of Puffin Island. The total core foraging areas at Puffin Island were found to be located around the colony itself and along the north-eastern/eastern coast of Anglesey in both seasons. These were of comparable sizes, and similar to the core foraging area estimated for the Bardsey Island colony. Overall, there was a 71% and 66% overlap in the 95% and 50% home ranges at Puffin Island, respectively, between the season of 2011 and 2012.

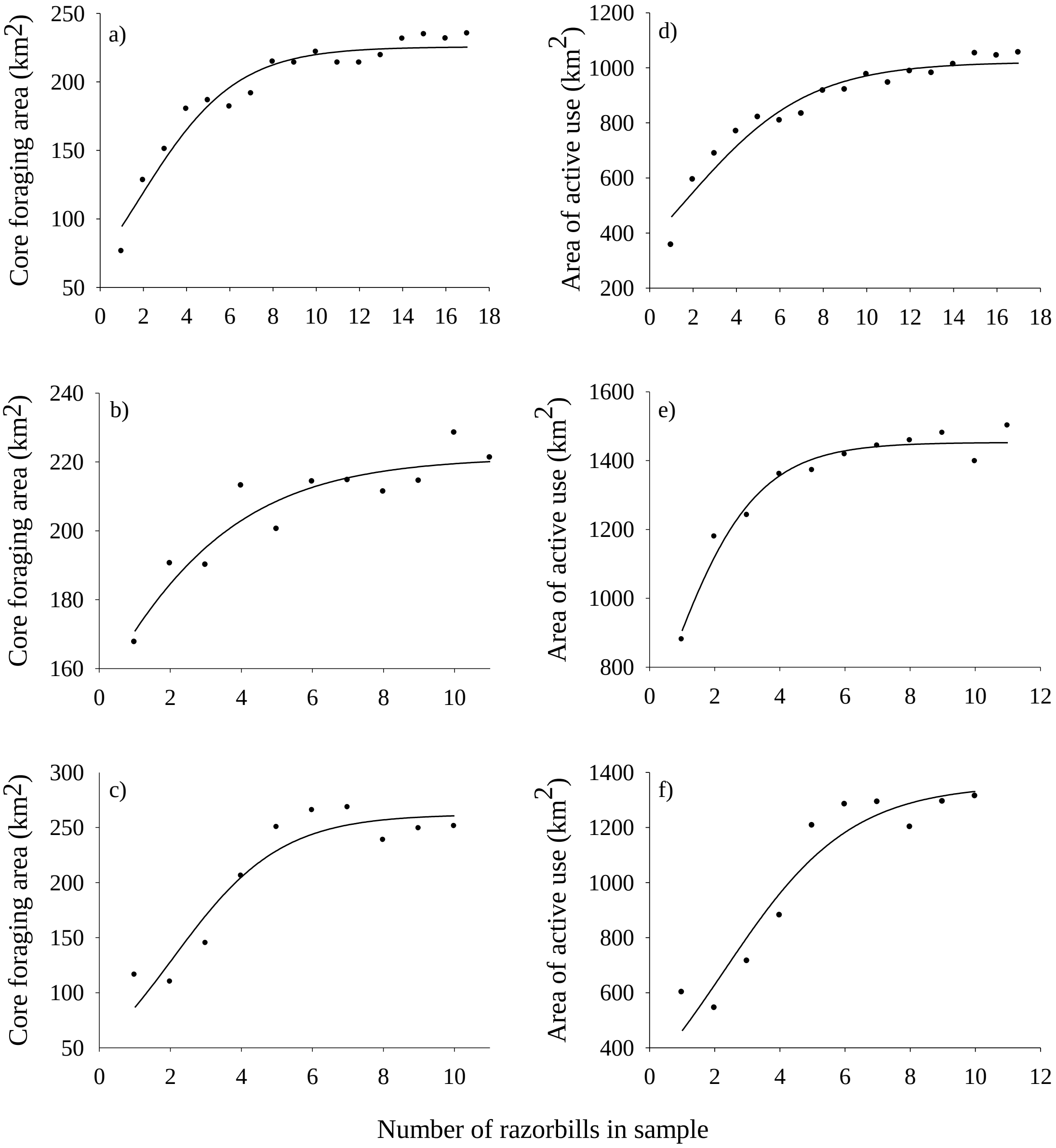

Figure 3.7 Change in estimated core foraging areas (a-c) and active-use areas (d-f) as predicted from analysis of all trips as a function of an increasing number of randomly chosen individual razorbills tagged at Bardsey Island 2011 (a, d), Puffin Island 2011 (b, e) and Puffin Island 2012 (c, f).

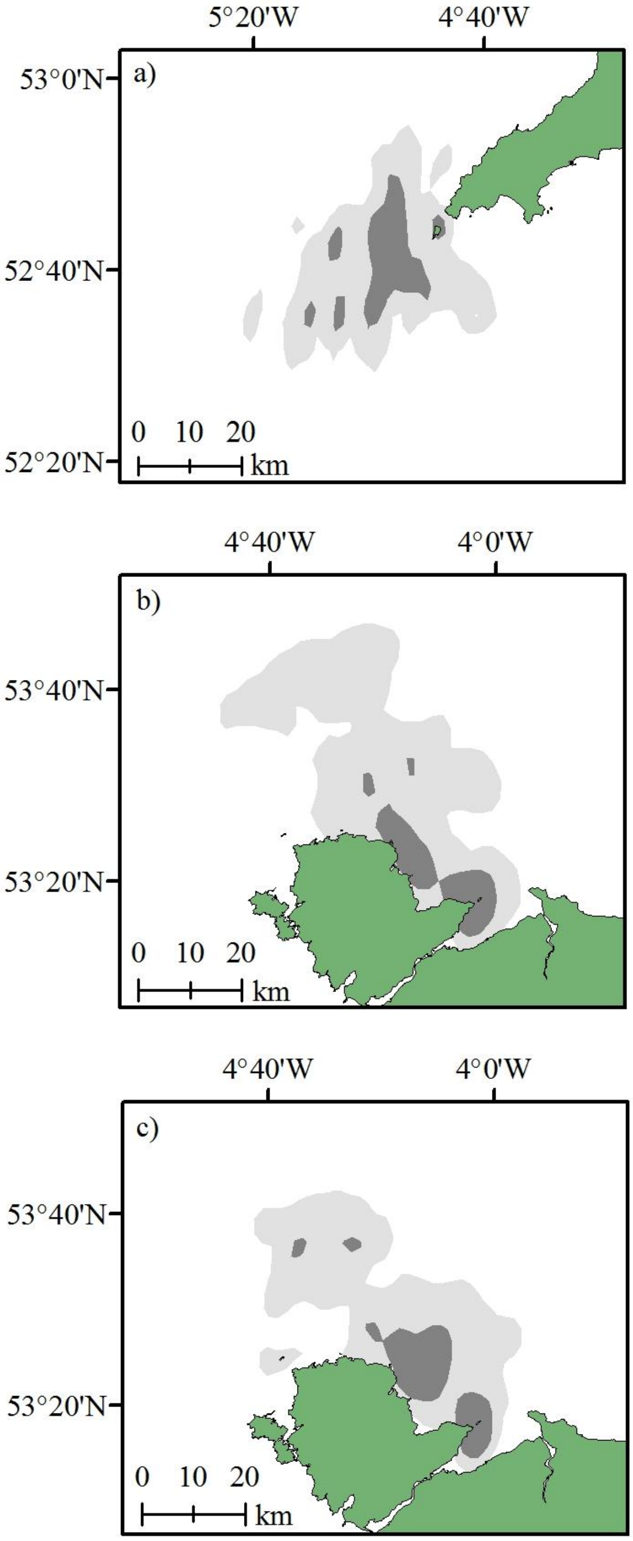

Figure 3.8 Total home-range of the razorbill colonies at Bardsey Island (2011) (a), Puffin Island 2011 (b) and Puffin Island 2012 (c). Light grey = 95% active-use area; dark grey = 50% core foraging area with hours of darkness fixes (22:00h-04:00h) removed from analysis.

Table 3.9 Summary of total (DN), diurnal (D) and nocturnal (N) home ranges (km^2) of the razorbill colonies at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11) and Puffin Island 2012 (PUF12). 95 = 95% active-use area, 50 = 50% core foraging area with hours of darkness (22:00h-04:00h) removed from analysis.

Colony /year	DN		D		N	
	95	50	95	50	95	50
BAR11	1059.0	232.0	468.6	118.3	1078.7	244.3
PUF11	1589.2	216.5	81.2	7.1	1590.0	368.0
PUF12	1314.9	246.7	40.9	6.6	1291.2	269.1

3.4.2. DIURNAL AND NOCTURNAL HOME-RANGE: SIZE AND DISTRIBUTION

Given the significant difference between diurnal and nocturnal trips, it was decided to also calculate the diurnal and nocturnal home-range estimates individually (Figure 3.9). Respective sizes of active-use and core foraging areas are summarised in Table 3.9. The saturation curves for BAR11, PUF11 and PUF12 home-range predictions all leveled off before the final samples were added to the analysis (Appendix 6.2, 6.3), suggesting that these home-range estimates are representative of their respective colonies with regards to the time period sampled.

The geographical distribution and sizes of the nocturnal active-use and core foraging areas were similar to those calculated for the total activity ranges at both colonies/ in both years. However, diurnal activity ranges showed a very different picture. At Bardsey, the diurnal home-range was roughly half the size of the nocturnal home-range, with the two showing roughly 37% and 8% overlap for the active-use and core foraging areas, respectively. A key diurnal foraging area was found to be located roughly 10 to 20 km southwest of the colony and in the waters immediately surrounding the colony. The main diurnal foraging area was found to be located at a greater distance from the colony than the main nocturnal foraging area, despite nocturnal forgaing trips having ranged significantly further distances. The reason for this discrepancy is most probably due to the furthest distances of nocturnal trips having coincided with hours of darkness, which had been removed for the purpose of this report.

At Puffin Island, the diurnal home-ranges in 2011 and 2012 were vastly smaller than their respective nocturnal home-ranges (Table 3.9), with diurnal and nocturnal home-ranges showing very little overlap in either year (For PUF11 and PUF12 respectively:

diurnal and nocturnal 95% FKD overlap = 5%, 3%; diurnal and nocturnal 50% FKD overlap = 2%, 0.5%). In both seasons, a single diurnal core foraging area was distributed around the colony itself. Although both seasons showed multiple nocturnal core foraging areas, the largest areas were situated both times near Point Lynas along the northeastern coast of Anglesey.

