The foraging behaviour of seabirds: defining and predicting home range areas

Thesis submitted in accordance
with the requirements of the
University of Liverpool for the
degree of Doctor in Philosophy

Louise Mary Soanes

August 2013

Abstract

In recent years, seabird tracking studies have become ever more popular as a means of informing and evaluating the effectiveness of marine protected areas and offshore energy developments as well as in understanding the ecology and behaviour of seabirds. This study uses tracking data collected from the European shag, Black-legged kittiwake, Northern gannet and Brown booby to identify important foraging areas around four seabird colonies located in the UK, Channel Islands and Anguilla and examines the impact of offshore renewable energy developments in the Channel Islands. As well as providing examples of how seabird tracking data can be useful in informing marine spatial planning, this study also considers the impact that sample size and the sample composition may have on the foraging areas predicted for any colony. Small sample sizes are a common feature of tracking studies, often due to logistical and financial constraints, meaning that seabirds are often tracked over short spatial and temporal scales which may not fully represent the important foraging areas and behaviours of the colony or individual. This study therefore provides recommendations to improve the predictions of area use and foraging strategy for future tracking studies to ensure the most representative and useful data is collected and used to inform marine spatial planning issues.

Table of contents

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

List of Figures

List of Tables

Chapter 1

General Introduction

Photograph by Johann Bourgeois 2012

Seabirds: Life history and conservation

There are 350 species of seabird which are entirely dependent on marine habitats for at least part of their life cycle (Croxall *et al.*, 2012). Seabirds are an important component of the marine ecosystem, with at least 15 species having more than 10 million individuals. This equates to a large biomass that consumes about 100 million tones of marine prey annually, which is very close to the overall global fishery extraction (Brooke, 2004). The defining feature of seabirds is that they must breed on land, and yet obtain their food from the sea. The constraints imposed individually by these very different habitats and the interactions of these constraints are the evolutionary drivers for a host of traits that are unique to seabirds, such as their longevity, delayed maturity, and low reproductive rates which in turn influence their ecology, behavior, physiology and life history (Ballance, 2007).

Globally seabirds as a group have become threatened at a faster rate than all other groups of birds and they represent the most threatened marine taxonomic group in the world. Currently about 30% of pelagic species are threatened with unsustainable population declines (Croxall *et al.*, 2012, Lewison *et al.*, 2012). For example, the extinction of the Balearic shearwater *Puffinus mauretanicus* is modeled to take place in 40 years if the impact of long-line fisheries on adult mortality is not minimized (Oro *et al.*, 2004). Globally, the most important identified threats to seabirds include: those acting at the breeding site such as (1) invasive species (Wanless *et al.*, 2012, Hervias *et al.*, 2013) (2) human disturbance (Viblanc *et al.*, 2012, Albores-Barajas & Soldatini, 2011) and (3) human infrastructure developments (Hill *et al.*, 1995) and those acting mainly at sea such as (1) fisheries by-catch (Votier *et al.*, 2004, Pierre *et al.*, 2012, Baker *et al.*, 2007); (2) pollution (Montevecchi *et al.*, 2012, Lindborg *et al.*, 2012) (3) hunting and trapping (Bakken and Mehlum, 2005) (4) energy production and mining (Burke *et al.*, 2012, Grecian *et al.*, 2010, Lindeboom *et al.*, 2011) and (5) climate change and severe weather incidences (Sydeman *et al.*, 2012, Chambers *et al.*, 2011, Barbraud *et al.*, 2008). The study of seabirds both, whilst at their breeding sites, and their behavior at sea, can aid in preventing, managing or predicting the impact of these identified threats to seabird populations.

Seabirds at their breeding colonies

The majority of seabird research up until the 1970's focused on studies at the breeding colony where parameters such as productivity, survival between years, feeding rates, prey types and demographic changes affecting seabird populations have been well documented for many species (Schuetz, 2011, Aebischer and Coulson, 1990, Gladbach *et al.,* 2009, Harris *et al.,* 1998).

Some impressively long-term datasets exist, such as the 30-year old database of the life-history characteristics of the Black-browed albatross *Thalassarche melanophrys,* breeding on Kerguelen, an island located in the Indian Ocean. This database has provided information on population growth rates and their relationship to climate change and changes in fishery practice over the study years (Rolland *et al.,* 2009). Similarly, surveys of breeding seabirds and coastal birds along the German North Sea coast began in the early 20th century, thereby enabling the examination of long-term population trends (Haelterlein and Suedbeck, 1996). Another long-term data set (1988-2009) which recorded the breeding success and clutch size of the endangered Californian least tern *Stemula antillarum browni* allowed Schueltz *et al.* (2011) to determine that both clutch size and fledgling productivity had declined over the years as a result of reduced food availability. There are also examples of national programmes in place, such as the UK's Joint Nature Conservancy Council (JNCC) Seabird Monitoring Programme (SMP), which is an ongoing annual monitoring programme, established in 1986. The SMP monitors 26 species of seabird that breed regularly within Britain and Ireland. The program aims to ensure that sample data on breeding numbers and the breeding success of seabirds are collected regularly, both regionally and nationally. This enables the conservation status of populations to be assessed and analysis of abundance, productivity, survival and diet data to be conducted together with interpretation of the likely causes of change (Mitchell and Dunn, 2004).

Ringing studies have aided in extending our understanding of seabird biology beyond the colony, and have also allowed the collection of some information on seabird migration routes, inter-colony dispersal; survival and wintering distribution (Baillie *et al.,* 1999, Frederiksen and Petersen, 2000). Through the effort of ringers broad-scale wintering grounds and migration routes of many British and Irish seabirds are well known (Harris and Tasker, 1999). Ringing recoveries have also proved extremely useful in highlighting seabird conservation issues, such as the killing of terns in West Africa (Mead, 1978) and the level of hunting of Brunnichs guillemots *Uria lomvia* in Greenland (Bakken 2005). Ringing has also enabled us to age birds, for example, the oldest reported Manx shearwater *Puffinuns puffinus* was at least 50 years old (Fransson *et al.* 2010). The use of ringing in long term capture-mark-recapture efforts can also provide important demographic information (Votier *et al.,* 2008), but the dispersal and movement information derived from them is often limited. This is because ringing recoveries documenting seabird movements typically occur in coastal areas where humans encounter them, and where incidences of recoveries tend to mirror human population distributions (Montevecchi *et al.,* 2012).

Seabirds at sea

Apart from the limited information gained from ringing recoveries, until recently very little was known about what seabirds do at sea both during the breeding and non-breeding season. This started to change in the 1970s (Tasker *et al.,* 1984, Briggs *et al.,* 1985) mainly due to the legal requirement in many countries to conduct Environmental Impact Assessments (EIAs) before any offshore developments. For example, studies of seabird marine ecology were given little attention in the USA until the 1970s when the designation of Exclusive Economic Zones (EEZs) by coastal countries and a push to develop petroleum resources became constrained by legislation such as the US National Environmental Policy Act of 1970. Due to this legislation, EIAs for activity on federal lands (including sea areas) were required (Ainley *et al.,* 2012). Likewise, in the UK, the JNCC’s Seabirds at Sea Team (SAST) began a programme of survey and research on seabirds and cetaceans in the marine environment in the north-east Atlantic in 1979, and in the south-west Atlantic between 1998 and 2002. In 1979, little was known about the offshore distribution and ecology of seabirds, yet they faced potential threats, such as the North Sea's rapidly expanding offshore oil industry. As such, much of the SAST's work has been driven and funded by the needs of the offshore oil and gas industry in the UK (Webb *et al.,* 1995).

Marine research efforts in the UK were entirely ship-based up until the early 1970s, with aerial surveys becoming more popular through the 1990s. Before 1984 seabird data were largely qualitative presence-absence surveys with large birds, e.g. gannets, over-emphasised because they could be seen farther away than smaller birds. After reviewing the previously used methods, Tasker *et al.* (1984) proposed a standardised technique of using well defined strips, with search effort broken temporally into fixed time segments. As a result our knowledge of distribution patterns of seabirds at sea is now substantially improved. However, Lewison *et al.* (2012) stated that there is still a lack of detailed knowledge about at-sea distribution of individuals across species, sex and age classes and that this presents one of the most substantial challenges to seabird ecology. Seabird habitat use at sea cannot be documented comprehensively by "snapshot" vessel and aerial surveys and the significance of tracking seabirds to detect more realistic spatial and temporal coverage of their remote oceanic distributions cannot be overstated (Montevecchi *et al*., 2012).

Tracking Technology

With the development of new miniaturised and affordable technologies such as radio transmitters, satellite transmitters, geolocators and Global Positioning Systems (GPS) devices a whole new area of seabird research has presented itself (Boyd, 2004, Weimerskirch *et al.,* 2009, Burger and Shaffer, 2008) enabling the foraging movements of seabirds to be monitored at a fine-scale both temporarily and spatially (Gremillet *et al.,* 2006).

The first seabird tracking studies were conducted using radio telemetry with the first papers published in the early 1970s, such as the study on foraging ranges of Herring gulls *Larus argentatus* (Southern, 1970). Radio tracking represents a relatively cheap way to locate birds and can be used on small species with the smallest radio transmitter currently available weighing about 4 grams. This method requires the use of portable directional receivers to monitor the animal's position and movements, by triangulation from two or more sites. As such, this method is labour intensive, does not provide frequent fixes, and transmitters can only be detected within a limited range, typically 15-20 km from a high vantage point, (Burger and Shaffer, 2008). Therefore, this method is more suitable in identifying short-term movements of seabirds. For example, to investigate the rafting locations of Manx shearwaters *Puffinus puffinus* around their colonies (Wilson *et al.,* 2009) and the foraging trip characteristics of the locally feeding Caspian tern *Hydroprogne caspia* (Sirdevan and Quinn, 1997). Bugoni *et al.* (2005) attempted to overcome the problems of limited range and triangulation associated with this method by tracking Common terns *Sterna hirundo* with transmitters attached to four aircraft and Irons *et al.* (1998)

tracked Black-legged kittiwake *Rissa tridactyla* by boat. However, it is not an appropriate method for most species due to the remote locations of colonies and the larger foraging areas of many seabird species.

In the early 1990s satellite transmitters using the ARGOS system became available; with the first papers using this tracking method published on Wandering albatross *Diomedea exulans* (Jouventin and Weimerskirch, 1990, Weimerskirch *et al.,* 1993), and Emperor penguins *Aptenodytes forsteri* (Ancel *et al.,* 1992). It has since been used many times since to study long-distance foragers and to determine migration routes and wintering areas (Wakefield et al., 2009, Hatch *et al.*, 2010, Hatch *et al.*, 2011). The benefit of satellite tags is that they do not require recapture of the study animal, hence are valuable for investigating dispersion of juveniles, which may not return to their natal breeding colony. They can weigh as little as 9 grams and typically transmit up to 20 locations per day with an accuracy of 1-3 km (Burger and Shaffer, 2008). However, this technology is expensive in terms of purchasing devices and accessing data.

Geolocators are the smallest device available to seabird trackers (can be as small as 1.5 grams) and work by determining the number of daylight hours, including sunrise and sunset times which can allow the calculation of an approximate latitudinal and longitudinal positions. Despite their small size, these tags have enough battery and memory capacity to store several years' worth of data. However geolocators have limited function close to the equator and around the equinoxes and rely on the bird returning to the breeding colony to enable retrieval of the device. The spatial resolution is also coarse, recording only one-or two locations per day with a typical error of 180-200 km (Phillips *et al.*, 2004, Shaffer *et al.*, 2005). Thus they are more suited for monitoring long distance movements.

Global positioning satellite (GPS) data loggers send digital signals to orbiting satellites to triangulate a position which is then stored within the device. GPS loggers record real-time positions with a frequency of up to every second and to an accuracy of meters. In recent years the price and size of GPS loggers has reduced, making this form of tracking evermore popular and available to researchers and as such, these devices have now been used on a range of species. The advantages of size, cost and fine spatial resolution are somewhat out-weighed by the need to retrieve these loggers to download data, although remote download stations are becoming more popular (Clark *et al*., 2006, Takeuchi *et al*., 2012). These loggers are also limited by battery life so unless a solar panel has been fitted (which generally increases the size of the logger) (Spencer and Miller, 2011) this type of tracking technology is usually best suited to work undertaken during the breeding season.

In addition to tracking technologies, other types of archival tags are often deployed on seabirds at the same time to gain more detailed information on physiology, habitat use and behaviour. For example, heart rate loggers and accelerometers have been deployed to investigate physiological changes whilst a bird is foraging (Woakes *et al.*, 1995, Halsey *et al.*, 2010, Kokubun *et al.*, 2011); dive loggers are deployed which enable researchers to determine where and when foraging actually takes place and to what depth birds dive (Cook *et al.*, 2012, Weimerskirch *et al.*, 2009); and camera loggers have been mounted on birds heads to examine habitat use (Watanuki *et al.*, 2008).

Why track seabirds?

These various tracking technologies have been used for a range of purposes to aid in our understanding of seabird biology and their conservation; these can be grouped into ten broad categories, described below with specific examples.

1) **Understanding migration and wintering areas**
   The use of geolocators has revealed the migration and pre-breeding behavior of the critically endangered Balearic shearwater *Puffinus mauretanicus* in the Mediterranean (Guilford *et al.*, 2012), and identified the different overwintering areas of the South polar skuas *Catharacta maccormicki* from a single breeding population (Kopp *et al.*, 2011). Geolocators have also been used to identify individual migratory schedules and wintering areas of Northern gannets *Morus bassunus* revealing that 18% wintered in the North Sea and the English Channel, 27% in the Bay of Biscay and the Celtic Sea, 9% in the Mediterranean Sea and 45% off West Africa (Kubetzki *et al.*, 2009).

2) **Identifying important foraging areas whilst breeding**
   Radio tracking of the threatened Olrags gull *Larus atlanticus* revealed that

individuals mostly foraged within 20 km of their colony and fed predominately on crab species (Suarez *et al.,* 2012); GPS loggers were used to identify the foraging behavior and important areas of Magellanic penguins *Spheniscus magellanicus* breeding in Patagonia (Sala *et al.,* 2012) and Hamer *et al.* (2000) used satellite telemetry to determine foraging ranges and feeding locations of Northern gannets breeding on Bass rock, Scotland.

3) **Designation and evaluation of marine protected areas**

Yorio *et al*. (2010) GPS tracked Imperial cormorants *Phalacrocorax atriceps* and Magellanic penguins *Spheniscus magellanicus* to assess the effectiveness of marine protected areas in Argentina and Trebilco *et al.* (2008) used satellite transmitters to determine how well protected Macquarie Island's Giant petrel *Macronectes halli* populations were by marine reserves during their breeding season.

4) **Assessing pollution risk**

Montevecchi *et al.* (2012) used geolocators to track three species of seabird to assess risk and to evaluate the consequences of the 2009 Gulf of Mexico Oil spill disaster and Gremillet *et al.* (2006) found using GPS and satellite transmitters that Northern gannets breeding at a French colony foraged exclusively within the western English Channel, with a strong preference for the tidal front between eastern and western Channel waters, northwest of Guernsey which is a major oil spill hotspot.

5) **To provide data for the Environmental Impact Assessment (EIA) process**

Perrow *et al.* (2006) radio tracked Little tern *Sternula albifrons* and determined that their foraging ranges overlapped with an offshore wind farm. Similarly, Harris *et al*. (2012) found using GPS technology that the foraging areas of Atlantic puffin *Fratercula arctica* breeding on Isle of May, Scotland also overlapped with proposed offshore wind farms in the area.

6) **To assess the effect of fisheries**

Votier *et al.* (2010) linked GPS tracking data to vessel monitoring systems (VMS) and found that fishing boats shape the at-sea foraging behavior of Northern gannets. Bertrand *et al*. (2012) determined using GPS technology that Peruvian booby *Sula variegata* significantly increased their foraging effort as the anchovy fishery in the region expanded. Picehgru *et al.* (2009) used GPS-recorders to assess the overlap in foraging range and fisheries of eight colonies containing 95% of the global Cape gannet *Morus capensis* and 60% of the global African penguin *Spheniscus demersus* populations and found that the main foraging areas of both species were located where purse-seine fisheries caught most fish, with most catches occurring during the birds' breeding season.

7) **Comparing the foraging behavior of different colonies**

Garthe *et al.* (2007) identified contrasting foraging tactics of Northern gannets breeding at different colonies in Canada; similarly Hamer *et al.* (2001) examined the foraging strategies of Northern gannets at a colony in the UK and found marked differences between colonies, in the duration of their foraging trips and foraging area fidelity, but found the average speed of travel during foraging trips was almost identical and birds at both colonies spent about half their time at sea in flight. Wienecke & Robertson (2006) found using satellite telemetry that King penguins *Aptenodytes patagonicus* breeding at two sites exhibited different at sea distributions related to differences in oceanographic and bathymetric conditions between the two sites.

8) **Sex specific differences**

Sex specific differences in foraging behavior have been well documented for sexually dimorphic species such as Brown boobies *Sula leucogaster* and Blue-footed boobies *Sula nebouxii,* with the larger females of both species tending to have longer foraging trips (Weimerskirch *et al.,* 2009). Differences have also been revealed in sexually monomorphic species such as the Common guillemot *Uria aalge* where males were found to have longer foraging trips than females (Thaxter *et al.,* 2009).

9) **Age-related differences**

Using satellite transmitters Weimerskirch *et al.* (2005) found that young, inexperienced Wandering albatross had foraging success and efficiency similar to those of older, experienced birds but exhibited a different foraging strategy, whereby they foraged more actively and caught more prey at night compared to experienced birds.

10) **Use as ecological indicators**

Durant *et al.* (2012) advocated the use of seabirds as ecological indicators stating that top predators such as seabirds provide an integrative view of the consequences of environmental variability. Ancel *et al.* (1992) monitored, by satellite, the routes taken by Emporer penguins for foraging and compared them with satellite images of sea-ice. The authors suggested that such bio-logging of penguins represented a cheap oceanographic sampling platform to investigate the Antarctic sea-ice habitat. Similarly, changes in sea-surface temperature (SST) including the position of the sub-tropical convergence of the southern Indian Ocean were ascertained using Wandering albatrosses fitted with temperature recorders and by satellite tracking systems (Weimerskirch *et al.,* 1995).

These are just a few examples of how seabird tracking studies have been applied to aid in our understanding of seabird ecology and behavior and highlight the possible conservation and management applications of such data.

Methodological considerations for tracking studies

Despite the vast amount of resources that are now invested in seabird tracking, researchers usually give little consideration to the design of their studies including factors such as sample size and sample composition. This is often due to limited financial resources and logistical restraints. However sample size recommendations and sampling designs have been developed for studies of most other parameters that describe seabird populations (Lindberg and Walker, 2007). For example, for nesting success and for counting populations, the JNCC's Seabird Monitoring Handbook (Walsh *et al.,* 1995) recommends the minimum number of nests to monitor and the frequency of monitoring for each species to accurately reflect the productivity of a population. For surveying seabirds at sea from ships or planes there are now guidelines in place concerning the frequency, and effort required (Camphuysen *et al.,* 2004, Tasker *et al.,* 1984). However, there are no such guidelines or common practices associated with the tracking of seabirds. Lindberg & Walker (2007) state "*if the interest is in making inferences to populations, little information will be gained* *by throwing out a few transmitters to see what happens*". This is particularly true if the composition of the sample is also not considered.

Inter-individual variation in foraging behavior has been widely reported for seabirds (Takahashi, 2004, Kato *et al.*, 2000, Wanless *et al.*, 1992) and other central place marine foragers (Staniland *et al.*, 2004, Austin *et al.*, 2004, Bonadonna *et al.*, 2001), caused by underlying physiology or individual quality. Environmental and ecological variables may also affect the foraging areas used by any sample of birds. For example, year of study (Chivers *et al.*, 2012, Garthe *et al.*, 2011), breeding site (Hipfner *et al.*, 2007, Lescroel and Bost, 2005) and timing of tracking may all have an influence on foraging behavior and should be considered before any inference is drawn on the foraging characteristics of any population when based on limited samples. The cost of transmitters and logistical challenges of working with some species at remote colonies can limit sample composition and strength of inferences. Therefore, careful study design including consideration of sample composition should be at the forefront of any researchers mind when conducting tracking work.

Scope of thesis and overall aims

The aim of this research was to determine the important foraging areas and foraging behavior of several seabird species related to marine spatial planning issues and to highlight the importance of considering sample size and the composition of a sample in any tracking study. The methods introduced aim to improve the data collected in this field, thus enabling any tracking data better able to inform conservation and management practices. Given the importance and prevalence of seabird tracking studies the time has come for a thorough examination of how tracking studies are conducted and the implications of inferences made from limited samples.

This thesis uses data collected from the European shag (*Phalacrocorax aristotelis*), and the Black-legged kittiwake (*Rissa tridactyla*) breeding on Puffin Island, Wales; Northern gannets *Morus bassunus* breeding in the Channel Islands and Brown boobies *Sula leucaster* breeding on Dog Island, Anguilla. Commonly used low-cost IGOTU GPS loggers (Mobile Action, Taiwan) were used on all species to track their movements during their breeding seasons.

Chapter 2 attempts to answer a theoretical question "*how many seabirds do we need to track to accurately predict foraging ranges*", with the aim of providing a relatively simple analysis for researchers to apply to their own data to determine how representative their tracking samples may be of the study population.

Chapters 3 and **4** use the analysis introduced in **Chapter 2** to relate to situations where tracking studies were conducted with the aim of identifying important foraging areas and the potential threats facing them. **Chapter 3** examines the foraging areas of Brown boobies, with the aim of identifying areas for marine protected area designation. Whilst **Chapter 4** relates the foraging areas of Northern gannets to renewable energy developments within their range.

Chapters 5 and 6 introduce further methodological considerations for seabird tracking studies. In **Chapter 5** the tracking datasets collected from the European shag over three years are used to identify which ecological factors (sex, number of chicks at time of tracking, age of chicks, year of study and breeding site) may affect foraging trip characteristics (trip duration, maximum distance travelled from the colony and area used). In **Chapter 6** foraging data from the Black-legged kittiwake is used to relate sex, stage of breeding, year, and wind speed to the foraging behavior of this species to highlight the need for researchers to carefully consider the individuals they select for tracking studies, and the time that they invest in tracking, particularly when considering offshore renewable energy developments areas in the region.

Chapter 6 summarises the main findings and puts them in the context of seabird conservation

References

Aebischer, N. J. & Coulson, J. C. 1990. Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *Journal of Animal Ecology,* **59:** 1063-1071.

Ainley, D. G., Ribic, C. A. & Woehler, E. J. 2012. Adding the ocean to the study of seabirds: a brief history of at-sea seabird research. *Marine Ecology-Progress Series,* **451:** 231-243.

Albores-Barajas, Y. V. & Soldatini, C. 2011. Effects of human disturbance on a burrow nesting seabird. *Revista Mexicana De Biodiversidad,* **82:** 1262-1266.

Ancel, L., Kooyman, G. L., Ponganis, P. J., Gendner, J. P., Lignon, J., Mestre, X., Huin, N., Thorson, P. H., Robisson, P. & Le Maho, Y. 1992. Foraging behaviour of emperor penguins as a resource detector in winter and summer. *Nature (London),* **360:** 336-339.

Austin, D., Bowen, W. D. & McMillan, J. I. 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos,* **105**: 15-30

Baillie, S. R., Boobyer, G., Perrins, C. M., Brenchley, A., Bryant, D. M., Ormerod, S. J., Rehfisch, M. M., Tasker, M. L. & Wilson, J. D. 1999. The conservation uses of ringing data. Conclusions of the JNCC/BTO workshop, 4-5 November 1995, Norwich. *Ringing and Migration,* **19:** 119-127.

Baker, G. B., Double, M. C., Gales, R., Tuck, G. N., Abbott, C. L., Ryan, P. G., Petersen, S. L., Robertson, C. J. R. & Alderman, R. 2007. A global assessment of the impact of fisheries-related mortality on shy and white-capped albatrosses: Conservation implications. *Biological Conservation,* **137:** 319-333.

Bakken, V. & Mehlum, F. 2005. Wintering areas and recovery rates of Brunnichs's guillemots *Uria lomvia* ringed in the Svalbard archipelago. *Arctic,* **58:** 268-275.

Ballance, L. T. 2007. Understanding seabirds at sea: Why and how? *Marine Ornithology,* **35:** 127-135.

Barbraud, C., Weimerskirch, H., Bost, C.-A., Forcada, J., Trathan, P. & Ainley, D. 2008. Are king penguin populations threatened by Southern Ocean warming? *Proceedings of the National Academy of Sciences of the United States of America,* **105:** 39-38

Bertrand, S., Rocıo, J., Arbulu Smet, C., Tremblay, Y., Barbraud, C. & Weimerskirch, H. 2012. Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology,* **49:** 1365-2664.

Bonadonna, F., Lea, M. A., Dehorter, O. & Guinet, C. 2001. Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal *Arctocephalus gazella*. *Marine Ecology- Progress Series,* **223**: 287-297.

Boyd, I. L., Kato, A., & Robert-Coudert, Y. 2004. Bio-logging science: Sensing beyond the boundaries. *Polar Research,* **58:** 1-4.

Briggs, K. T., Tyler, W. B. & Lewis, D. B. 1985. Comparison of ship and aerial surveys of birds at sea. *Journal of Wildlife Management,* **49**: 405-411

Brooke, M. d. L. 2004. The food consumption of the world's seabirds. *Proceedings. Biological sciences / The Royal Society,* **271 Suppl 4:** S246-8.