Comparing between years for the Puffin Island colony, both nocturnal and diurnal home-ranges were somewhat bigger in 2011 compared to the following year, although to varying degrees (see Table 3.9). The diurnal active-use and core foraging areas of 2011 and 2012 showed a 32% and 42% overlap, respectively, whilst the nocturnal active-use and core foraging areas of PUF11 and PUF12 showed a 56% and 22% overlap, respectively. Comparing between colonies, the nocturnal active-use and core foraging areas are respectively approximately 1.7 times and 1.5 times bigger at PUF11 than at BAR11. With regards to the diurnal home-range, however, the active-use and core-foraging areas are respectively about 6 and 17 times smaller at PUF11 compared to at BAR11.

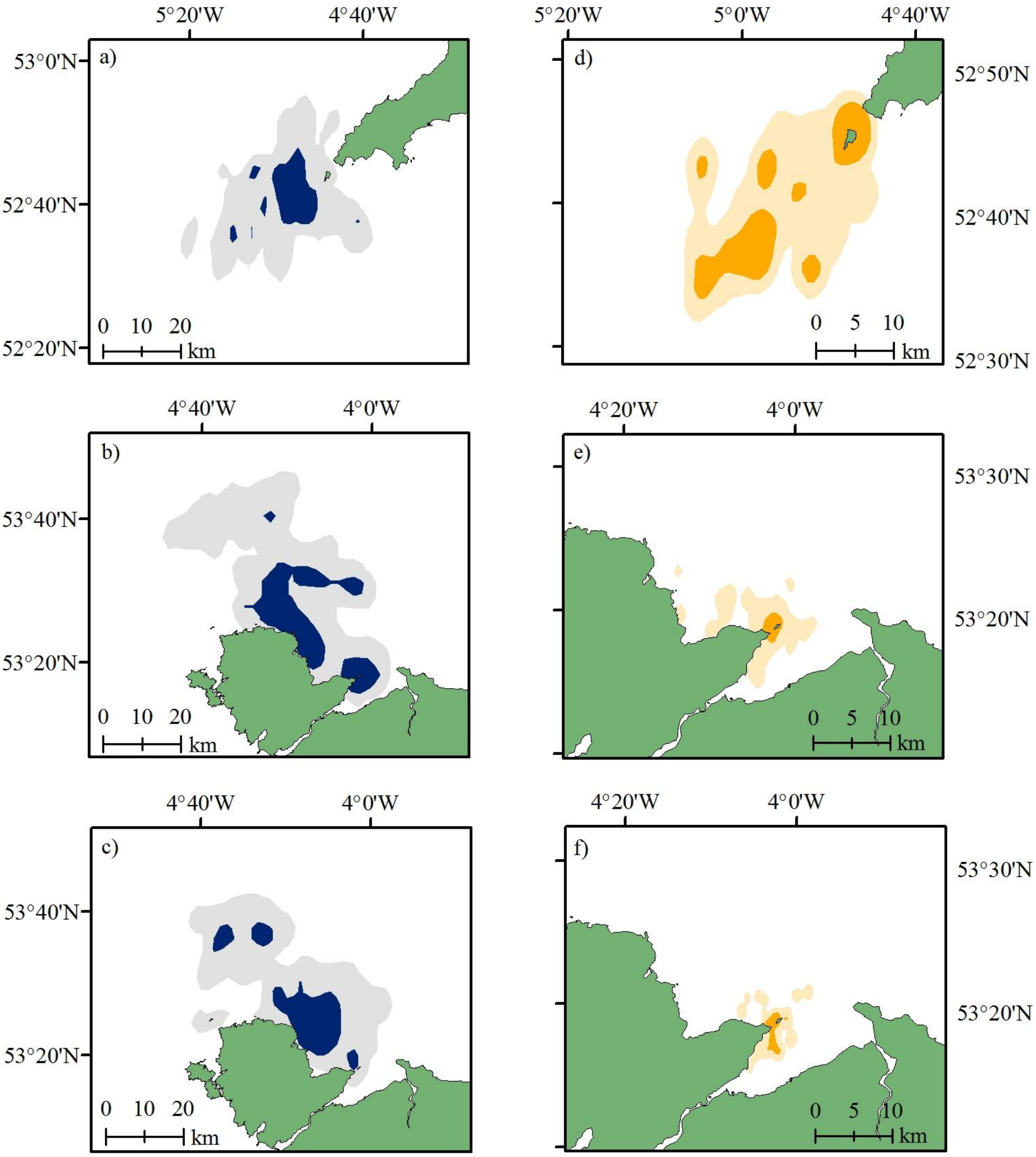

Figure 3.9 Nocturnal (a-c) and diurnal (d-f) home-ranges of razorbills at Bardsey Island 2011 (a, d), Puffin Island 2011 (b, e) and Puffin Island 2012 (c, f). Light blue/orange area = 95% active-use area; dark blue/orange = 50% core foraging area with hours of darkness fixes (22:00h-04:00h) removed for analysis. Note the difference in scale between nocturnal and diurnal home-range maps, introduced to facilitate visualisation of the diurnal home-range at Puffin Island.

3.4.3. *DIURNAL AND NOCTURNAL FORAGING RANGES IN RELATION TO ENVIRONMENTAL VARIABLES*

Given the considerable difference in the distribution of the core foraging areas for diurnal and nocturnal foraging trips, they were each related separately to depth (Figure 3.10) and substrate type (Figure 3.11) for BAR11, PUF11 and PUF12. At Bardsey, both nocturnal and diurnal core foraging areas predominantly overlay depths between 50-100 m, with shallower depths only accessed in waters immediately surrounding the colony during diurnal trips (Figure 3.10; Table 3.10). In terms of bottom type, the diurnal core foraging area overlapped much more extensively with sandy substrate, whilst the nocturnal core foraging area overlapped predominantly with coarse sediments (Figure 3.11; Table 3.11).

At Puffin Island the diurnal foraging area extended exclusively over waters of less than 20 m depth in both 2011 and 2012. The nocturnal foraging areas, on the other hand, were predominantly located in waters deeper than 35 m (maximum 67 and 85 m in 2011 and 2012, respectively) (Figure 3.10; Table 3.10). As was the case for BAR11, the diurnal core foraging areas of PUF11 and PUF12 showed much greater overlap with sandy sediments compared to the nocturnal core foraging areas, which predominantly overlapped with coarse sediments (Figure 3.11; Table 3.11).

Table 3.10 Percentage (%) overlap of diurnal and nocturnal foraging areas (50% FKD) with particular depths for the razorbill colonies at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11), and Puffin Island 2012 (PUF12), as shown in Figure 3.10.

Colony/year	% overlap with water depth of < 20 m		% overlap with water depth of > 35 m	
	D	N	D	N
BAR11	0	0	77	100
PUF11	100	21	0	85
PUF12	100	6	0	94

Table 3.11 Percentage (%) overlap of diurnal and nocturnal foraging areas (50% FKD) with particular substrate types for the razorbill colonies at Bardsey Island 2011 (BAR11), Puffin Island 2011 (PUF11), and Puffin Island 2012 (PUF12), as shown in Figure 3.11.

Colony/year	% overlap with sandy substrate		% overlap with coarse substrate		% overlap with other substrate	
	D	N	D	N	D	N
BAR11	49	20	35	78	16	2
PUF11	83	30	17	66	0	4
PUF12	86	23	14	68	0	9

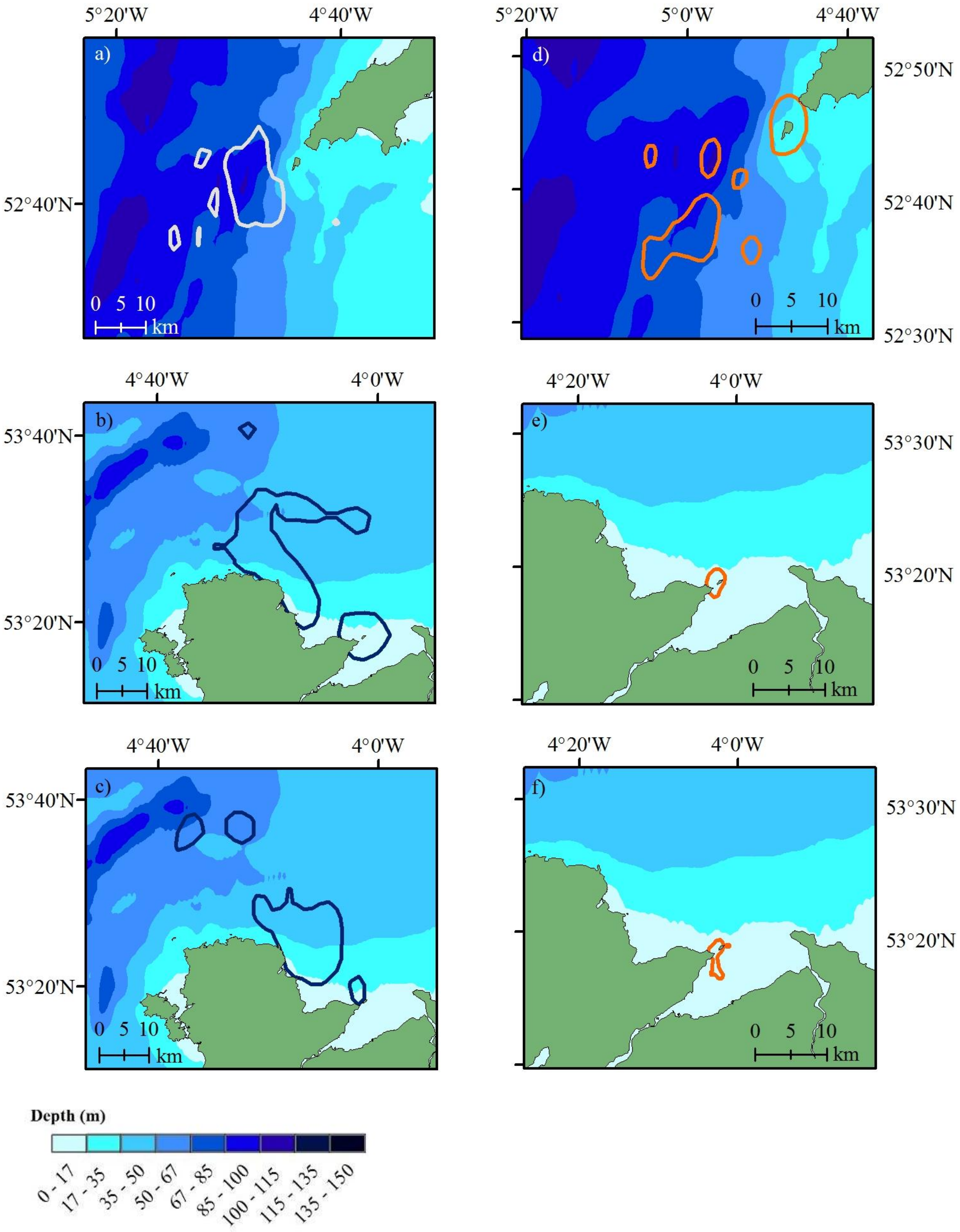

Figure 3.10 Nocturnal (a-c; dark-blue outline) and diurnal (d-f; orange outline) core foraging areas (50% FKD) of razorbill colonies at Bardsey Island 2011 (a, d), Puffin Island 2011 (b, e) and Puffin Island 2012 (c, f) in relation to depth. Core foraging area estimates calculated with hours of darkness fixes (22:00h-04:00h) removed from analysis. Note the difference in scale between nocturnal and diurnal home-range maps, introduced to facilitate visualisation of the diurnal foraging are at Puffin Island.

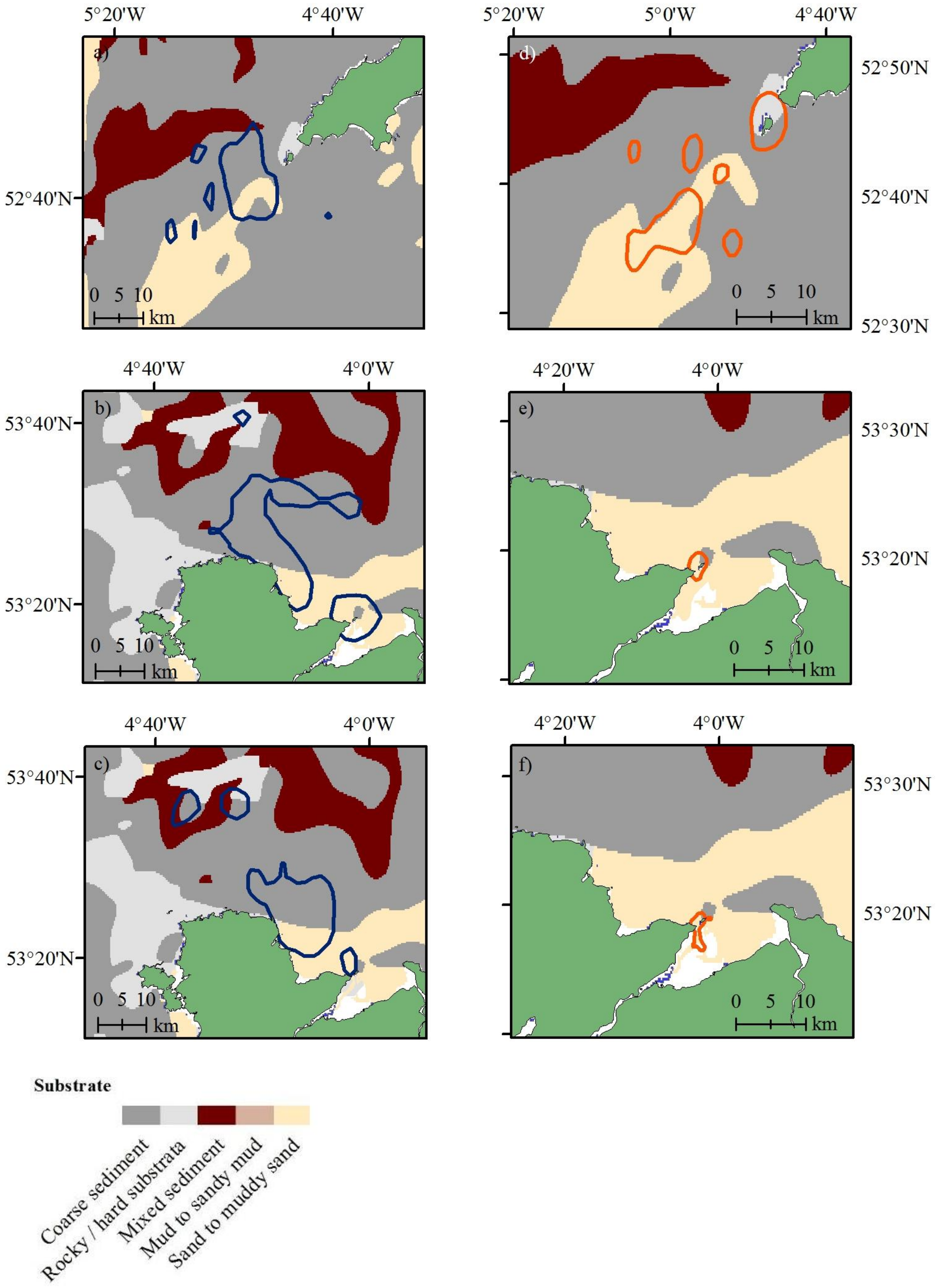

Figure 3.11 Nocturnal (a-c; dark-blue outline) and diurnal (d-f; orange outline) core foraging areas (50% FKD) of razorbill colonies at Bardsey 2011 (a, d), Puffin Island 2011 (b, e) and Puffin Island 2012 (c, f) in relation to bottom type. Core foraging area estimates calculated with hours of darkness fixes (22:00h-04:00h) removed from analysis. Note the difference in scale between nocturnal and diurnal home-range maps, introduced to facilitate visualisation of the diurnal foraging area at Puffin Island.

4. DISCUSSION

The GPS-tracking of razorbills at Bardsey Island (2011) and Puffin Island (2011 and 2012) has proven very informative, providing an enhanced understanding of the at-sea foraging behaviour of these animals at these particular colonies. In line with the aims and objectives, this study has successfully determined and compared the foraging patterns of these two colonies (Bardsey and Puffin Island) and, for Puffin Island compared between years (2011 and 2012) in terms of maximum and total foraging trip distance, trip duration and trip timing. It has also refined, on a quantitative basis, the home-range and likely foraging areas used by these colonies, and has identified potentially important foraging habitat types for razorbills in terms of depth and substrate type.

4.1. FORAGING TRIP PARAMETERS

When all foraging trips were analysed together (i.e. diurnal and nocturnal trips combined), overall average foraging parameters were remarkably similar between colonies, and for Puffin Island, between years, averaging approximately 13 km maximum distance, 37 km total distance and 5.5-6 hours duration. This may explain the historically similar population parameters of these two colonies, with approximately 500 and 600 individuals at Bardsey and Puffin Island, respectively, in the mid-1980s (Barnes, 1997).

Although patterns within the Puffin Island colony remained very similar across the two seasons when diurnal and nocturnal trips were considered separately, a different pattern emerged between colonies in terms of maximum distance travelled. At Bardsey, diurnal trips were of significantly longer mean maximum distance, whilst nocturnal trips were of significantly shorter mean maximum distance compared to trips from Puffin Island birds. The maximum foraging distance is the most commonly reported foraging trip variable in other razorbill studies, and appears to vary somewhat between colonies in the British Isles and elsewhere (Table 4.1). As is the case for the variation observed between other colonies, the difference in maximum distance seen between the Bardsey and Puffin Island colonies is most likely to be a consequence of one or more of the reasons listed below. It should be noted that, with regard to the present study, whilst one might expect that some of these reasons would have affected diurnal and nocturnal trips similarly, possible explanations for the diurnal and nocturnal discrepancies are discussed in Section 4.3.

Firstly, varying proximities and/or distribution of prey availability depending on, amongst others, the oceanographic conditions surrounding the colony, can affect the foraging behavior of marine predators (Pyke, 1984; Bell, 1991; BirdLife International, 2000). As shown by Garthe *et al.* (2007) foraging tactics of GPS-tracked northern gannets (*Sula bassana*), differed significantly between colonies breeding in different oceanographic domains with different prey fields. Puffin Island and Bardsey Island are located in very different locations, environmentally, with Puffin Island being situated in shallow waters surrounded by sandy substrate, whereas Bardsey Island lies within deeper waters primarily surrounded by coarse sediment (Figure 3.11, 3.12). The potential relationship between these environmental variables and core foraging sites is discussed in more detail in Section 4.5.

Secondly, the difference in maximum forging distance observed between Bardsey Island and Puffin Island may be due to the difference in their present colony sizes, with Bardsey holding 3 times as many. A number of studies have suggested that at least in some places, larger colonies have to forage further afield and tend to deplete local food supplies more than is the case for small colonies (Lewis *et al.*, 2001; Ainley *et al.*, 2003; Gaston, 2004; Grémillet *et al.*, 2004). However, these usually involve very large colonies (>50’000 individuals), or large differences between colony sizes.

Lastly, other reasons to consider with regard to the difference observed in diurnal and nocturnal maximum foraging distances between Bardsey and Puffin Island are a series of temporal effects, potentially introduced through data at Bardsey having been collected for an additional six days in June. Although no differences in trip parameters were found between birds on eggs and birds on chicks, studies on e.g. kittiwakes have shown that birds on older chicks fly further than birds on smaller chicks (Chivers *et al.*, 2012). Hence, if only diurnal foraging trips were used for chick provisioning (see Section 4.3), the difference between Bardsey and Puffin Island birds may have been caused by differing proportions of young versus older chicks due to some sampling at Bardsey having taken place when the breeding season was slightly more advanced.

However, no direct effect of chick age on trip distance was found in razorbills studied by Dall'Antonia *et al.* (2001), nor in the closely-related common guillemot (Uttley *et al.*, 2008), and the sample number of large chicks in the present study was most likely too low (BAR11: n = 2; PUF11, n = 1) to have influenced the overall pattern found. Other temporal effects may include the tendency of older razorbills to breed earlier in the season compared to younger ones (Lloyd, 1979; Hipfner *et al.*, 1997), and, because they are more experienced, may show different patterns to younger razorbills (Lloyd, 1979; Hipfner *et al.*, 1997). Perhaps the most likely temporal effect, however, may have been a deterioration in feeding conditions as the season progressed, forcing the birds to forage at greater distances, as has been found in other colonies (Hedgren and Linnman, 1979; also see Dall'Antonia *et al.*, 2001).