Bugoni, L., Cormons, T. D., Boyne, A. W. & Hays, H. 2005. Feeding grounds, daily foraging activities, and movements of common terns in southern Brazil, determined by radio-telemetry. *Waterbirds,* **28:** 468-477.

Burger, A. E. & Shaffer, S. A. 2008. Application of tracking and data-logging technology in research and conservation of seabirds. *Auk,* **125:** 253-264.

Burke, C. M., Montevecchi, W. A. & Wiese, F. K. 2012. Inadequate environmental monitoring around offshore oil and gas platforms on the Grand Bank of Eastern Canada: Are risks to marine birds known? *Journal of Environmental Management,* **104:** 121-126.

Camphuysen, K. C., Fox, T. A., Leopold, M. M. & Petersen, I. B. 2004. Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K. Royal Netherlands Institute for Sea Research.

Chambers, L. E., Devney, C. A., Congdon, B. C., Dunlop, N., Woehler, E. J. & Dann, P. 2011. Observed and predicted effects of climate on Australian seabirds. *Emu,* **111:** 235-251.

Chivers, L. S., Lundy, M. G., Colhoun, K., Newton, S. F., Houghton, J. D. R. & Reid, N. 2012. Foraging trip time-activity budgets and reproductive success in the Black-legged kittiwake. *Marine Ecology-Progress Series,* **456**; 269-267.

Clark, P. E., Johnson, D. E., Kniep, M. A., Jermann, P., Huttash, B., Wood, A., Johnson, M., McGillivan, C. & Titus, K. 2006. An advanced, low-cost, GPS-based animal tracking system. *Rangeland Ecology & Management,* **59:** 334-340.

Cook, T. R., Hamann, M., Pichegru, L., Bonadonna, F., Gremillet, D. & Ryan, P. G. 2012. GPS and time-depth loggers reveal underwater foraging plasticity in a flying diver, the Cape Cormorant. *Marine Biology,* **159**: 373-387.

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A. & Taylor, P. 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International,* **22:** 1-34.

Durant, J. M., Hjermann, D. O., Frederiksen, M., Charrassin, J. B., Le Maho, Y., Sabarros, P. S., Crawford, R. J. M. & Stenseth, N. C. 2009. Pros and cons of using seabirds as ecological indicators. *Climate Research,* **39:** 115-129.

Fransson, T., Kolehmainen, T., Kroon, C., Jansson, L. & Wenninger, T. 2010. EURING list of longevity records for European birds. British Trust for Ornithology, UK.

Frederiksen, M. & Petersen, A. 2000. The importance of natal dispersal in a colonial seabird, the Black Guillemot *Cepphus grylle*. *Ibis,* **142:** 48-57.

Garthe, S., Montevecchi, W. A., Chapdelaine, G., Rail, J. F. & Hedd, A. 2007. Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. *Marine Biology,* **151:** 687-694.

Garthe, S., Montevecchi, W. A. & Davoren, G. K. 2011. Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnology and Oceanography,* **56**: 802-812.

Gladbach, A., Braun, C., Nordt, A., Peter, H. U. & Quillfeldt, P. 2009. Chick provisioning and nest attendance of male and female Wilson's storm petrels *Oceanites oceanicus*. *Polar Biology,* **32:** 1315-1321.

Grecian, W. J., Inger, R., Attrill, M. J., Bearhop, S., Godley, B. J., Witt, M. J. & Votier, S. C. 2010. Potential impacts of wave-powered marine renewable energy installations on marine birds. *Ibis,* **152:** 683-697.

Gremillet, D., Pichegru, L., Siorat, F. & Georges, J. Y. 2006. Conservation implications of the apparent mismatch between population dynamics and foraging effort in French northern gannets from the English Channel. *Marine Ecology-Progress Series,* **319:** 15-25.

Guilford, T., Wynn, R., McMinn, M., Rodriguez, A., Fayet, A., Maurice, L., Jones, A. & Meier, R. 2012. Geolocators Reveal Migration and Pre-Breeding Behaviour of the Critically Endangered Balearic Shearwater *Puffinus mauretanicus*. *Plos One,* **7:** 8.

Haelterlein, B. & Suedbeck, P. 1996. Monitoring of breeding seabirds and coastal birds along the German North Sea coast. *Vogelwelt,* **117:** 277-285.

Halsey, L. G., Butler, P. J., Fahlman, A., Bost, C. A. & Handrich, Y. 2010. Changes in the foraging dive behaviour and energetics of king penguins through summer and autumn: a month by month analysis. *Marine Ecology-Progress Series,* **401:** 279-289.

Hamer, K. C., Phillips, R. A., Hill, J. K., Wanless, S. & Wood, A. G. 2001. Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology-Progress Series,* **224:** 283-290.

Hamer, K. C., Phillips, R. A., Wanless, S., Harris, M. P. & Wood, A. G. 2000. Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. *Marine Ecology-Progress Series,* **200:** 257-264.

Harris, M. P., Murray, S. & Wanless, S. 1998. Long-term changes in breeding performance of Puffins *Fratercula arctica* on St Kilda. *Bird Study,* **45:** 371-374.

Harris, M. P. & Tasker, M. L. 1999. Conservation value of ringing seabirds in Britain and Ireland. *Ringing and Migration,* **19:** 95-106.

Harris, M. P., Bogdanova, M. I., Daunt, F. & Wanless, S. 2012. Using GPS technology to assess feeding areas of Atlantic Puffins *Fratercula arctica*. *Ringing & Migration,* **27**: 43-49

Hatch, S. A., Gill, V. A. & Mulcahy, D. M. 2010. Individual and colony-specific wintering areas of Pacific northern fulmars (*Fulmarus glacialis*). *Canadian Journal of Fisheries and Aquatic Sciences,* **67:** 386-400.

Hatch, S. A., Gill, V. A. & Mulcahy, D. M. 2011. Migration and wintering sites of Pelagic Cormorants determined by satellite telemetry. *Journal of Field Ornithology,* **82:** 269-278.

Hervias, S., Henriques, A., Oliveira, N., Pipa, T., Cowen, H., Ramos, J. A., Nogales, M., Geraldes, P., Silva, C., Ruiz de Ybanez, R. & Oppel, S. 2013. Studying the effects of multiple invasive mammals on Cory's shearwater nest survival. *Biological Invasions,* **15:** 143-155.

Hill, G., Rosier, J. & Dyer, P. 1995. Tourism development and environmental limitations at Heron Island, Great Barrier Reef – a response. *Journal of Environmental Management,* **45:** 91-99.

Hipfner, J. M., Charette, M. R. & Blackburn, G. S. 2007. Subcolony variation in breeding success in the tufted puffin (*Fratercula cirrhata*): Association with foraging ecology and implications. *Auk,* **124:** 1149-1157.

Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology,* **79:** 647-655.

Jouventin, P. & Weimerskirch, H. 1990. Satelite tracking of wandering albatrosses. *Nature* **343:** 746-748.

Kato, A., Watanuki, Y., Nishiumi, I., Kuroki, M., Shaughnessy, P. & Naito, Y. 2000. Variation in foraging and parental behavior of King Cormorants. *Auk,* **117:** 718-730.

Kokubun, N., Kim, J. H., Shin, H. C., Naito, Y. & Takahashi, A. 2011. Penguin head movement detected using small accelerometers: a proxy of prey encounter rate. *Journal of Experimental Biology,* **214:** 3760-3767.

Kopp, M., Peter, H. U., Mustafa, O., Lisovski, S., Ritz, M. S., Phillips, R. A. & Hahn, S. 2011. South polar skuas from a single breeding population overwinter in different oceans though show similar migration patterns. *Marine Ecology-Progress Series,* **435:** 263-267.

Kubetzki, U., Garthe, S., Fifield, D., Mendel, B. & Furness, R. W. 2009. Individual migratory schedules and wintering areas of northern gannets. *Marine Ecology-Progress Series,* **391:** 257-265.

Lescroel, A. & Bost, C. A. 2005. Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Marine Ecology-Progress Series,* **302**: 245-261.

Lewison, R., Oro, D., Godley, B. J., Underhill, L., Bearhop, S., Wilson, R. P., Ainley, D., Arcos, J. M., Boersma, P. D., Borboroglu, P. G., Boulinier, T., Frederiksen, M., Genovart, M., Gonzalez-Solis, J., Green, J. A., Gremillet, D., Hamer, K. C., Hilton, G. M., Hyrenbach, K. D., Martinez-Abrain, A., Montevecchi, W. A., Phillips, R. A., Ryan, P. G., Sagar, P., Sydeman, W. J., Wanless, S., Watanuki, Y., Weimerskirch, H. & Yorio, P. 2012. Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research,* **17:** 93-123.

Lindberg, M. S. & Walker, J. 2007. Satellite telemetry in avian research and management: Sample size considerations. *Journal of Wildlife Management,* **71:** 1002-1009.

Lindborg, V. A., Ledbetter, J. F., Walat, J. M. & Moffett, C. 2012. Plastic consumption and diet of Glaucous-winged Gulls (*Larus glaucescens*). *Marine Pollution Bulletin,* **64:** 2351-2356.

Lindeboom, H. J., Kouwenhoven, H. J., Bergman, M. J. N., Bouma, S., Brasseur, S., Daan, R., Fijn, R. C., de Haan, D., Dirksen, S., van Hal, R., Lambers, R. H. R., Ter Hofstede, R., Krijgsveld, K. L., Leopold, M. & Scheidat, M. 2011. Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. *Environmental Research Letters,* **6:** 1-13.

Mead, C. J. 1978. Tern mortality in West-Africa as shown by British and Dutch ringing results. *Ibis,* **120:** 110-110.

Mitchell, P. I., Newton, S. F., Ratcliffe, N. & Dunn, T. E. (2004) *Seabird Populations of Britain and Ireland,* London: T & AD Poyser.

Montevecchi, W., Fifield, D., Burke, C., Garthe, S., Hedd, A., Rail, J.-F. & Robertson, G. 2012. Tracking long-distance migration to assess marine pollution impact. *Biology Letters,* **8**: 218-221.

Oro, D., Aguilar, J. S., Igual, J. M. & Louzao, M. 2004. Modelling demography and extinction risk in the endangered Balearic shearwater. *Biological Conservation,* **116:** 93-102.

Perrow, M. R., Skeate, E. R., Lines, P., Brown, D. & Tomlinson, M. L. 2006. Radio telemetry as a tool for impact assessment of wind farms: the case of Little Terns *Sterna albifrons* at Scroby Sands, Norfolk, UK. *Ibis,* **148:** 57-75.

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V. & Briggs, D. R. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology-Progress Series,* **266:** 265-272.

Pichegru, L., Ryan, P. G., Le Bohec, C., van der Lingen, C. D., Navarro, R., Petersen, S., Lewis, S., van der Westhuizen, J. & Gremillet, D. 2009. Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas. *Marine Ecology-Progress Series,* **391:** 199-208.

Pierre, J. P., Abraham, E. R., Richard, Y., Cleal, J. & Middleton, D. A. J. 2012. Controlling trawler waste discharge to reduce seabird mortality. *Fisheries Research,* **131:** 30-38.

Rolland, V., Nevoux, M., Barbraud, C. & Weimerskirch, H. 2009. Respective impact of climate and fisheries on the growth of an albatross population. *Ecological Applications,* **19:** 1336-1346.

Sala, J. E., Wilson, R. P., Frere, E. & Quintana, F. 2012. Foraging effort in Magellanic penguins in coastal Patagonia, Argentina. *Marine Ecology-Progress Series,* **464**: 273-287.

Schuetz, J. 2011. Reproductive Declines in an Endangered Seabird: Cause for Concern or Signs of Conservation Success? *Plos One,* **6:** 9.

Shaffer, S. A., Tremblay, Y., Awkerman, J. A., Henry, R. W., Teo, S. L. H., Anderson, D. J., Croll, D. A., Block, B. A. & Costa, D. P. 2005. Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology,* **147:** 833-843.

Sirdevan, J. E. & Quinn, J. S. 1997. Foraging patterns of caspian terns (*Sterna caspia*) determined using radio-telemetry. *Colonial Waterbirds,* **20:** 429-435.

Southern, W. E. 1970. En route behaviour of homing Herring gulls as determined by radio tracking. *Wilson Bulletin,* **82:** 189-&.

Spencer, H. J. & Miller, T. 2011. A proposal for using GPS-logger equipped flying-foxes as monitors of change in tropical rainforest resource distribution. *Biology and Conservation of Australasian Bats***:** 195-201.

Staniland, I. J., Reid, K. & Boyd, I. L. 2004. Comparing individual and spatial influences on foraging behaviour in Antarctic fur seals *Arctocephalus gazella*. *Marine Ecology-Progress Series,* **275:** 263-274.

Suarez, N., Retana, M. V. & Yorio, P. 2012. Spatial patterns in the use of foraging areas and its relationship with prey resources in the threatened Olrog's Gull (*Larus atlanticus*). *Journal of Ornithology,* **153**: 861-871.