Variability in local feeding conditions can also occur over more long-term periods, and has the potential to cause inter-annual difference in foraging behaviour within colonies (e.g. razorbills: Dall'Antonia *et al.*, 2001 (Table 4.1); black-legged kittiwakes: Chivers *et al.*, 2012). Although average foraging parameters were extremely similar at Puffin Island in both years, suggesting overall comparable feeding conditions in these seasons, a slight difference in pattern was nevertheless observed with birds in 2011 having made an increased number of trips and, probably related, having lost more weight over the course of the study period, compared to birds sampled in 2012.

Table 4.1 Summary of razorbill foraging trip parameter values as found by various studies. D = diurnal, N = nocturnal; values are given as mean ± standard deviation (SD). Ranges (min-max) are indicated in brackets. In Maximum distance, values in *italics* represent distance of reported highest densities. B = Birds, T = Trips, NA= Non-applicable; BT = boat transect, CL = compass loggers, RT = radio-telemetry, GPS = Global Positioning System. *based on flight speed of 58km/h (Pennycuick, 1987).

Location	Year	Sample no.	Max. distance (km)	Total distance (km)	Duration (h)	Method	Reference
Flamborough Head, England	1984	NA	(up to28) *1, 26-28*	-	-	BT	Webb *et al.*, 1985
North Rona and Sula Sgeir, Scotland	1986	NA	(up to 15) *< 5*	-	-	BT	Benn *et al.*, 1987
St. Kilda, Scotland	1987	NA	(up to 38) < *5*	-	-	BT	Leaper *et al.*, 1988
Pembrokeshire Islands, S. Wales	1990; 1992	NA NA	(up to 45) *10;* (up to 25) *5*	- -	- -	BT	Stone *et al.*, 1992
Græsholmen, Denmark	1998	B:7; T: 8N, 34D	D: (1-28)* N: (10-35)*	- -	D: 1.9 ±1.4 (0.25- 4.7) N: 8.9 ± 1.3 (7.2 – 10.7)	CL	Benvenuti *et al.*, 2001
Latrabjarg, Iceland	1997; 1998	B: 11, T: 13; B: 18, T: 34	(20-110)*; 29.0 ± 17.3 (4-90)*	133 ± 41 (40-220); 70 ± 41	17.1 ± 7.4 (4.0-30.8); 13.1 ± 6.3 (1.6-30.4)	CL	Dall'Antonia *et al.*, 2001
Isle of May, Scotland	1990	B: 3; T:35	(>10) *>10*	-	-	RT	Wanless *et al.*, 1990
Isle of May, Scotland	1997	NA	(up to 35) < *5*	-	-	BT	Wanless *et al.*, 1998
Isle of May, Scotland	2002-2006	B: 14; T:76	18.4 ± 4.8 (up to 40) *<10*	47.8 ± 45.5	5.1 ± 5.6	CL	Thaxter *et al.*, 2010
Fair Isle, Scotland	2011	unpublished	(up to 300)	unpublished	unpublished	GPS	R. Hughes, RSPB, *pers.comm*

Generally, only a few trips exceeded 40 km from the colony at Bardsey, and, whereas at Puffin Island trips of maximum distance of more than 40 km were not uncommon in both years, they very rarely exceeded 60 km. Similar to results from Bardsey, the vast majority of the current literature reports the maximum foraging trip distance of breeding razorbills to be within 40 km of the colony (Figure 4.1). However, past records on razorbill foraging distance have predominantly originated from observational studies (Figure 4.1), which may have run the risk of having missed birds beyond the transect distance (see Wanless *et al.,* 1998; Hamer *et al.,* 2000), may have erroneously assumed birds to be from the nearest colony (Hamer *et al.,* 2000), or may have provided a biased understanding of foraging ranges due to dispersion invariably leading to reduced densities with increasing distance from the colony (Perrow *et al.,* 2011). Furthermore, these observational studies are unlikely to have recorded data from birds on nocturnal trips (Wilson *et al.,* 2009), which in the few studies available, have shown a considerable higher foraging range compared to diurnal foraging trips (Benvenuti *et al.,* 2001; present study). Indeed, much greater foraging distances have recently been reported from remote sensing studies with a GPS-tracked razorbill from Muckle Skerry in the Pentland Firth, NE Scotland, having been recorded to travel up to 144 km from its nest site (RSPB, 2011), and several GPS-tracked razorbills from Fair Isle having been found to forage 250-300 km from the colony off the coast of Aberdeenshire (R. Hughes, RSPB, *pers. comm*.). However, such great distances do not seem to be the norm, as other remote sensing studies from razorbill colonies in Iceland (Latrabjarg), Denmark (Græsholmen), and Scotland (Isle of May) have also reported maximum foraging distances of within 40 km (Benvenuti *et al.,* 2001; Dall'Antonia *et al.,* 2001; Thaxter *et al.* 2010; Table 4.1).

This relatively restricted foraging range is likely to be related to razorbills facing a high energetic cost in long-distance flights (Camphuysen *et al.,* 2011). Compared to many other seabirds, the wings of razorbills and other alcids are extremely short relative to their body mass, as they are adapted to diving rather than flying (Wanless *et al.,* 1990, Gaston, 2004; Thaxter *et al.,* 2010). This results in a reduction of powered flight efficiency and adaptation to long-distant foraging (Pennycuick, 1987). With a changing environment and reported scarcity in food availability, however, it is possible that the proportion of long trips, such as recorded at Muckle Skerry and Fair Isle, will increase and push the physiological limits of these birds. Whilst there is strong evidence from a number of seabird species, including alcids, that adults can markedly increase trip distance and duration in response to low prey availability (e.g. Hamer *et al.*, 1993; Ronconi and Burger, 2008), clear thresholds have been shown to exist, whereby foraging flexibility can no longer buffer breeding success with very low food availability (e.g. marbled murrelets *Brachyramphus marmoratus*: Ronconi and Burger, 2008*;* black-legged kittiwakes: Chivers *et al.,* 2012). Such a threshold may also have been reached by the razorbill colony from Fair Isle, which, historically very successful, has recently experienced dramatic declines and breeding failures (3500 individuals in 2005 to 1,365 individuals in 2010; P.G.H. Evans, *pers. comm*.). Given, therefore, that the vast majority of foraging trips from birds at Bardsey and Puffin Island were recorded to be within 40 and 50 km, respectively, suggests that the foraging conditions for these colonies were favourable during the period of this study.

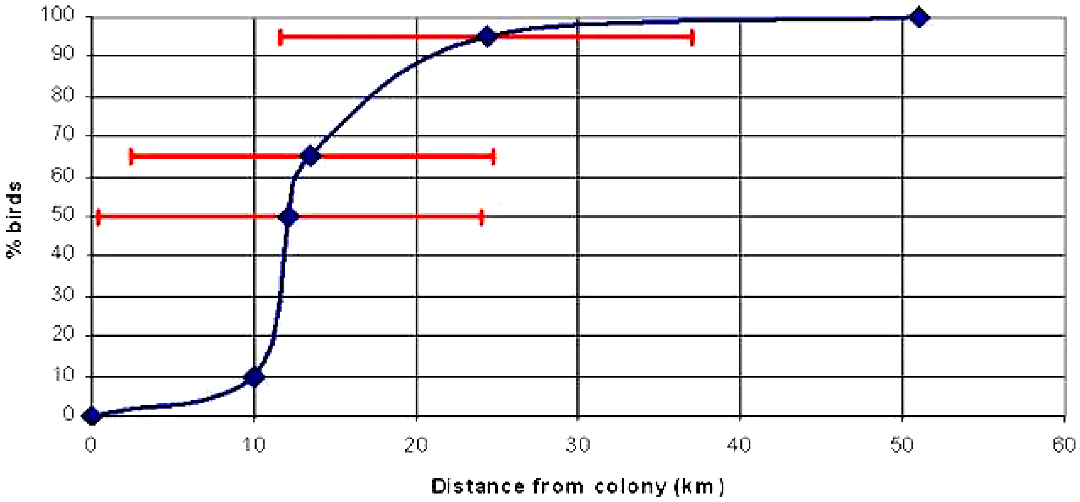

Figure 4.1 Cumulative frequency (with standard deviation) and proportion of razorbills found foraging at different distances from their colonies. Source: Birdlife Seabird Foraging Range Database.

Very few razorbill studies contain reports on total trip distance or trip duration (but see Table 4.1). However, the significantly positive correlation between maximum distance, total distance and trip duration is a common pattern found in marine central place foragers (Harcourt *et al*., 2002; Page *et al*., 2006; McLeay *et al.*, 2010), and this feature has been exploited to determine one parameter on the basis of another (razorbills: Dall'Antonia *et al.,* 2001; Benvenuti *et al.*, 2001; Thaxter *et al.*, 2010; gannets: Hamer *et al.*, 2000, 2001). This study shows, however, that the degree of correlation between these parameters may vary between colonies, as despite the significant difference in maximum trip distance between Bardsey and Puffin Island, trip durations remained very similar between these colonies.

4.2. TRIP TIMING

Nocturnal trips showed a clear diel pattern that was consistent across both colonies and years in this study, and were in agreement with findings by Benvenuti *et al.* (2001), with nocturnal trips generally starting before sunset (around 18:00h to 20:00h) and ending just after sunrise (between 06:00h and 09:00h). This pattern suggests a crepuscular foraging behaviour associated with nocturnal trips, as will be discussed in more detail in Section 4.3.

In 2011 at both Bardsey and Puffin Island, after the peak in return times early in the morning from nocturnal trips, birds appeared to perform diurnal foraging trips through the day, between sunrise and sunset, with no obvious pattern. With foraging range being relatively close to the colonies, the trends in departure and return times were similar. Puffin Island (2012), on the other hand, showed a marked peak in diurnal trips before 09:00h, possibly reflecting a change in feeding conditions and perhaps in prey type, with birds taking advantage of early morning peaks in prey availability.

Trip return times are likely to be associated with potential nest duties such as chick provisioning, and previous studies have reported chick provisioning in razorbills to peak in the early morning (e.g. Látrabjarg, NW Iceland: Dall'Antonia *et al.*, 2001; Græsholmen, central Baltic: Benvenuti *et al.*, 2001; Lundy Island, SW England: Perry, 1940; Skomer Island, SW Wales: Lloyd, 1976; Isle of May, SE Scotland: Harris and Wanless, 1986; Kerry Islands, SW Ireland: P.G.H. Evans, *pers. comm.*; Gannet Islands, Labrador, E Canada: Paredes *et al.*, 2006; 2008).