Sydeman, W. J., Thompson, S. A. & Kitaysky, A. 2012. INTRODUCTION Seabirds and climate change: roadmap for the future. *Marine Ecology-Progress Series,* **454:** 107-110.

Takahashi, A. 2004. Individual variation in foraging behaviour and reproductive performance of seabirds. *Japanese Journal of Ornithology,* **53:** 22-35.

Takeuchi, T., Matsuki, R. & Nashimoto, M. 2012. GPS cell phone tracking in the Greater Tokyo Area: A field test on raccoon dogs. *Urban Ecosystems,* **15:** 181-193.

Tasker, M. L., Jones, P. H., Dixon, T. & Blake, B. F. 1984. Counting seabirds at sea from ships – A review of methods employed and a suggestion for a standardised approach. *Auk,* **101**. 564-577.

Thaxter, C. B., Daunt, F., Hamer, K. C., Watanuki, Y., Harris, M. P., Gremillet, D., Peters, G. & Wanless, S. 2009. Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalge*: nest defence, foraging efficiency or parental effort? *Journal of Avian Biology,* **40**: 75-84.

Viblanc, V. A., Smith, A. D., Gineste, B. & Groscolas, R. 2012. Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors. *BMC ecology,* **12:** 10.

Votier, S. C., Bearhop, S., Witt, M. J., Inger, R., Thompson, D. & Newton, J. 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology,* **47:** 487-497.

Votier, S. C., Birkhead, T. R., Oro, D., Trinder, M., Grantham, M. J., Clark, J. A., McCleery, R. H. & Hatchwell, B. J. 2008. Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *Journal of Animal Ecology,* **77:** 974-983.

Votier, S. C., Furness, R. W., Bearhop, S., Crane, J. E., Caldow, R. W. G., Catry, P., Ensor, K., Hamer, K. C., Hudson, A. V., Kalmbach, E., Klomp, N. I., Pfeiffer, S., Phillips, R. A., Prieto, I. & Thompson, D. R. 2004. Changes in fisheries discard rates and seabird communities. *Nature,* **427:** 727-730.

Wakefield, E. D., Phillips, R. A. & Matthiopoulos, J. 2009. Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology-Progress Series,* **391:** 165-182.

Walsh, P., Halley, D., Harris, M., del Nevo, A., Sim, L. & Tasker, M. (1995) *Seabird monitoring handbook for Britain and Ireland: a compilation of methods for survey and monitoring of breeding seabirds,* Peterborough: JNCC / RSPB /ITE / Seabird Group.

Wanless, R. M., Ratcliffe, N., Angel, A., Bowie, B. C., Cita, K., Hilton, G. M., Kritzinger, P., Ryan, P. G. & Slabber, M. 2012. Predation of Atlantic Petrel chicks by house mice on Gough Island. *Animal Conservation,* **15:** 472-479.

Wanless, S., Harris, M. P. & Morris, J. A. 1992. Diving behaviour and diet of the Blue-eyed shag at South-Georgia. *Polar Biology,* **12:** 713-719.

Watanuki, Y., Daunt, F., Takahashi, A., Newei, M., Wanless, S., Sat, K. & Miyazaki, N. 2008. Microhabitat use and prey capture of a bottom-feeding top predator, the European shag, shown by camera loggers. *Marine Ecology-Progress Series,* **356:** 283-293.

Webb, A., Stronach, A., Tasker, M. L. & Stone, C. J. 1995. Vulnerable concentrations of seabirds south and west of Britain. Peterborough: JNCC.

Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. 1993. Foraging strategy of Wandering albatross through the breeding season – A study using satelitte telemetry. *Auk,* **110:** 325-342.

Weimerskirch, H., Wilson, R. P., Guinet, C. & Koudil, M. 1995. Use of seabirds to monitor sea-surface temperatures and to validate satellite remote-sensing measurements in the Southern-Ocean. *Marine Ecology-Progress Series,* **126:** 299-303.

Weimerskirch, H., Gault, A. & Cherel, Y. 2005. Prey distribution and patchiness: Factors in foraging success and efficiency of wandering albatrosses. *Ecology,* **86:** 2611-2622.

Weimerskirch, H., Shaffer, S. A., Tremblay, Y., Costa, D. P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K. & Aurioles, D. 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Marine Ecology-Progress Series,* **391:** 267-278.

Wienecke, B. & Robertson, G. 2006. Comparison of foraging strategies of incubating king penguins *Aptenodytes patagonicus* from Macquarie and Heard islands. *Polar Biology,* **29:** 424-438.

Wilson, L. J., McSorley, C. A., Gray, C. M., Dean, B. J., Dunn, T. E., Webb, A. & Reid, J. B. 2009. Radio-telemetry as a tool to define protected areas for seabirds in the marine environment. *Biological Conservation,* **142:** 1808-1817.

Woakes, A. J., Butler, P. J. & Bevan, R. M. 1995. Implantable data logging system for heart-rate and body temperature – its application to the estimation of field metabolic rates in antartcic predators. *Medical & Biological Engineering & Computing,* **33:** 145-151.

Yorio, P., Quintana, F., Dell'Arciprete, P. & Gonzalez-Zevallos, D. 2010. Spatial overlap between foraging seabirds and trawl fisheries: implications for the effectiveness of a marine protected area at Golfo San Jorge, Argentina. *Bird Conservation International*, **20,** 320-334.

Chapter 2

How many seabirds do we need to track to define home-range area?

Soanes, L.M.[a], Arnould, J.P.Y.[b], Dodd, S.G.[c], Sumner, M.D.[d] and Green, J.A.[a]

[a] School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP. [b] School of Life and Environmental Sciences, Deakin University, Melbourne, 3215, Australia.[c] Royal Society for the rotection of Birds, North Wales Office, Bangor, LL57 4FD.[d] Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, Tasmania, 8001.

Published in the Journal of Applied Ecology (2013), Vol 50 (3) pages 671-679

Photograph Louise Soanes 2010

Author contributions: LMS & JAG conceived and designed the study, LMS & SGD conducted fieldwork, LMS, JAG & MDS analysed data, JPYA provided financial assistance, LMS wrote the manuscript with editorial advice from co-authors,

Abstract

In recent years marine predator and seabird tracking studies have become ever more popular. However, they are often conducted without first considering how many individuals should be tracked and for how long they should be tracked in order to make reliable predictions of a population's home-range area. Home-range area analysis of two seabird-tracking data sets was used to define the area of active use (where birds spent 100% of their time) and the core foraging area (where birds spent 50% of their time). Analysis was conducted on the first foraging trip undertaken by the birds and then the first two, three and four foraging trips combined. Appropriate asymptotic models were applied to the data and the calculated home-range areas were plotted as a function of an increasing number of individuals and trips included in the sample. Data were extrapolated from these models to predict the area of active use and the core foraging area of the colonies sampled. Significant variability was found in the home-range area predictions made by analysis of the first foraging trip and the first four foraging trips combined. For shags, the first foraging trip predicted a 56% smaller area of active use when compared to the predictions made by combining the first four foraging trips. For kittiwakes a 43% smaller area was predicted when comparing the first foraging trip with the four combined trips. The number of individuals that would be required to predict the home range area of the colony depends greatly on the number of trips included in the analysis. This analysis predicted that 39 (confidence interval 29–73) shags and 83 (CI 109–161) kittiwakes would be required to predict 95% of the area of active use when the first four foraging trips are included in the sample compared to 135 (CI 96–156) shags and 248 (164-484) kittiwakes when only the first trip is included in the analysis.

Introduction

The biology and behaviour of seabirds has been widely studied, but is often limited to periods when the birds are on the nest within their breeding colonies. It was not until the late 1970s that scientists began collating and recording information on what seabirds were actually doing at sea. Whilst surveys of presence and abundance at sea are important for identifying potential ‘hot-spots’ of activity, they provide little or no information on where birds recorded have come from and often only represent a snapshot in time, day and season. However, with recent advances in the technology of satellite tracking and the availability of relatively low-cost GPS loggers, the field of seabird biology has become increasingly focused on investigating the foraging behaviour of seabirds away from their breeding colonies (Burger & Shaffer 2008; Wakefield, Phillips & Matthiopoulos 2009).

Recent studies have ranged from determining the differences in foraging behaviour between species (Young *et al.* 2010), sexes (Thaxter *et al.* 2009; Weimerskirch *et al.* 2009; Quintana *et al.* 2011) and age classes (Votier *et al.* 2011) to detecting inter-colony (Zavalaga, Halls & Dell'Omo 2010) and inter-individual variation (Hatch, Gill & Mulcahy 2010). As well as these behavioural studies, the use of seabird tracking data are also being applied to define important habitat types used by species (Wakefield, Phillips & Matthiopoulos 2009; McLeay *et al.* 2010) and to define important foraging areas (Harris *et al.* 2007; Yorio 2009).

Around the world, seabird tracking studies have already provided insights to aid in the designation of Marine Protected Areas (Garthe & Skov 2006; Louzao *et al.* 2006; Gremillet & Boulinier 2009; Wakefield, Phillips & Matthiopoulos 2009; Wilson *et al.* 2009) and to assess the effectiveness of such areas (Harris *et al.* 2007; Yorio 2009; Yorio *et al.* 2010) .

The widespread use of GPS and satellite tracking devices has led to the publication of studies that reveal the importance of the effect of sampling regime (Seaman *et al.* 1999; Girard *et al.* 2002; Taylor, Terauds & Nicholls 2004; Nicholls, Robertson & Naef-Daenzer 2005; Borger *et al.* 2006) and to warnings that tracking studies often compromise good study design and may overestimate the importance of fine-scale data (Hebblewhite & Haydon 2010). Despite these concerns, the number of devices deployed in any particular study is often governed by time and economic factors rather than standard experimental design principles. In the majority of published studies, little or no consideration is given as to how long to deploy the tracking devices for and how many individuals from a population should be tracked to make the most reliable predictions of home-range area. This is particularly important when considering the use of the low-cost data loggers, which only have the capacity to collect data over days rather than weeks. Whilst several foraging trips may be recorded for localised feeders, this approach may not reveal the potential variability in the foraging areas of species that make foraging trips of longer duration. Often in tracking studies only one foraging trip may be recorded per individual, or only the first trip made by individuals is used to make predictions on foraging behaviour and preferred habitats (Gremillet *et al.* 2008; McLeay *et al.* 2010; Yorio *et al.* 2010; Quintana *et al.* 2011). Similarly, data loggers may be left on birds for longer periods than necessary, which may not add to the information that could have been gained from a shorter deployment if the birds are consistent in their foraging habits. The study by Taylor *et al.* (2004) on the foraging behaviour of two species of albatross suggested a relationship between sample size and kernel density area, indicating that at small sample sizes the foraging behaviour of a single individual on a single trip can produce hotspots in regions not frequented by any other individuals, but by using larger samples the influence of a single individual is reduced.

The data collected by seabird tracking studies has already revealed interesting and important information such as seabirds' use of particular oceanic habitats (Louzao *et al.* 2006; Bugoni, D'Alba & Furness 2009; Soanes *et al.* 2012) and their foraging behaviour (Gremillet *et al.* 2004; Lewis *et al.* 2005; McLeay *et al.* 2010; Grecian *et al.* 2012; Lewison *et al.* 2012). However, with the increasing importance and ecological application of seabird tracking data it is now time to consider how we can make the best use of resources that are being invested into this field. This will ensure that the data collected are used to make the most reliable and useful predictions to aid in the designation of Marine Protected Areas, and will help ensure we do not miss potentially important foraging areas.

This study develops a simple approach to enable researchers to determine:

1. How many individuals should be used to predict the home-range area of a colony?
2. How many trips should be used to predict the home range area of a colony?
3. What is the optimum combination of individuals and trips to include in a sampling protocol?

Materials and methods

Data collection

Seabird-tracking data sets from two species with different foraging modes were used: 19 European shags *Phalacrocorax aristotelis* (Linnaeus, 1761), representing an inshore benthic diving seabird, and 21 Black- legged kittiwakes *Rissa tridactyla* (Linnaeus, 1758), representing an offshore surface feeding seabird. Birds were tracked from their breeding colony on Puffin Island, Wales, (53.3ºN, 4.0ºW) using IgotU GT-120 GPS data loggers (Mobile Action, Taiwan) during the chick-rearing period of 2010 for shags and 2011 for kittiwakes. All loggers were attached to the back feathers with waterproof tape (Wilson *et al.* 1997). The GPS devices did not always record a position every 120 seconds as programmed to do, in part due to the diving activity of shags. This may provide a biased sample of the spatial distribution of foraging activity (McLeay *et al.* 2010), and so GPS fixes were interpolated to every 10 seconds using the R package *trip* (Sumner 2011). This process and interval ensured that all cells (see *home range analysis* below) flown over by birds were included in the spatial analysis since fixes recorded every 120 seconds could be greater than 1 km apart for a rapidly flying bird, and thus entire cells could have been excluded from the analysis. Any GPS positions recorded at the breeding colony or within 300 m of it were excluded from the analysis. The number of foraging trips recorded per individual ranged from 1–16 for shags, and 1–11 for kittiwakes, with a mean number of 8 and 5 foraging trips made per species respectively. Eighteen individual shags and 14 individual kittiwakes made at least four foraging trips and these data were used in further analysis as a compromise between maximising both the number of individuals included in a sample and the number of foraging trips made by each individual.

Home range analysis

For the purpose of this paper the term ‘home range’ refers to “a minimum area in which an animal has some specified probability of being located” (Worton 1989). The 95% home-range area is considered to be the area of active use of an individual or sample of individuals whilst the 50% area is considered to be the core foraging area (Ford 1979). The calculation of home-range areas of animals is often performed using kernel density methods (Calenge 2007). However, these methods are reliant on the appropriate use of smoothing parameters and the type of kernel used (Worton 1989; Row & Blouin-Demers 2006) and often do not perform well on auto-correlated data (Blundell, Maier & Debevec 2001). In the present study we attempted to analyse our data using kernel density methods, trialling the *ad hoc*, the Least Squares Cross Validation (LSCV) and the Brownian Bridge kernel methods (Calenge 2007). However as in the studies mentioned above these methods were found to be unsuitable for our data. As such, home-range areas in this study were represented using a time-based approach spent in a pre-defined grid of 1x1 km cells surrounding the breeding colony (Page *et al.* 2006). The area of active use was defined as the sum of all grid cells used (Casper *et al.* 2010 Hindell *et al.* 2003). We then ranked all cells used in order of time spent in each one, and defined the core foraging areas as the cells which encompassed the first 50% of the cumulative frequency distribution. The R package *trip* (Sumner 2012) was used to perform the analysis. Maps of time spent in pre-defined grids for both species were plotted using ArcGIS software (Esri 2011, ArcGIS Desktop: Release 10, CA: Environmental Systems Research Institute).

Predicting the home range area of a colony

One of the main aims of most tracking studies is to predict the home-range area of a population from a colony using a sample of individuals. Here we consider the relationship between the number of individuals in a sample and the predicted size of the colony’s home-range area. We suggest three possible relationships: (a) There is no overlap in home-range area used by individuals and the colony’s home range area is fully defined only when all individuals have been sampled (b) individuals use distinctive areas to forage, but with some overlap, until a sufficient number of individuals have been included in the sample for all available habitat to be used (an asymptote is met) or (c) all individuals from a colony forage in the same area, and home-range area estimates are the same once one individual has been adequately sampled (Fig. 2.1). Scenario (b) is the most likely relationship between the theoretical extremes of (a) and (c).

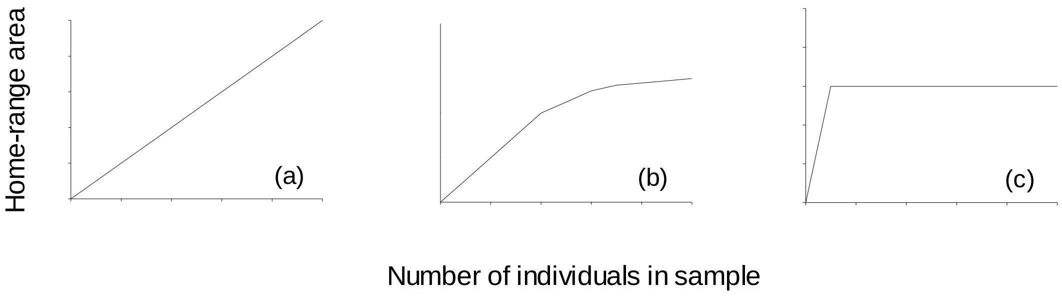


Figure 2.1. Hypothetical relationships between number of seabirds and the home-range area under three scenarios: (a) all birds have different home-range areas and the colony's home-range area is defined only when all individuals have been sampled (b) there is some overlap between individuals in their home-range area and a limit to the amount of favourable habitat available (c) all birds have the same home-range area.

The areas of active use and the core foraging areas were calculated for the first foraging trip individually and for the first two, three and four foraging trips combined. These areas were calculated for an increasing sample of individual shags or kittiwakes (up to 18 shags and up to 14 kittiwakes). Using the statistical software R (R Core Team 2012) the individuals included in each sample were selected at random a total of 18 times for shags and 14 times for kittiwakes (to match the total sample of birds), then this data bootstrapped 10000 times, with replacement, using the R package *boot* (Canty & Ripley 2007) to determine the mean and upper and lower percentile values of home-range area. The lower (2.5%) and upper (97.5%) percentile values for each number of individuals included in a sample represented the 95% confidence intervals of this estimate. A range of linear and asymptotic models (see Table S1), appropriate to the scenarios described in figure 1, were fitted to the data using the statistical software R and the most appropriate model selected based on AIC values of the models tested. These models included the Michaelis-Menten (Equation 1) and the 3-parameter asymptotic exponential (Equation 2) models. A sensitivity analysis was performed to evaluate the differences in the home-range area predictions made by each of the models.

Equation 1: Michaelis- Menten: $y = \frac{a*x}{(b+x)}$

Where a=the asymptotic value of the y axis, and b=the value of x at which half of the maximum response is attained.

Equation 2: 3 Parameter-asymptotic exponential: $y = a - b * e^{-cx}$

Where a= the asymptotic value of the y-axis, b= a-the value of y when x=0, and c= $-\frac{\log((a-y)/b}{x}$ where y= value of y axis and x= value of x axis when the curve is rising most steeply.

Using the relationship from the first four trips made by our full sample of shags and kittiwakes we extrapolated each of the non-linear model functions to estimate the populations' area of active use and core foraging area based on the colony size. We then used each non-linear function to calculate the home range size for each combination of number of birds and number of trips and expressed this as a percentage of the prediction for the full number of birds and trips. Plotting these percentages as a three dimensional surface allowed rapid visual evaluation of the amount of the true home range size that would be estimated using different sampling protocols.

Finally for each species we used our models to calculate how many birds would need to be tracked in order to estimate 50% and 95% of the population's core foraging area and area of active use under scenarios where only the first trip or the first four trips were analysed.

Results

Of the 16 relationships between sample size and home range area, the Michaelis-Menten model was the best fitting model in 12 cases with the 3-parameter model the best fit in the remaining four cases (see Table S1). Examples of the fits of different types of model are shown in Figure S1 in Supporting Information. This supports our theoretical prediction that an asymptotic model would be the best predictor of the relationship between birds sampled and home range area (Fig. 2.1). A sensitivity analysis indicated some difference (< 30%) between these two models in terms of the prediction of home range areas for the full population when compared to the other models fitted (Table 2.1). However, these differences were substantially less than the differences between each of these and the other models tested. As a result we used the Michaelis-Menten model for all further analysis.

Table 2.1. Sensitivity analysis of the predictions of area of active use from the different linear and non-linear models tested. Using all four trips made by 18 shags and 14 kittiwakes, where y= the home-range area predicted for 484 shags and 892 kittiwakes breeding on Puffin Island.

	Shags	Kittiwakes
	y	y
2-parameter asymptotic	176.5	1130.1
3-parameter asymptotic	202.9	1193.0
Michaelis-Menten	228.5	1539.3
Linear	3580.4	54096.5
2-parameter logistic	179.6	1059.9

Comparing the predicted areas of active use and the core foraging areas of trip 1, trips 1–2, trips 1–3 and all four trips combined of all 18 shags and 14 kittiwakes revealed differences in the model asymptote predictions of number of cells used. In general, as the number of trips included in the sample increased, the asymptotic prediction increased and number of individuals required to define half of the asymptote decreased (Fig. 2.2).

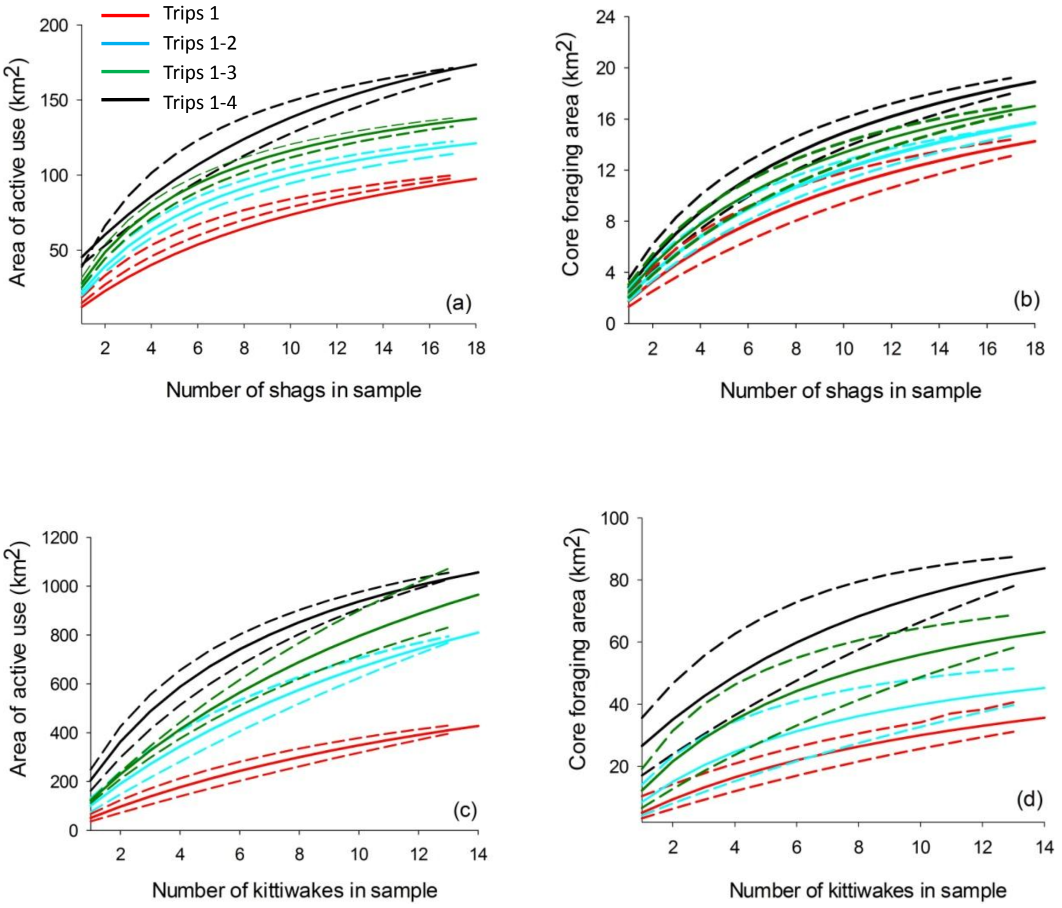


Figure 2.2. Comparisons of home-range areas predicted by using the first, first two, first three or all four foraging trips for analysis with all four trips combined for (a) the area of active use of shags (b) the core foraging area of shags (c) the area of active use of kittiwakes and (d) the core foraging area of kittiwakes. Upper (97.5%) and lower (2.5%) confidence intervals are represented by the dashed lines.

Particularly large differences were found when comparing the asymptote predictions of the number of cells from trip 1 only, trips 1–2 and trips 1–3 when compared to all four trips combined for the area of active use of shags and between trip 1 and all 4 trips combined to predict the core foraging area of kittiwakes (Table S2). This indicates that using the first trip only and including few individuals in a sample for home-range analysis may have implications in under-estimating the area used (Fig. 2.3 & 2.4).