Foraging patterns in relation to the tide were not determined, but the strong diel pattern of nocturnal trips, and the fact that most individuals performed multiple diurnal trips per day, suggests that razorbills from Bardsey and Puffin Island may not be timing their foraging trips to coincide with a particular tidal state. However, tidal effects may be very time- and site-specific, and more investigation is required to determine potential tidal influences on razorbill foraging patterns.

4.3. DIURNAL VERSUS NOCTURNAL FORAGING TRIPS

The pattern of multiple ‘short’ diurnal trips and a single more distant nocturnal trip over the course of a day, as was observed in razorbills from both Puffin Island and Bardsey Island, has previously been reported from the razorbill colonies at Græsholmen (Benvenuti *et al.,* 2001; Table 4.1) and Gannet Islands (Parades *et al.*, 2006, 2008), and has also been found to occur in other seabird species such as guillemots (Paredes *et al.,* 2006, 2008) and kittiwakes (Kotzerka *et al.,* 2010).

Diurnal and nocturnal trips were found to be of significantly different distances, with nocturnal trips ranging to substantially further distances, especially at Puffin Island. In the closely-related Brünnich’s guillemot and crested auklet (*Aethia cristella*) such differences between diurnal and nocturnal trips have been shown to be the effect of a sex-specific pattern in timing of breeding site attendance during the incubation and brooding period, with males generally being on nest duty during the night, and females during the mid-day period (Fraser *et al.,* 2002; Paredes *et al.,* 2006, 2008). However, with most of the individuals in the present study having performed both diurnal and nocturnal trips, such a sex-specific pattern is not likely to be the case in razorbills. In line with this, Benvenuti *et al.* (2001) found both males and females to perform nocturnal trips in an apparently unpredictable manner. Also, although Paredes *et al.* (2006) reported a sex-difference in razorbill parental role, with females being the main meal providers and males being mostly involved in brooding and chick defence, a sex-difference in the timing of nest attendance has not been found in razorbills (Isle of May: Wanless and Harris, 1986; Skomer Island: Wagner, 1992; Gannet Island, Labrador: Paredes *et al.,* 2006).

So-called dual-foraging strategies have also been widely observed in chick-rearing Procellariiformes (Weimerskirch *et al*., 2001; Hyrenbach *et al*., 2002; Congdon *et al.,* 2005) albeit at a different temporal scale, with short trips lasting 1 to 4 days, and longer trips lasting up to 8 days. In these cases, it was established that the shorter trips were used for chick-provisioning, while the longer trips were used for self-feeding by adults. Although in the present study, short diurnal foraging trips were also recorded in birds on eggs, there is the potential that the same theory applies to egg incubation duty. Further investigation is needed to confirm this possibility in razorbills.

The difference in the distribution of foraging distances of diurnal and nocturnal trips may also reflect prey distribution. This was suggested to be the case in black-legged kittiwakes which were found to forage on two types of fish species (Kotzerka *et al.*, 2010). Dietary preferences for razorbills at Bardsey and Puffin Island have not been established in the present study, nor have they been reported previously. However, the diet of razorbills has been shown to be similar to that of guillemots (Harris and Wanless, 1986; Thaxter *et al.*, 2009). Guillemot chick diet data collected at South Stack, Anglesey, in 2011 by Emery (2011) consisted of approximately 20% sandeels (most likely lesser sandeels *Ammodytes marinus*) and 80% clupeids (mainly sprat *Sprattus sprattus*). Given the relative proximity of the colonies, it is probably safe to assume that the razorbills at Bardsey and Puffin Island also fed on these two species, which may be available at a different time of day and at different distances from the colonies. In order to explore this theory further, it is useful to consider the previously reported activity patterns of razorbills during diurnal and nocturnal trips, as well as the ecology of sandeels and sprat.

Using activity recorders (Benvenuti *et al.*, 2001) and time-depth loggers (TDRs; Paredes *et al.*, 2006, 2008), the authors were able to determine that razorbill dives ceased during the darkest hours of the night when birds remained inactive at sea. This lack of activity over night could also be determined by the extensive long, straight and low-speed tracks in the present study, which mirrored the ebb and flow of the tidal currents and suggested that the birds were simply drifting with the tide. However, Benvenuti *et al.* (2001) and Paredes *et al.* (2006, 2008) also found that dive frequency on nocturnal trips increased at twilight with dives being much shallower than dives performed on diurnal trips. Such crepuscular foraging behaviour has also been reported in the closely-related Brünnich's guillemot (thick-billed murres in North America, *Uria lomvia*) (Croll *et al.* 1992; Falk *et al.*, 2000; Mehlum *et al.*, 2001; Paredes *et al.*, 2006) and common guillemot (Regular *et al.*, 2010), and has been attributed to the vertical migration of their prey in the evenings, allowing the birds to reach them with shallower dives. Sprat show diel vertical migrations with schools moving to the surface waters at dusk (Nilsson *et al.*, 2003; Cardinale *et al.*, 2003). Sandeels, on the contrary, although largely burrowed in the sediment from September to March (Macer, 1966; Gauld and Hutcheon, 1990) are known to be distributed within the water column during the summer months, when they feed on zooplankton in the upper layer of the sea (Wright, 1996; Furness, 2002). Being light-sensitive, however, sandeels only roam the water column during daytime (Ostrand *et al.*, 2005). It is therefore possible that the razorbills from Bardsey and Puffin Island foraged on sandeels during diurnal trips, switching to more accessible sprat during crepuscular foraging on nocturnal trips. This hypothesis remains to be investigated but will be further discussed in relation to environmental factors in Section 4.5.

4.4. HOME-RANGE

Determining the extent and intensity of use of specific areas by seabirds is crucial to our understanding of their foraging ecology (Weimerkirch *et al*., 1997; Wood *et al*., 2000; Thaxter *et al.*, in press.) and can be important in marine spatial planning such as in relation to offshore wind farms (Garthe and Hüppop, 2004). Furthermore, the identification of important feeding areas for breeding colonies is considered fundamental as a preliminary tool for identifying candidate Marine Protected Areas (Thaxter *et al*., in press.).

Here, a kernel analysis has been used to calculate the contour lines of the home-range distribution estimates, allowing the identification of areas most likely to be used for foraging by razorbills from the colonies at Bardsey Island and Puffin Island. At Bardsey Island, the 95% active-use area extended predominantly in a south-western direction, with key foraging areas being located west and south-west of the colony approximately 10 and 20 km from the colony for nocturnal and diurnal core foraging areas, respectively. Interestingly, the diurnal foraging area appeared to coincide with the foraging area of Manx shearwater from Skomer, as shown in the GPS-tracking study by Guilford *et al.* (2008). At Puffin Island, patterns of home-range were similar in both seasons. The overall, as well as the nocturnal 95% active-use area, spanned predominantly north/northwest-wards along the coast of Anglesey, with the main nocturnal foraging areas being located along the eastern/northeastern coast of Anglesey.

In line with the much shorter ranging diurnal trips, the diurnal active-use area of the Puffin Island colony was distributed close to Puffin Island along the southeastern tip of Anglesey, with core foraging areas being located in the waters immediately surrounding the colony. Despite this similarity in broad patterns, however, the actual overlap in foraging areas used in both seasons was not absolute, especially for nocturnal forgaing, suggesting a slight shift in prey distribution to have occurred.

Both colonies showed multiple core foraging areas, which are likely to be related to temporal variations in prey distribution (see e.g. Boyd, 1996). Indeed, there was some evidence from track patterns that particular areas were favoured by different birds over the short term. Multiple core foraging areas may also have been caused by individual bird variation in foraging patterns, as preliminary analyses in the present study found considerable between-, as well as within-individual variation (Appendix 6.1; also see Wanless *et al.*, 1990, 1998). Also, Paredes *et al.* (2008) showed that male and female diving patterns were slightly different in razorbills, possibly related to their sex-specific roles as discussed above, and they suggested that this may cause males and females to forage in slightly different areas. In both colonies, core foraging areas included the water close to the colony, and it cannot be ruled out that some of the usage may have been related to non-foraging activities such as grooming, socializing, and resting near the colony (Owen, 2012).

The overall active-use and core foraging areas were larger for the Puffin Island colony compared to the Bardsey Island colony, although the diurnal active-use and foraging areas at Bardsey were considerably bigger. The active-use and core foraging areas of razorbills from the Isle of May, as calculated by Thaxter *et al.* (2010) based on pooled data from 76 trips from 14 razorbills over four seasons, were 2201 km^2 and 155 km^2 in size, respectively. Hence, the 95% active-use areas at Bardsey and Puffin Island were approximately two and 1.5 times smaller than at the Isle of Man, whilst the 50% core use areas were approximately 1.5 and two times larger, respectively. These size differences in activity ranges are likely to be linked to one or more of the potential reasons listed above to explain the differences in maximum foraging trip distances: A difference in the proximity of suitable feeding grounds, varying levels of intra-colony competition, as well as a series of potential temporal effects.

4.5. FORAGING AREAS IN RELATION TO ENVIRONMENTAL PARAMETERS

The GPS-data can indicate where the birds went, but the critical question is why. Matching habitat types with core foraging areas can help identify potentially important habitats for specific species/colonies (Owen, 2012). As Owen (2012) explains, the habitat type often influences the type and reliability of prey, which are crucial to seabirds when under pressure to feed themselves whilst providing for chicks.

At Bardsey, both diurnal and nocturnal core foraging areas overlapped with depths of approximately 50 to 100 m, and, despite shallower waters having been available at equally accessible distances, the only potential foraging area situated in shallow waters was the area immediately surrounding the colony. As mentioned above, this core-use area surrounding Bardsey may, however, not be exclusively associated with foraging activities. At Puffin Island, diurnal core foraging areas were located in depths of no greater than approximately 20 m, whilst nocturnal core foraging areas were located in waters of up to approximately 80 m deep, and especially in 2012, overlapped little with shallow waters (<20 m). Stone *et al*. (1995) observed very few razorbills beyond the continental shelf during the breeding season in north-west European waters, with highest densities recorded within the 100 m isobath. Although the relationship of razorbill densities and depth may partly be related to distance from the colony, particularly during the breeding season when birds need to regularly return to the nest, Stone *et al.* (1995) found, similar to the present study for the Bardsey colony, a distinct peak in razorbill numbers in waters between 50 to 100 m deep. At Puffin Island, waters of 50 m and deeper are only encountered at distances of 35 to 40 km from the colony. The fact that these were used only during nocturnal trips suggests that the shallower waters used during diurnal trips still provided suitable foraging grounds, implying that factors other than depth are likely to also play an important role in constituting suitable feeding grounds for razorbills.