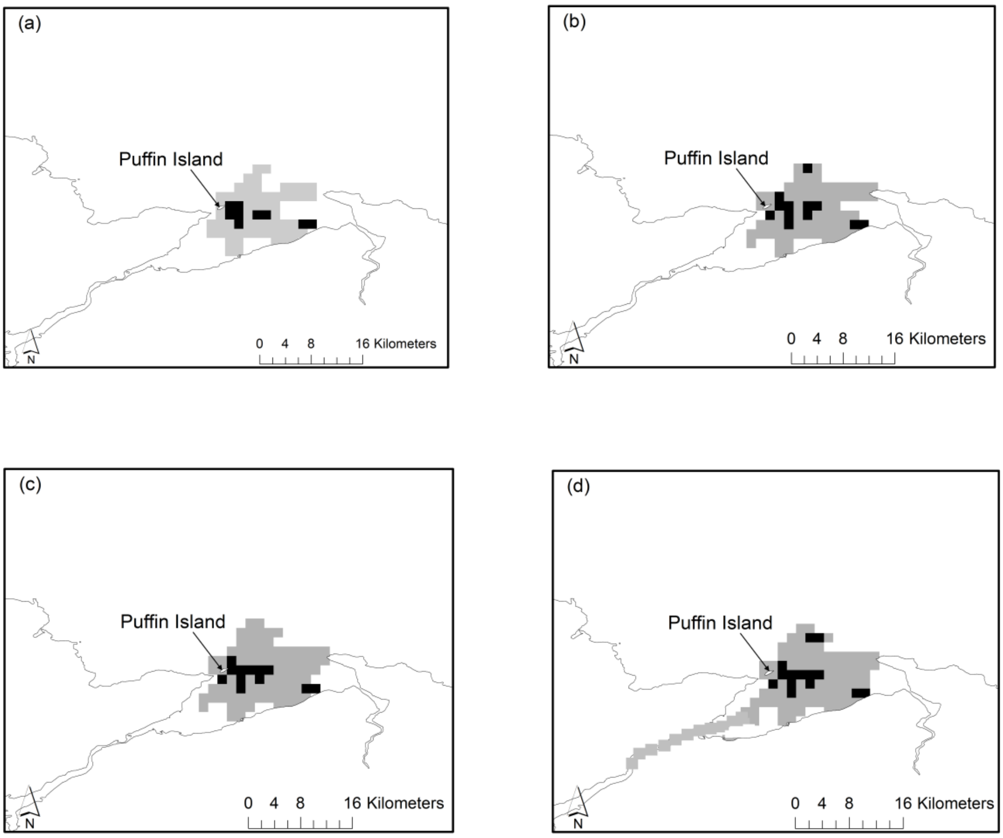


Figure 2.3. Home-range area maps of the area of active use predicted from analysis of (a) the first foraging trip and (b) the first two foraging trips (c) the first three foraging trips and (d) all four foraging trips combined of 18 shags. Black squares = areas where birds spent 50% of their time, Grey squares = areas where birds spent 100% of their time. (See Figure S2(a) for actual plotted tracks)

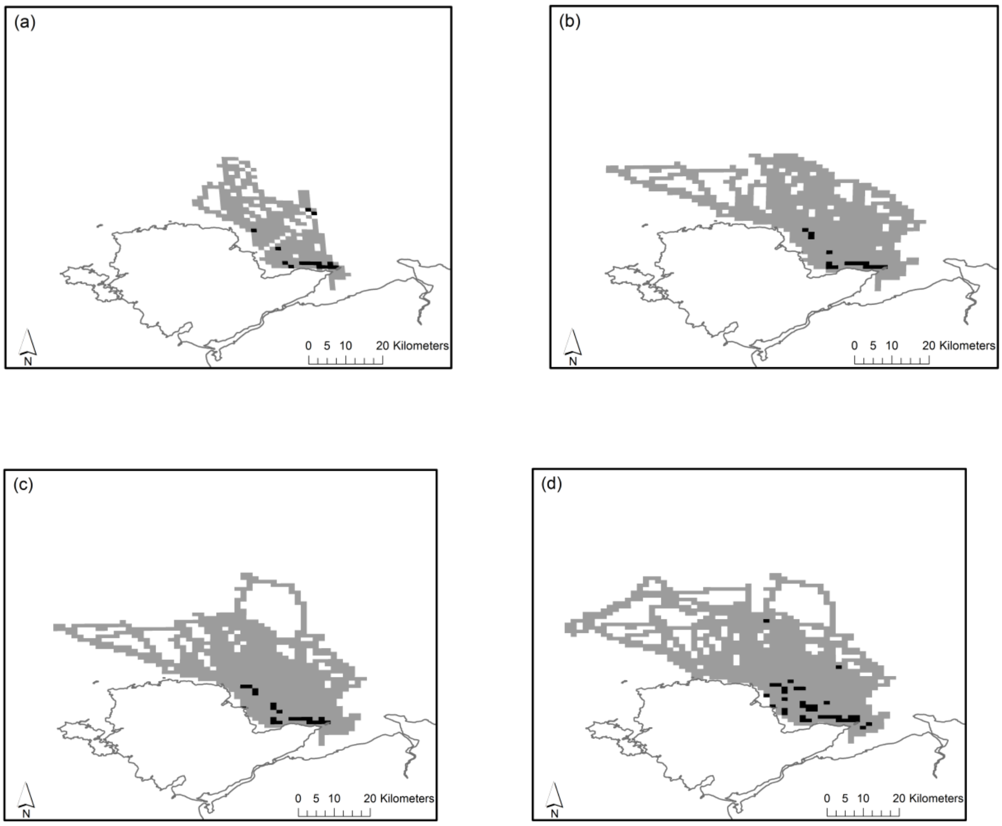


Figure 2.4. Home-range area maps of the area of active use predicted from analysis of (a) the first foraging trip and (b) the first two foraging trips (c) the first three foraging trips and (d) all four foraging trips combined of 14 kittiwakes. Black squares = areas where birds spent 50% of their time, Grey squares = areas where birds spent 100% of their time. (See Figure S2(b) for actual plotted tracks).

Using several trips from fewer birds for home-range analysis is likely to yield the same conclusion as using one trip from many more birds. The exact relative importance of the number of birds and trips is likely to vary between species and/or populations. Indeed, in our data there are some differences between shags and kittiwakes. For shags, four trips from one bird predicted a similar size core foraging area as using one trip from all 18 birds. For kittiwakes, four trips from three birds predicted the same core foraging area as one trip from 14 birds (Fig. 2.5).

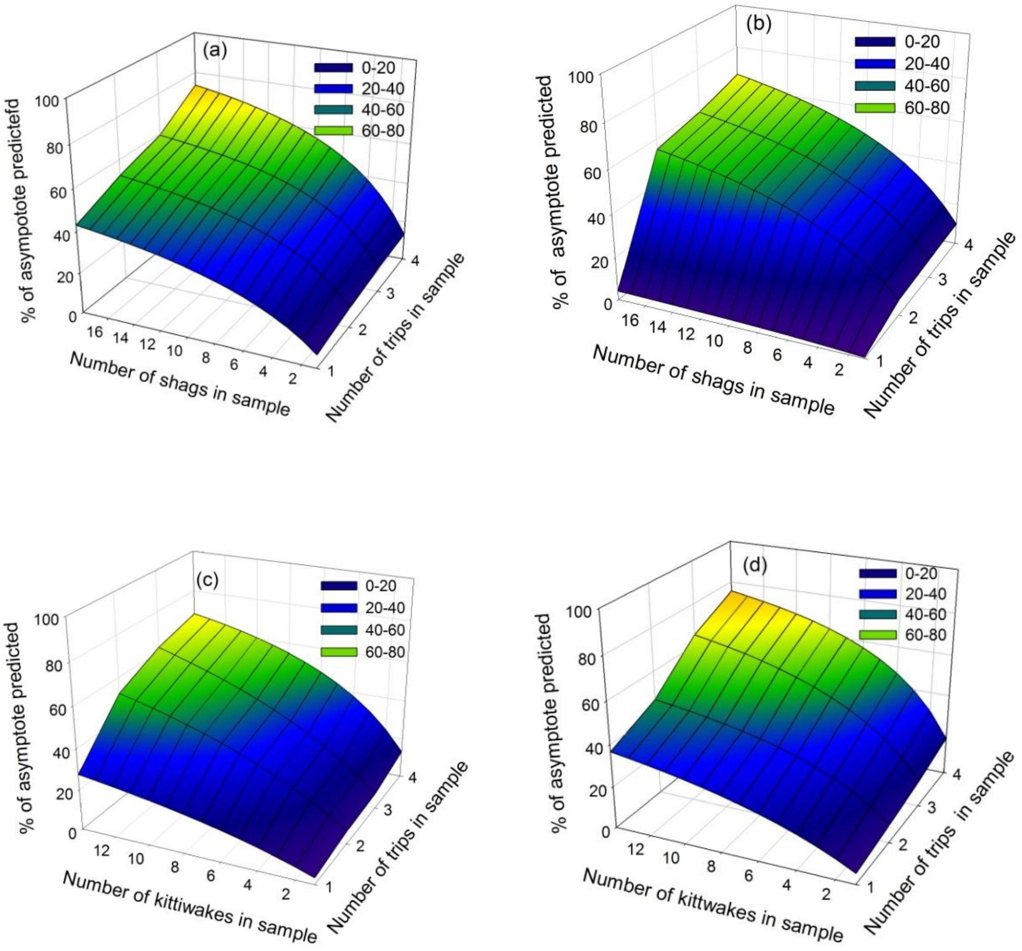


Figure 2.5. The percentage of the home-range area asymptote predicted by different numbers of trips and numbers of individuals included in a sample (a) the area of active use of shags (b) the core foraging area of shags (c) the area of active use of kittiwakes and (d) the core foraging are of kittiwakes.

If using all four trips in analysis, relatively few individuals from the population of shags and kittiwakes breeding on Puffin Island would need to be tracked to predict the colony's area of active use and core foraging areas (Table 2.2). There are quite large confidence intervals around these estimates suggesting some variability in the home-range areas used by individuals. The estimates range from 6–15% of the shag population and 12–18% of the kittiwake population to predict 95% of the area of active use, and 5–9% of the shag population and 1–6% of the kittiwake population to predict 95% of the colony's core foraging area. However using only the first trip for analysis of home-range area would increase the number of individuals required to predict the area of active use to 20–28% of the shag colony and 18–54% of the kittiwake colony and would require 22–54% of the shag colony and 3–27% of the kittiwake colony to predict the core foraging areas.

Table 2.2. The number of individuals required to represent 50% and 95% of the core foraging areas and area of active use for each of our study populations when all four foraging trips are included in the analysis compared to when just the first foraging trip is included (based on population size of 484 shags and 892 kittiwakes and model derived parameters from Equation 1).

Number of individuals required to represent:					
	Number of trips included in sample	**50% of core foraging area (CI)**	**95% of core foraging area (CI)**	**50% of area of active use (CI)**	**95% of area of active use (CI)**
European shag	1	12 (7-18)	159 (106-259)	9 (6-12)	135 (96-156)
	4	6 (5-9)	30 (24-45)	5 (5-8)	39 (29-73)
Black-legged kittiwake	1	18 (10-52)	182 (27-237)	11 (5-30)	248 (164-484)
	4	4 (2-11)	22 (12-51)	7 (5-10)	83 (109-161)

Discussion

To date, there have been few cases where seabird-tracking data has been used to aid the designation of Marine Protected Areas, but several studies have suggested that their data may be used for this purpose. For example Birdlife International (Taylor, Terauds & Nicholls 2004) pooled 90 datasets of Procellariiformes tracking data from around the world with the aim of identifying the important feeding areas of this group. Wilson *et al.* (2009) radio tracked between 19–30 Manx shearwaters *Puffinus puffinus* at three UK colonies to determine their rafting locations with a view to promoting their protection. There are more published examples where tracking data have been used to evaluate the effectiveness of already designated areas. For example, Trebilco *et al.* (2008) tracked 9 Northern and 10 Southern giant petrel (*Macronectes halli* & *Macronectes giganteus*, respectively), and concluded that the foraging areas of breeding adult petrels, represented by 8 individuals in their sample, were covered by already existing marine protected areas, whereas the main foraging areas of recently fledged juveniles, represented by 11 individuals in their sample, were outside of protected areas. Pichegru *et al.* (2010) compared the foraging effort of two penguin colonies; one which had recently been surrounded by a Marine Protected Area and one that had not, after analysing the first trip of 91 individuals (in total from both colonies). They concluded that the designation of the Marine Protected Area had reduced the foraging effort of the colony closer to it. For future studies, it will be important to consider the number of individuals tracked and the number of foraging trips included in any analysis before generalised conclusions are drawn regarding the designation or effectiveness of Marine Protected Areas.

Our analysis reveals that the common practice of using only the first foraging trip made by individuals for subsequent analysis, often performed to avoid pseudo-replication or long deployments on smaller species (e.g. Pichegru *et al.* 2010; e.g. Yorio *et al.* 2010), is likely to under-estimate the size of a population's area of active use and core foraging areas. This also applies to studies comparing the foraging behaviour of individuals or between sexes or age classes (Weimerskirch *et al.* 2009; Quintana *et al.* 2011; Votier *et al.* 2011). Including more than just the first foraging trip in these analyses is more likely to be representative of the foraging behaviour of the particular individual, sex or age class. Our results suggest that analysis of the first trip made by both shags and kittiwakes predicted significantly smaller home range area when compared to combining up to four trips (Fig. 2.3, 2.4 & 2.5).