The sand banks surrounding Puffin Island are known to contain high abundances of sandeels (*pers. observ*.), supporting the theory that the razorbills from Puffin Island may be foraging on sandeels at least on diurnal trips. This is also likely to hold true for birds from Bardsey, as diurnal foraging areas are predominantly located over sandy sediment, which is the preferred substrate of sandeels (Macer, 1966). Conversely, nocturnal foraging areas from both colonies are much less associated with sandy substrate. They are, however, located in areas of tidal mixing and high productivity, which have also been shown to attract relatively high densities of marine mammals (Baines and Evans, 2012). This supports observations by Begg and Reid (1997) and Durazo *et al.* (1998) who found razorbills, like many other seabirds, to be associated with shallow tidal mixing fronts and areas of high primary productivity. Central place foragers generally utilise areas where prey species aggregate, influenced either by physical factors (Guinet *et al*., 1997; Awkerman *et al*., 2005; Simmons *et al*., 2007) and/or enhanced primary productivity (Hyrenbach *et al*., 2002; Weimerskirch *et al*., 2004; Page *et al*.; 2006, Suryan *et al*., 2006). Therefore, whilst diurnal foraging areas may be associated with sandeels aggregating over sandy substrate, nocturnal foraging may be associated with clupeids whose abundance has been shown to relate to areas of high primary productivity (Martin *et al*., 2008; Tsagarakis *et al*., 2008).

The ecological interactions in the marine environment are complex, and the distribution of both predator and prey organisms is generally determined by various interacting biological, physical and chemical factors (Begg and Reid, 1997). The present study only compared foraging areas to substrate type and depth, two very constant environmental variables. However, other studies have also shown seabird distributions to be associated with spatially and temporally more variable parameters such as chlorophyll *a* concentrations and sea surface temperatures (e.g. Begg and Reid, 1997). These more variable parameters may have been the cause for the slight shift in core foraging areas at Puffin Island between 2011 and 2012.

4.6. POTENTIAL LIMITATIONS OF THE STUDY

This study presents some of the most detailed data currently available for the razorbill colonies at Bardsey Island and Puffin Island. However, it is important to consider the potential limitations of the information presented here.

4.6.1. POSSIBLE EFFECTS OF GPS DEVICES ON THE BIRDS

Data collected from animal-borne devices can only be used in conservation if the recorded behaviour of the study animal is not altered by the device. Hence, the use of animal-borne devices should always be coupled with consideration of possible negative reactions and impacts on the animal's normal behaviour (Dall'Antonia *et al.,* 2001). In the case of razorbills, bird-borne devices have the potential to decrease efficiency of flight and diving, due to increased wing loading and drag (Dall'Antonia *et al.,* 2001). Although it is impossible to completely rule out at least some impact, there are numerous reasons to assume that the loggers used in the present study recorded normal foraging behaviour:

(1) Instruments weighing less than 5% of the bird's body mass are considered to have negligible impacts on behaviour (Croll *et al.,* 1992; Benvenuti, 1993; Benvenuti *et al*., 2001). The mass of the device used in this study weighed only 2.6-3.4% of total body mass. Although razorbills may be more vulnerable to extra weight compared to other seabirds, given their high wing loading, no relationship was found between duration of carrying the device and percentage weight loss.

(2) Although no control birds were used in this study, some of the birds actually gained weight whilst carrying the device. Furthermore, the weight losses recorded are comparable to those reported in similar studies such as on Brünnich's guillemots (Croll *et al*., 1992) and razorbills (Dall'Antonia *et al.,* 2001; Benvenuti *et al.,* 2001), despite a difference in devices used. The loss of adult body mass may be a normal phenomenon in razorbills during the breeding season, even in the absence of attachments, as has been shown to be the case for both Brünnich's and common guillemots (Gaston, 1985; Croll *et al*., 1991).

(3) When on land, tagged birds observed showed normal behaviour and did not appear to be handicapped or in discomfort by the device (*pers. observ*). They were not observed to preen their backs intensively, as would be expected if birds were disturbed by the device (Wilson *et al*., 1990).

4.6.2. REPRESENTATIVENESS AND QUALITY OF DATA

Representativeness of data is another key consideration to keep in mind when conducting a remote-sensing study, where only the behavior of a subsample of the whole colony is being studied (Wood *et al.*, 2000). Soanes *et al.* (in review.) highlighted the importance of data quality checks, in particular with regard to seabird home-range studies, in order to determine how much credence can be given to the results obtained and conclusions drawn. Based on the home-range saturation curves produced for data of this study, we can be confident that the data are representative for the individual colonies with regard to the time period sampled.

However, economic and time constraints limited data collection to only parts of the breeding season (late egg incubation/early chick rearing period), particularly at Puffin Island. It is therefore very possible that the home-ranges of breeding razorbills from Bardsey and Puffin Island, as reported in the present study, are an underestimate of the total extent used by these colonies over the entire breeding season, due to potential temporal variations in suitable foraging areas, as discussed in Section 4.1. The extent of any underestimate is unknown and may not be the same for BAR11, PUF11 and PUF12, especially given the difference in sampling dates. Similarly, it is unknown how widely other foraging variables (including distance, duration and trip timing) of razorbills may differ across the entire breeding season at Bardsey and Puffin Island. Furthermore, the Bardsey and Puffin Island colonies were only sampled over one and two years, respectively, and it is unknown how foraging patterns might differ over an extended time scale.

Finally, the criteria applied in this study for selecting foraging trips (i.e. trips of >300 m maximum distance and >10 min duration) may have resulted in some miss-assignments – the exclusion of some foraging trips, or, conversely, the inclusion of other trips as foraging trips when they were made for other maintenance activities. However, there is no evidence for a bias in one direction or the other and so it is unlikely that this will have influenced broad patterns of foraging behaviours observed.

4.7. CONCLUSION AND FUTURE STUDIES

In a period where many seabird species of the British Isles are experiencing serious population declines with successive years of breeding failure, an enhanced understanding of species-specific foraging behaviours and the identification of colony-specific home-ranges to aid the safeguarding of core foraging areas is crucial (Thaxter *et al.*, in press.). This study highlights the usefulness of GPS technology for such purposes in medium-sized seabirds such as the razorbill, and provides an insight into the foraging patterns and key foraging areas of two colonies in North Wales. The following points are worth noting for future studies and conservation efforts:

(1) Razorbills perform both diurnal and nocturnal trips, and it was found that these can differ significantly in trip parameters, leading to substantially different diurnal and nocturnal home-ranges and foraging areas within colonies. This highlights the importance of bird-borne data loggers such as GPS devices, as the limitations of observational studies and radio-telemetry (see Thaxter *et al.*, in press.) would almost certainly not have allowed the data collection of significantly farther-ranging nocturnal foraging trips. The ability to record data without range-constraints is currently of particular relevance where birds appear to have to travel further in search of food (e.g. Fair Isle; P.G.H. Evans, *pers.comm.*)

(2) The colony differences found in the present study in terms of diurnal and nocturnal foraging distances and home-range sizes highlight the need to consider inter-colony differences when recommending conservation measures for this species. Whilst foraging behaviour remained very stable in the two consecutive seasons at Puffin Island, the relatively small percentage in overlap of core foraging areas between the two years, as well as the significant annual differences found in other colonies in previous studies (see Dall'Antonia *et al.*, 2001), suggest that any future studies seeking to determine the foraging patterns and core foraging areas of razorbills, or other seabirds, should ideally include data from multiple seasons.

(3) Since diurnal and nocturnal foraging areas were found to be broadly associated with different substrate types, and in the case of Puffin Island, with depth, the separate consideration of diurnal and nocturnal trips may help to clarify trends of habitat usage during foraging in future studies. Although this was not specifically tested for in the present study, the nocturnal foraging areas of both the Bardsey and the Puffin Island colony were found to be located in areas of high productivity (Baines and Evans, 2012). Given the complexity of the marine ecosystem, future studies are therefore encouraged to analyse their data considering a wide range of parameters, including also sea temperature and chlorophyll *a* (see e.g. Begg and Reid, 1997).

(4) The present study found the immediate waters surrounding Bardsey and Puffin Island to represent core-use areas, highlighting the importance of these zones to the colonies for the purpose of foraging or other maintenance behaviour. This supports the

proposal of Marine Protected Areas to also provide extensions to existing protected breeding colonies to safeguard their immediate marine areas (Thaxter *et al.*, in press.).

(5) As representativeness of data is essential for the purpose of conservation, future studies should always ensure the availability of enough equipment and manpower for the capture and recapture of birds in representative numbers and over a representative time period. Furthermore, whilst GPS-devices clearly provide detailed data on foraging patterns of seabirds such as razorbills, future studies using this technique would benefit from complementary behavioural data that would allow a more complete insight into the relationship between the GPS-recorded foraging patterns and potential biological, physical, and temporal factors. These could include, for example, additional measurements on dive depth using time-depth recorders (TDR) (Benvenuti *et al.*, 2001; Dall'Antonia *et al.*, 2001; Paredes *et al.*, 2008; Thaxter *et al.*, 2010) which can provide a three-dimensional insight into the foraging behaviour of razorbills, particularly relevant for these diving seabirds. Data on hatching dates and chick size might shed light on how foraging patterns change as the season progresses, whilst information on fledging success could be used to link foraging behaviour to breeding success. The collection of dietary data would allow a more complete analysis of the requirements of these birds, and might assist in making more informed conservation decisions in areas where tracking studies have not yet been performed. This may be especially relevant since poor feeding conditions are often cited as a major cause of recent, widespread breeding failures and population declines (Tasker *et al.*, 2000; Montevecchi, 2002; Mitchell *et al.*, 2004; Heath *et al.*, 2009).

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6. APPENDICES

6.1. BETWEEN AND WITHIN-INDIVIDUAL VARIATION

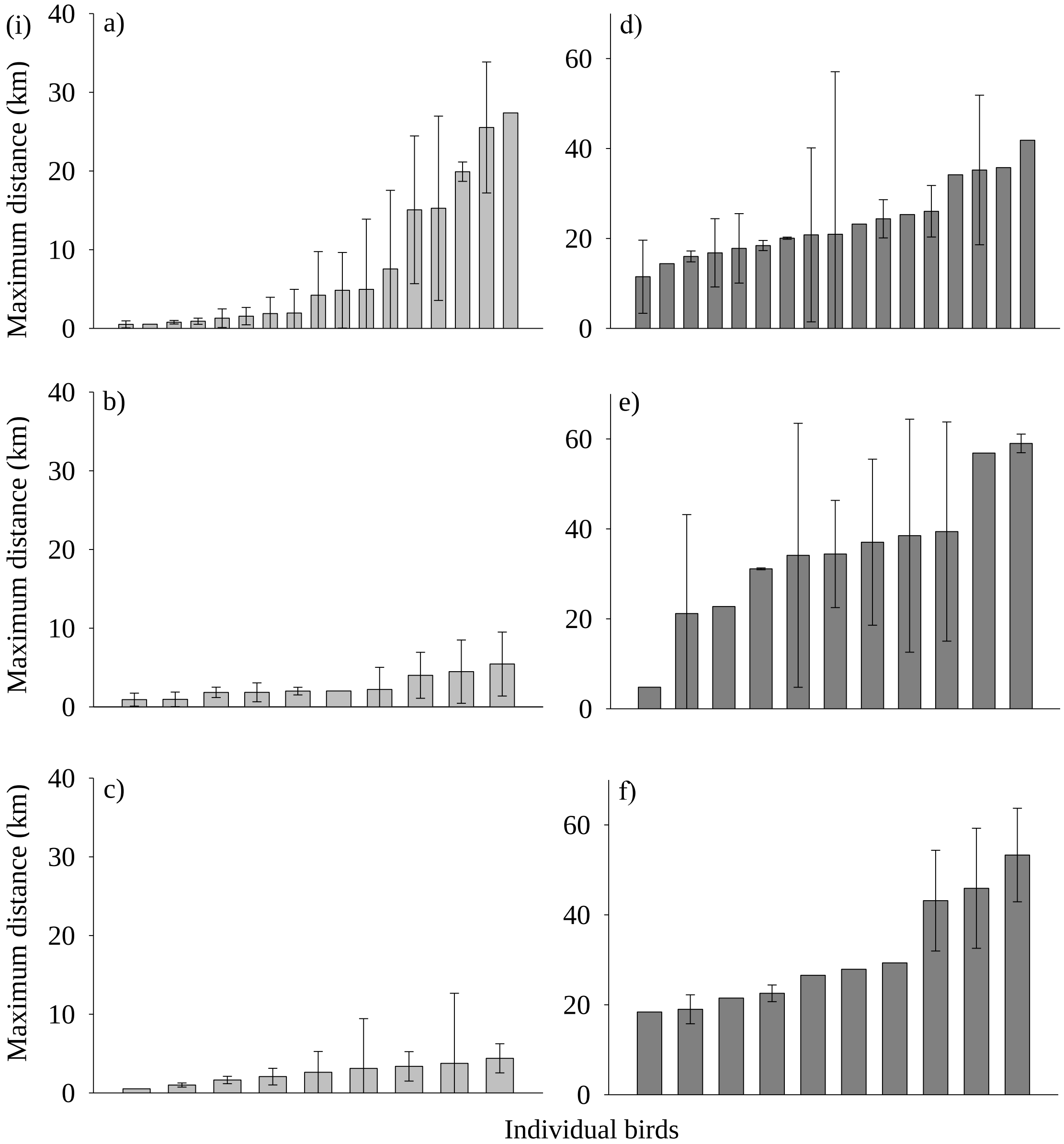

Figure 6.1 Mean ± standard error of (i) maximum distance (km), (ii) total distance (km) and (iii) tip duration (h) of individual birds' diurnal (a-c) and nocturnal (d-f) foraging trips for razorbills from the colonies at Bardsey Island 2011 (a, d), Puffin Island 2011 (b, e) and Puffin Island 2012 (c, f). Individual bars represent individual birds within each colony, hence the x-scale is arbitrary, and there is no connection between birds in each figure. Note the difference in scale between diurnal (a-c) and nocturnal (e-f) figures.

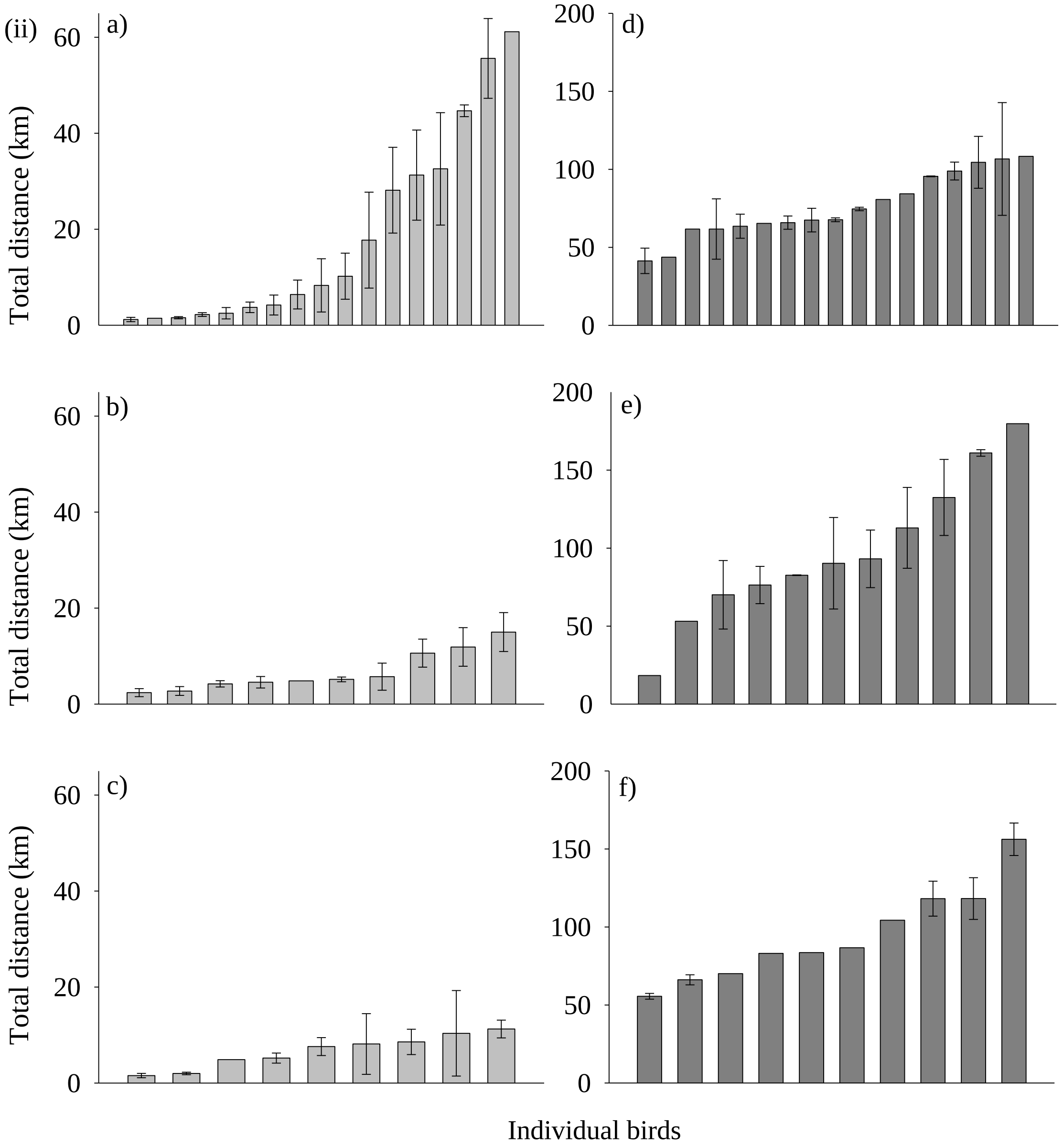

Figure 6.1 Mean ± standard error of (i) maximum distance (km), (ii) total distance (km) and (iii) tip duration (h) of individual birds' diurnal (a-c) and nocturnal (d-f) foraging trips for razorbills from the colonies at Bardsey Island 2011 (a, d), Puffin Island 2011 (b, e) and Puffin Island 2012 (c, f). Individual bars represent individual birds within each colony, hence the x-scale is arbitrary, and there is no connection between birds in each figure. Note the difference in scale between diurnal (a-c) and nocturnal (e-f) figures.