In many tracking studies, the number of individuals tracked is often dependent upon the number of devices available to deploy. However, our analysis has revealed that the number of individuals required to predict the area of active use and the core foraging area of a colony can fall within a reasonable value for species that are localised feeders such as the kittiwakes and shags in this study, if enough foraging trips are also included in the sample (Table 2.2). Those species with larger foraging areas represent more of a challenge as larger numbers of individuals may be required to estimate their foraging areas due to a larger available area to forage within. The predicted areas of use determined in this analysis were based on the foraging trips of birds made over one breeding season and only included individuals that were rearing chicks. Further developments of this approach might include the analysis of the number of individuals required to predict home-range areas at different times of the breeding season (i.e. incubating vs. chick rearing), over different years and to determine the numbers required to predict wintering areas of seabird populations. In the case of long, wholly pelagic migrations the concept of different foraging trips might not be relevant, but the larger areas available to individuals during the winter when they are not constrained to a breeding colony are likely to require many individuals from a population to be tracked to be able to make assumptions on important wintering areas of the population. Whilst tracking a large number of individuals may not be possible in some cases given time and economic constraints, it is important that in these situations researchers recognise the possible limitations of the data they present.

Our results indicate that the most likely relationship between the number of individuals and their associated foraging area is an asymptotic one (Fig. 2.1, Table 2.1). This is not surprising given the limited availability of suitable habitat within the foraging range of a colony and the energetic constraints of central place foragers (Orians & Pearson 1979). The parameters derived from these asymptotic equations can be applied to datasets as an approach to compare the home-range areas of different species, the same species between years and colonies and between individuals. There are few published studies on the repeatability of seabird colony foraging behaviour between years. Hamer *et al.* (2007) found that whilst there was a high degree of consistency in the bearing of foraging trips between years, foraging trip duration and total trip distance differed markedly for a colony of Northern gannets between the 3 years of study (data collected from 17 individuals in year one, 14 in year two and 22 in year three). Similar patterns have been shown for other central-place foragers such as pinnipeds. McDonald & Crocker (2006) found that average trip duration did not differ for the Antarctic Grey seal *Halichoerus grypus* between years but foraging area did (data collected from 27 individuals in both years). Cordes *et al.* (2011) found that the foraging areas of breeding female Harbour seals *Phoca vitulina* were comparable in 1989 and 2009 using a combination of VHF and GPS-GSM telemetry. Meanwhile, other studies have found significant differences in the foraging behaviour between years of central place foragers and have related this to environmental variables (Boyd 1999; Georges, Bonadonna & Guinet 2000; Skern-Mauritzen *et al.* 2009). We suggest that before drawing conclusions on the similarities or differences in a colony's foraging behaviour between years, that an appropriate number of individuals are tracked in each year to ensure that the assumed foraging areas determined by a sample are representative of the colony before inter-year comparisons can be fairly made. Our analysis can help to overcome the problems of small datasets by providing a means of predicting the foraging area of a sample that can then be used to make comparisons of the predicted foraging area and variability in foraging areas between individuals, colonies, or years.

The approach described in this paper is a relatively straightforward procedure to carry out and as such we propose that this should be an integral part of analysing the tracking data of seabirds and other central-place foragers. With the increasing value of tracking studies of seabirds and pinnipeds in Marine Protected Area designation, it is important that the data provided to inform these management decisions are as precise as possible. The purpose of this analysis is not to reveal actual foraging locations, but instead to provide a framework that can be used by researchers aiming to discover important foraging locations and allow them to evaluate the accuracy of their predictions and to determine how representative any tracking study is of the colony in question. This approach can be used to inform the planning of future years of study by striving for an optimum balance between longer deployment periods on fewer individuals versus shorter deployments on many more individuals.

Acknowledgements

This project was funded by a Doctoral Training Grant from the Natural Environment Research Council, with support from the RSPB's FAME project. We would like to thank Dr. Charles Bishop, Ashley Tweedale, Dr. Rachel Taylor (Bangor University), and volunteers from both the University of Liverpool and Bangor University for assistance with planning and fieldwork as well as Dr. Mark Bolton, Dr. Phillip Taylor, Dr. Norman Ratcliffe and Dr. Tony Knights for helpful discussions on this work and Dr. Josu Alday for assistance with analysis. Data collection on Puffin Island would not have been possible without permission to carryout fieldwork from Sir Richard Williams-Bulkeley. Permission was granted by the Countryside Council for Wales to conduct bird capture and tagging work on Puffin Island

References

Blundell, G.M., Maier, J.A.K. & Debevec, E.M. (2001) Linear home ranges: Effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs,* **71,** 469-489.

Borger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. (2006) Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology,* **75,** 1393-1405.

Boyd, I.L. (1999) Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. *Behavioral Ecology,* **10,** 198-208.

Bugoni, L., D'Alba, L. & Furness, R.W. (2009) Marine habitat use of wintering spectacled petrels Procellaria conspicillata, and overlap with longline fishery. *Marine Ecology-Progress Series,* **374,** 273-285.

Burger, A.E. & Shaffer, S.A. (2008) Application of tracking and data-logging technology in research and conservation of seabirds. *Auk,* **125,** 253-264.

Calenge, C. (2007) Exploring habitat selection by wildlife with adehabitat. *Journal of Statistical Software,* **22,** 1-19.

Canty, A. & Ripley, B. (2011). boot: Bootstrap R (S-Plus) Functions. R package version 1.3- 2.

Casper, R.M., Sumner, M.D., Hindell, M.A., Gales, N.J., Staniland, I.J. & Goldsworthy, S.D. (2010) The influence of diet on foraging habitat models: a case study using nursing Antarctic fur seals. *Ecography,* **33** (4): 748-749.

Cordes, L.S., Duck, C.D., Mackey, B.L., Hall, A.J. & Thompson, P.M. (2011) Long-term patterns in harbour seal site-use and the consequences for managing protected areas. *Animal Conservation,* **14,** 430-438.

Ford, R.G. (1979) The analysis of Space use Patterns. *Journal of Theroetical Biology***,** 76 125-155.

Garthe, S. & Skov, H. (2006) Selection of suitable sites for marine protected areas for seabirds: a case study with Special Protected Areas (SPAs) in the German Baltic Sea. *Waterbirds around the world: a global overview of the conservation, management and research of the world's waterbird flyways. International conference on waterbirds held in Edinburgh in April 2004.* (eds G.C. Boere, C.A. Galbraith & D.A. Stroud), pp. 739-742. The Stationery Office. Edinburgh.

Georges, J.Y., Bonadonna, F. & Guinet, C. (2000) Foraging habitat and diving activity of lactating Subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. *Marine Ecology-Progress Series,* **196,** 291-304.

Girard, I., Ouellet, J.P., Courtois, R., Dussault, C. & Breton, L. (2002) Effects of sampling effort based on GPS telemetry on home-range size estimations. *Journal of Wildlife Management,* **66,** 1290-1300.

Grecian, J., Witt, M., Attrill, M., Bearhop, S., Godley, B., Gremillet, D., Hamer, K. & Votier, S. (2012) A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern gannets breeding in the North East Atlantic. *Biological Conservation,* **156,** 43-52.

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

Gremillet, D., Dell'Omo, G., Ryan, P.G., Peters, G., Ropert-Coudert, Y. & Weeks, S.J. (2004) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Marine Ecology-Progress Series,* **268,** 265-279.

Gremillet, D., Lewis, S., Drapeau, L., van Der Lingen, C.D., Huggett, J.A., Coetzee, J.C., Verheye, H.M., Daunt, F., Wanless, S. & Ryan, P.G. (2008) Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology,* **45,** 610-621.

Hamer, K.C., Humphreys, E.M., Garthe, S., Hennicke, J., Peters, G., Gremillet, D., Phillips, R.A., Harris, M.P. & Wanless, S. (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology-Progress Series,* **338,** 295-305.

Harris, J., Haward, M., Jabour, J. & Woehler, E.J. (2007) A new approach to selecting Marine Protected Areas (MPAs) in the Southern Ocean. *Antarctic Science,* **19,** 189-194.

Hatch, S.A., Gill, V.A. & Mulcahy, D.M. (2010) Individual and colony-specific wintering areas of Pacific northern fulmars (Fulmarus glacialis). *Canadian Journal of Fisheries and Aquatic Sciences,* **67,** 386-400.

Hebblewhite, M. & Haydon, D.T. (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **365,** 2303-2312.

Hindell, M.A., Bradshaw, C.J.A., Sumner, M.D., Michael, K.J. & Burton, H.R. (2003) Dispersal of female southern elephant seals and their prey consumption during the austral summer: relevance to management and oceanographic zones. *Journal of Applied Ecology,* **40,** 703-715.

Lewis, S., Schreiber, E.A., Daunt, F., Schenk, G.A., Orr, K., Adams, A., Wanless, S. & Hamer, K.C. (2005) Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis,* **147,** 408-414.

Lewison, R., Oro, D., Godley, B.J., Underhill, L., Bearhop, S., Wilson, R.P., Ainley, D., Arcos, J.M., Boersma, P.D., Borboroglu, P.G., Boulinier, T., Frederiksen, M., Genovart, M., Gonzalez-Solis, J., Green, J.A., Gremillet, D., Hamer, K.C., Hilton, G.M., Hyrenbach, K.D., Martinez-Abrain, A., Montevecchi, W.A., Phillips, R.A., Ryan, P.G., Sagar, P., Sydeman, W.J., Wanless, S., Watanuki, Y., Weimerskirch, H. & Yorio, P. (2012) Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research,* **17 (2),**93-121.

Louzao, M., Hyrenbach, K.D., Arcos, J.M., Abello, P., Gil De Sola, L. & Oro, D. (2006) Oceanographic habitat of an endangered Mediterranean procellariiform: Implications for marine protected areas. *Ecological Applications,* **16,** 1683-1695.

McDonald, B.I. & Crocker, D.E. (2006) Physiology and behavior influence lactation efficiency in northern elephant seals (Mirounga angustirostris). *Physiological and Biochemical Zoology,* **79,** 484-496.

McLeay, L.J., Page, B., Goldsworthy, S.D., Paton, D.C., Teixeira, C., Burch, P. & Ward, T. (2010) Foraging behaviour and habitat use of a short-ranging seabird, the crested tern. *Marine Ecology-Progress Series,* **411,** 271-283.

Nicholls, D.G., Robertson, C.J.R. & Naef-Daenzer, B. (2005) Evaluating distribution modelling using kernel functions for northern royal albatrosses (Diomedea sanfordi) at sea off South America. *Notornis,* **52,** 223-235.

Orians, G.H., AND Pearson, N. E (1979) *On the theory of central place foraging, in "Analysis of Ecological Systems,"* Ohio State Univ. Press, Columbus, Ohio.

Page, B., McKenzie, J., Sumner, M.D., Coyne, M. & Goldsworthy, S.D. (2006)

Spatial separation of foraging habitats among New Zealand fur seals. *Marine Ecology-Progress Series,* **323,** 263-279.

Pichegru, L., Gremillet, D., Crawford, R.J.M. & Ryan, P.G. (2010) Marine no-take zone rapidly benefits endangered penguin. *Biology Letters,* **6,** 498-501.

Quintana, F., Wilson, R., Dell'Arciprete, P., Shepard, E. & Gomez Laich, A. (2011) Women from Venus, men from Mars: inter-sex foraging differences in the imperial cormorant Phalacrocorax atriceps a colonial seabird. *Oikos,* **120,** 350-358.

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Row, J.R. & Blouin-Demers, G. (2006) Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia***,** 797-802.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. (1999) Effects of sample size on kernel home range estimates. *Journal of Wildlife Management,* **63,** 739-747.

Skern-Mauritzen, M., Kirkman, S.P., Olsen, E., Bjorge, A., Drapeau, L., Meyer, M.A., Roux, J.P., Swanson, S. & Oosthuizen, W.H. (2009) Do inter-colony differences in Cape fur seal foraging behaviour reflect large-scale changes in the northern Benguela ecosystem? *African Journal of Marine Science,* **31,** 399-408.

Soanes, L., Gauvain, R., Atkinson, P. & Green, J. (2013) Individual consistency in the forgaing behaviour of Northern gannets: implications for interactions with offshore renewable energy developments. *Marine Policy,* ***38,*** 505-514.

Sumner, M.D. (2011). trip: Spatial analysis of animal track data. R package version 1.1-10.

Taylor, F., Terauds, A. & Nicholls, D. (2004) Tracking ocean Wanderers: *the global distribution of albatross and petrels. Results from the global Procellariform Tracking Workshop 1-5 September 2003. Gordon's Bay, South Africa.* Birdlife International, Cambridge.

Thaxter, C.B., Daunt, F., Hamer, K.C., Watanuki, Y., Harris, M.P., Gremillet, D., Peters, G. & Wanless, S. (2009) Sex-specific food provisioning in a monomorphic seabird, the common guillemot Uria aalge: nest defence, foraging efficiency or parental effort? *Journal of Avian Biology,* **40 (1),** 75-81**.**

Trebilco, R., Gales, R., Baker, G.B., Terauds, A. & Sumner, M.D. (2008) At sea movement of Macquarie Island giant petrels: Relationships with marine protected areas and Regional Fisheries Management Organisations. *Biological Conservation,* **141,** 2942-2958.

Votier, S.C., Grecian, W.J., Patrick, S. & Newton, J. (2011) Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology,* **158,** 355-362.