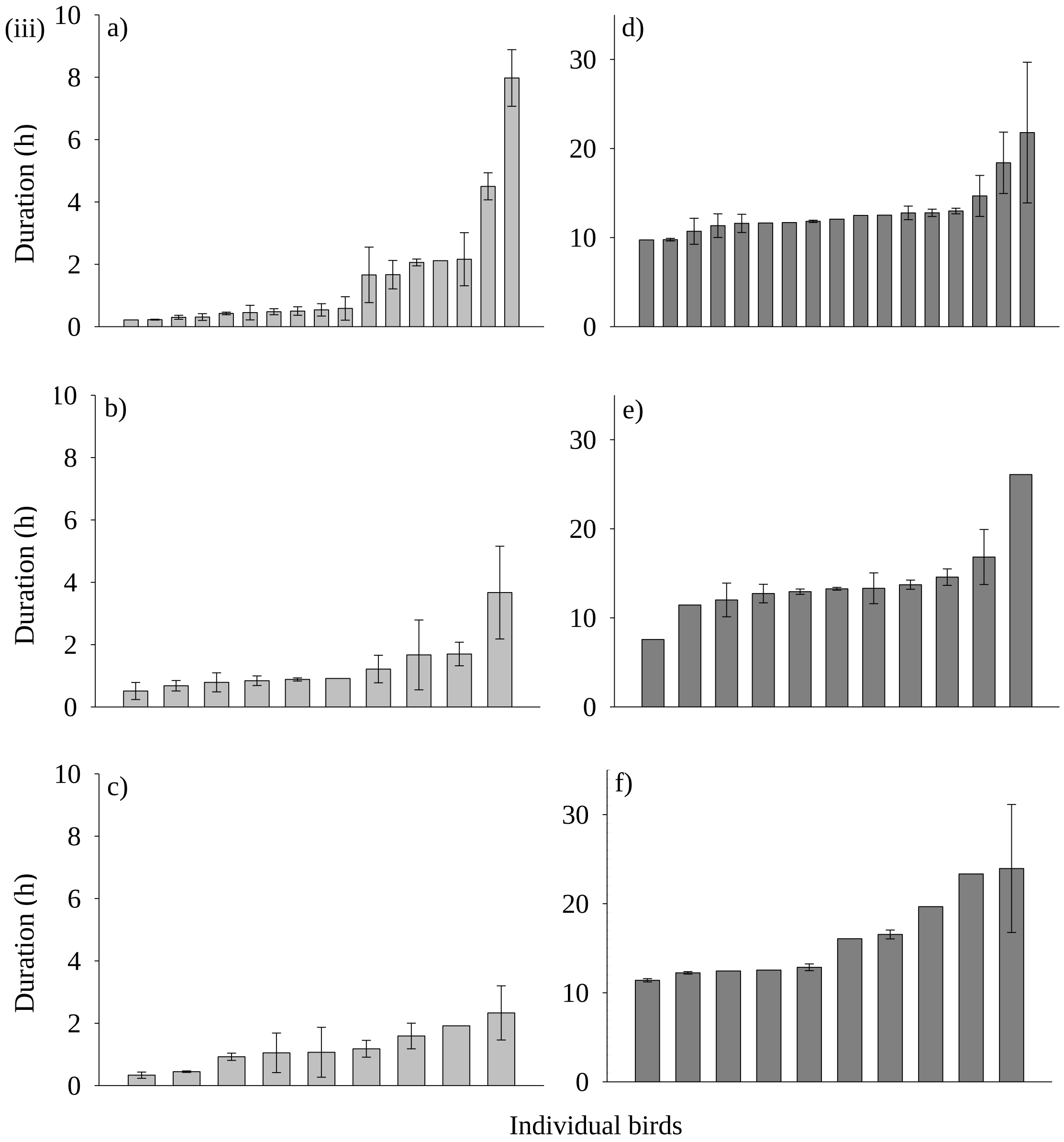

Figure 6.1 Mean ± standard error of (i) maximum distance (km), (ii) total distance (km) and (iii) tip duration (h) of individual birds' diurnal (a-c) and nocturnal (d-f) foraging trips for razorbills from the colonies at Bardsey Island 2011 (a, d), Puffin Island 2011 (b, e) and Puffin Island 2012 (c, f). Individual bars represent individual birds within each colony, hence the x-scale is arbitrary, and there is no connection between birds in each figure. Note the difference in scale between diurnal (a-c) and nocturnal (e-f) figures.

6.2. DIURNAL HOME-RANGE SATURATION CURVES

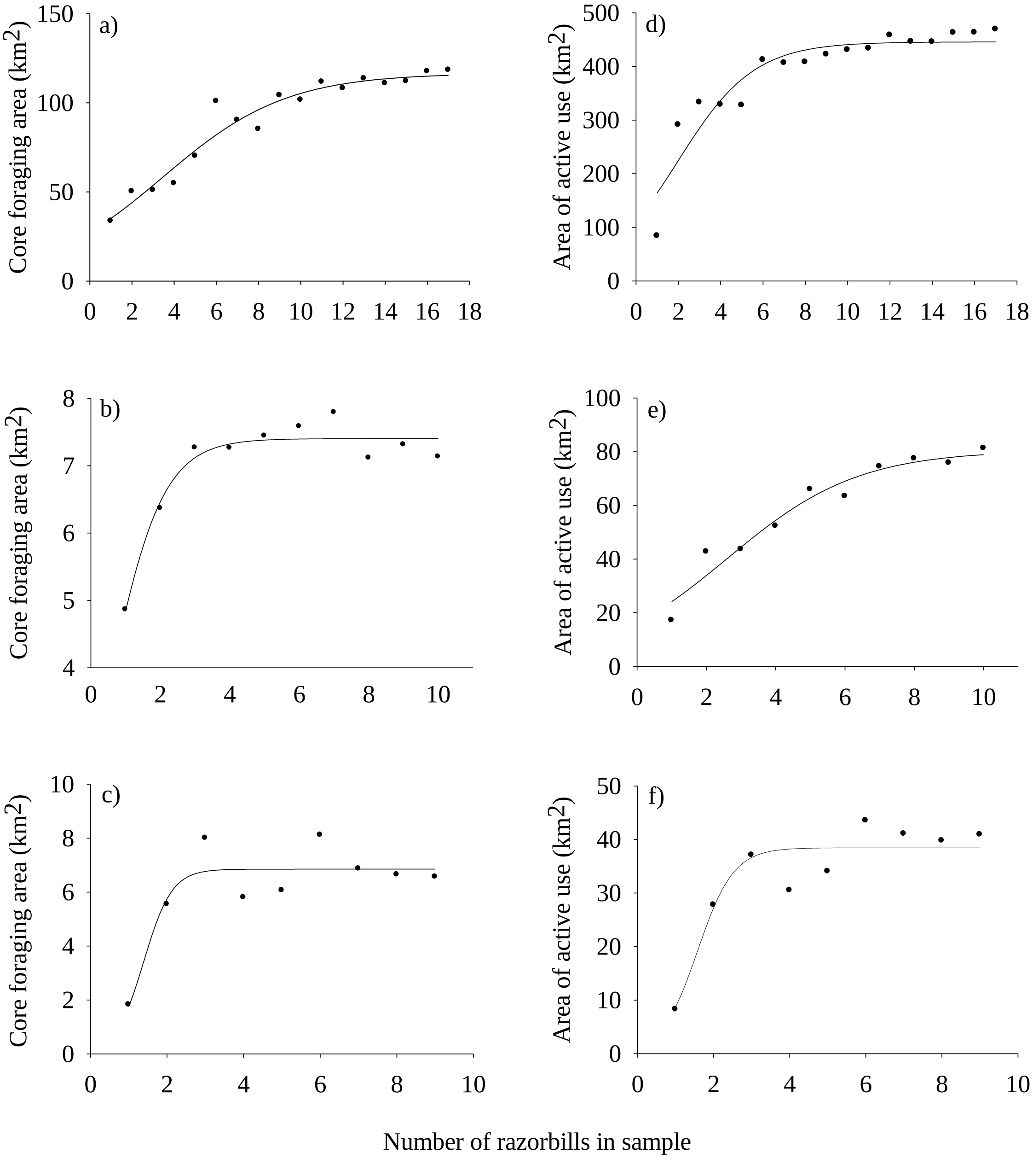

Figure 6.2 Change in estimated diurnal core foraging areas (a-c) and active-use areas (d-f) as predicted from analysis of all diurnal trips as a function of an increasing number of randomly chosen individual razorbills tagged at Bardsey Island 2011 (a, d), Puffin Island 2011(b, e) and Puffin Island 2012 (c, f).

6.3. NOCTURNAL HOME-RANGE SATURATION CURVES

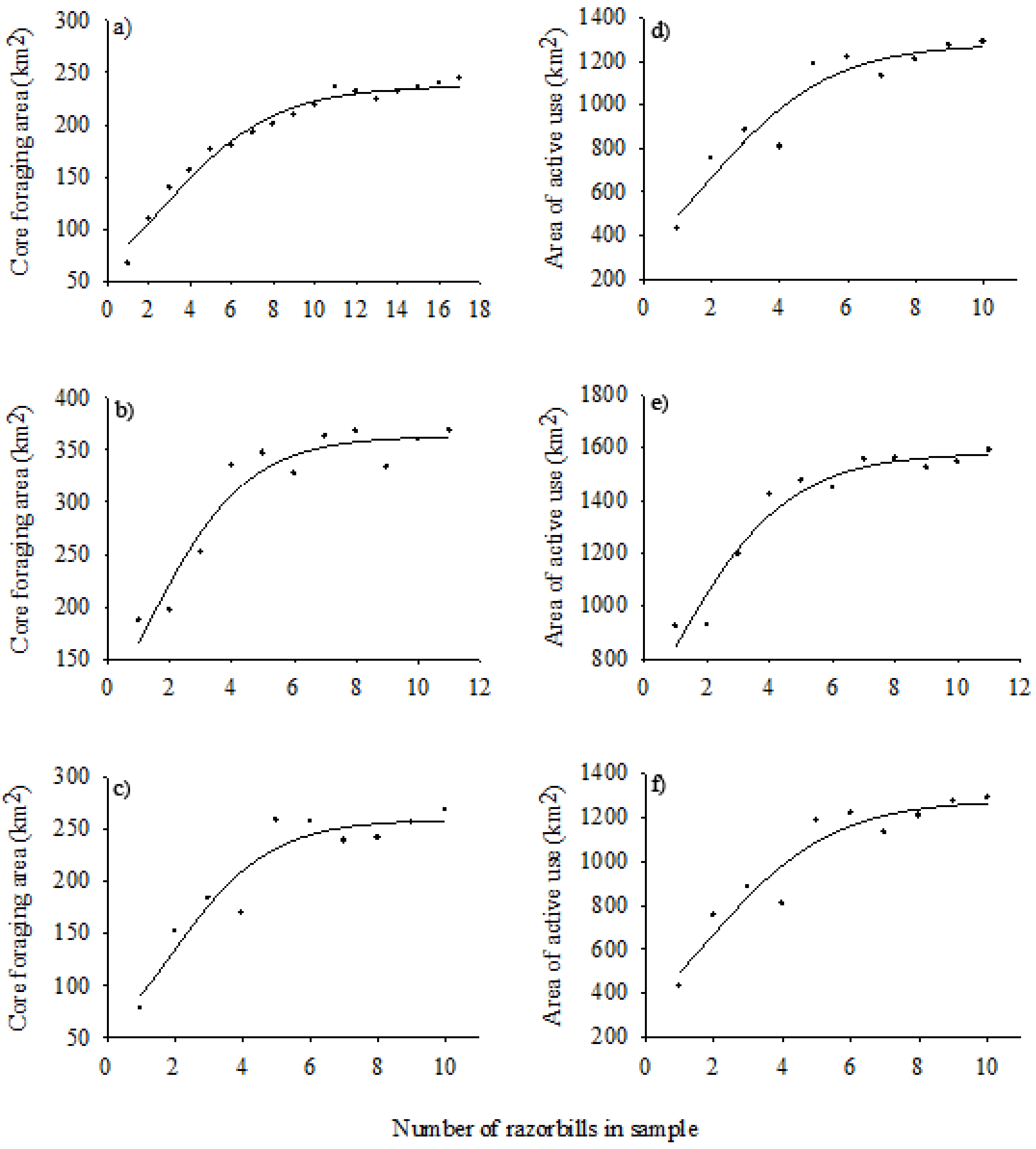

Figure 6.3 Change in estimated nocturnal core foraging areas (a-c) and active-use areas (d-f) as predicted from analysis of all nocturnal trips as a function of an increasing number of randomly chosen individual razorbills tagged at Bardsey Island 2011 (a, d), Puffin Island 2011(b, e) and Puffin Island 2012 (c, f).