Wakefield, E.D., Phillips, R.A. & Matthiopoulos, J. (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology-Progress Series,* **391,** 165-182.

Weimerskirch, H., Shaffer, S.A., Tremblay, Y., Costa, D.P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K. & Aurioles, D. (2009) Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Marine Ecology-Progress Series,* **391,** 267-278.

Wilson, L.J., McSorley, C.A., Gray, C.M., Dean, B.J., Dunn, T.E., Webb, A. & Reid, J.B. (2009) Radio-telemetry as a tool to define protected areas for seabirds in the marine environment. *Biological Conservation,* **142,** 1808-1817.

Wilson, R.P., Putz, K., Peters, G., Culik, B., Scolaro, J.A., Charrassin, J.B. & RopertCoudert, Y. (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin,* **25,** 101-106.

Worton, B.J. (1989) Kernel methods for estimating for utilization distribution in home-range studies. *Ecology,* **70,** 164-168.

Yorio, P. (2009) Marine protected areas, spatial scales, and governance: implications for the conservation of breeding seabirds. *Conservation Letters,* **2,** 171-178.

Yorio, P., Quintana, F., Dell'Arciprete, P. & Gonzalez-Zevallos, D. (2010) Spatial overlap between foraging seabirds and trawl fisheries: implications for the effectiveness of a marine protected area at Golfo San Jorge, Argentina. *Bird Conservation International,* **20,** 320-334.

Young, H.S., Shaffer, S.A., McCauley, D.J., Foley, D.G., Dirzo, R. & Block, B.A. (2010) Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. *Marine Ecology-Progress Series,* **403,** 291-301.

Zavalaga, C.B., Halls, J. & Dell'Omo, G. (2010) Marine habitat use of Peruvian boobies: a geographic and oceanographic comparison between inshore and offshore islands. *Ices Journal of Marine Science,* **67,** 940-951.

Supporting Information

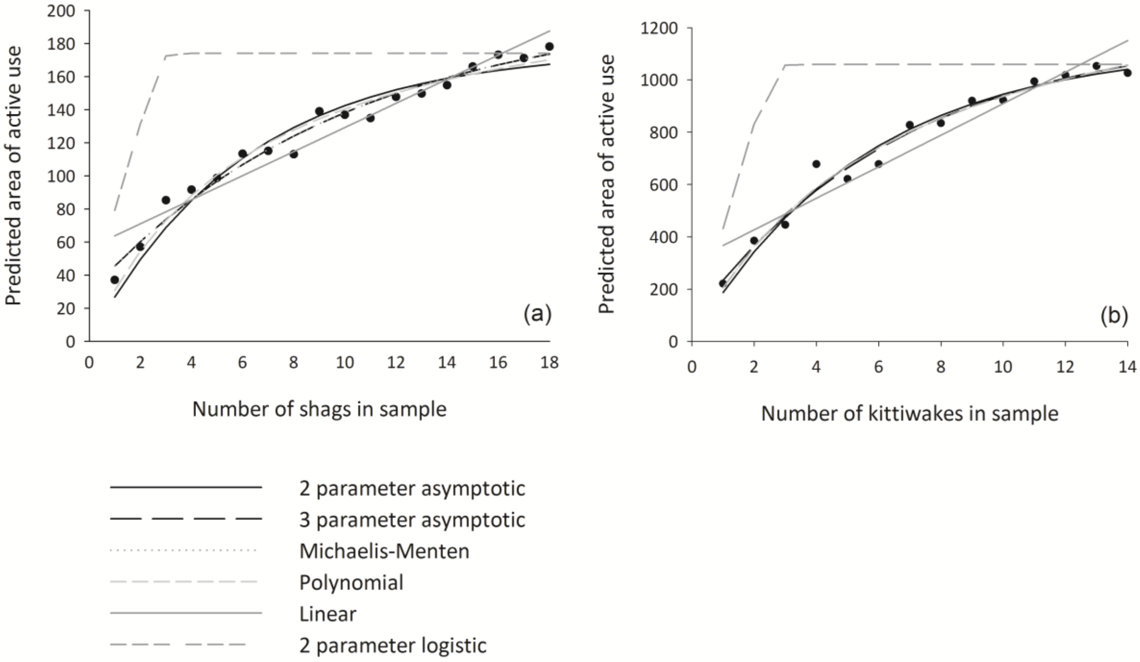


Figure S1. Example of the fit of the tested models to foraging data representing the areas of active use (km^2).

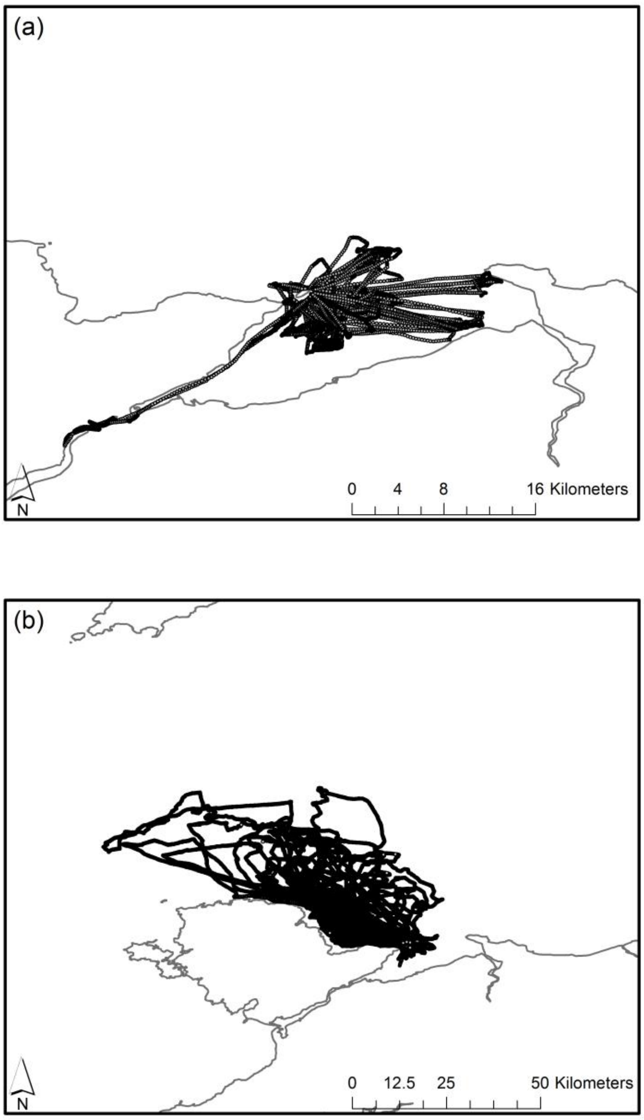


Figure S2. Actual foraging trips plotted for (a) European shag and (b) Black-legged kittiwake.

Table S1. The AIC values of different models tested with data representing the area of active use (AAU) and core foraging areas (CFA).

Shags	**Model equation**	**CFA 1st Trip**	**AAU 1st Trip**	**CFA Trips 1-2**	**AAU Trips 1-2**	**CFA Trips 1-3**	**AAU Trips 1-3**	**CFA 4 trips**	**AAU 4 trips**
2-parameter asymptotic	$y = a(1 - e^{bx})$	42.6	104.6	31.9	95.0	30.5	103.2	45.8	134.1
3-parameter asymptotic	$y = a - be^{-cx}$	39.9	105.6	28.3	89.9	25.1	96.3	40.4	125.6
Michaelis - Menten	$y = \frac{ax}{b + x}$	41.6	102.4	27.8	89.9	18.6	86.7	40.3	124.4
Linear	$y = a + bx$	50.9	128.7	43.0	138.6	56.4	141.5	61.3	140.1
Polynomial	$y = a + x - x^2$	43.6	110.2	30.2	108.6	19.9	114.3	43.5	128.1
2-parameter logistic	$y = \frac{e^{a+bx}}{1 + e^{1+bx}}$	50.7	115.3	37.4	112.4	28.7	116.2	50.6	133.7
Kittiwakes									
2-parameter asymptotic	$y = a(1 - e^{bx})$	62.3	120.4	78.8	128.9	97.4	153.9	90.4	150.0
3-parameter asymptotic	$y = a - be^{-cx}$	61.4	120.1	77.6	129.8	96.8	153.5	86.4	148.0
Michaelis - Menten	$y = \frac{ax}{b + x}$	61.2	122.0	77.7	128.8	96.1	153.0	83.9	149.7
Linear	$y = a + bx$	61.3	130.6	80.6	147.08	96.2	155.3	92.51	166.2
Polynomial	$y = a + x - x^2$	61.6	122.2	77.6	129.08	96.8	153.6	84.2	150.5
2-parameter logistic	$y = \frac{e^{a+bx}}{1 + e^{1+bx}}$	64.5	128.4	78.0	134.88	97.6	157.1	85.2	154.2

Table S2. Parameter estimates (with 95% confidence intervals) for Michalis-Menten model

	Shag CFA		Shag AAU		KI CFA		KI AAU	
	a	b	a	b	a	b	a	b
Trip 1	24.3 (20.9-29.6)	12.8 (7.7-21.5)	149.8 (136.4-164.6)	9.1 (6.23-12.4)	66.7 (49.5-80.9)	12.2 (3.67-32.5)	992.0 (783.6-2204.3)	18.5 (10.7-59.5)
Trips 1-2	25.04 (21.6-26.4)	10.7 (7-13.6)	161.9 (160.1-163.9)	6.3 (5.2-7.1)	67.9 (66.0-139.6)	7.0 (3.4-32.7)	1768.3 (1374.1-3320.6)	16.6 (9.5-43.2)
Trips 1-3	25.7 (23.8-29.0)	9.2 (6.8-13.2)	178.4 (174.3-180.0)	5.3 (4.5-6.1)	93.1 (87.6-165.6)	6.6 (3.6-24.0)	2068.3 (1786.2-2916.2)	16.0 (15.1-22.4)
Trips 1-4	28.4 (26.6-32.2)	9.1 (6.6-13.4)	231.5 (217.3-236.7)	6.5 (4.6-8.1)	108.6 (102.5-144.3)	4.5 (2.35-11.6)	1550.7 (1445.5-1853.8)	6.6 (4.8-10.5)

Chapter 3

Identifying the key foraging areas of seabirds breeding in the Caribbean

Soanes, L.M.[a], Bright, J.A,[b], Bolton, M.[b], Millett, J.[b], Muhkida, F.[c], Green, J.A.[a]

[a] School of Environmental Sciences, University of Liverpool, L69 3GP, UK.[b] Royal Society for the Protection of Birds, Sandy, Bedfordshire, SG19 2DL, UK. [c] Anguilla National Trust, P.O. Box 1234, The Valley, AI-2640 Anguilla, British West Indies.

Manuscript in review Biological Conservation International (2013)

Photograph by Louise Soanes 2012

Author contributions: LMS & JAB planned the project, FM, JM & MB contributed to organisation and logistics of the fieldwork, LMS & JAB conducted fieldwork, LMS analysed and wrote the manuscript with support from JAG & JAB.

Abstract

Seabird populations breeding in Caribbean UK Overseas Territories are relatively under-studied compared to UK seabird populations despite many being of international importance. Here we present the results of one of the first seabird tracking studies in the Caribbean region of the Lesser Antilles. Brown boobies breeding on the Important Bird Area (IBA) of Dog Island, Anguilla were tracked using GPS devices for 5-7 days during the chick-rearing period, to identify important foraging areas and to determine any differences in foraging behaviour between males and females. Foraging trips were on average 125.3 ± 54.4 (SD) km long and lasted for an average duration of 5.6 ± 1.95 (SD) hrs. Foraging areas extended outside Anguilla's territorial waters to the neighbouring islands of Saint Barthélemy, Saba and Sint Maarten/Saint Martin. The sexes differed in the direction travelled, and the total distance travelled by males was longer than that of females. However, trip duration and maximum foraging range from the colony of males did not exceed that of females indicating that males spent a higher proportion of their foraging trip time in flight. Our analysis suggests that our sample of 16 tracked individuals of a population of 1231 pairs identifies 64% of the core foraging area and 38% of the area of active use. We suggest that 121 (CI 61-421) individuals would be required to accurately predict 95% of the core foraging area of the colony and 417 (CI 262-672) individuals would be required to predict 95% of the area of active use.

Introduction

The tracking of seabirds has become an increasingly widespread tool to help identify and define the conservation priorities for seabird species and populations around the world (Burger and Shaffer, 2008, Lewison *et al*., 2012). Such studies have been able to reveal important information on summer (Hamer *et al*., 2007) and winter foraging areas and migration routes (Bugoni *et al*., 2009). These in turn can define important habitat types (Wakefield *et al*., 2011, McLeay *et al*., 2010), identify the possible impacts of marine renewable energy developments (Soanes *et al*., 2012a) and aid in the designation and/or monitoring of marine protected areas (Pichegru *et al*., 2010, Trebilco *et al*., 2008). Tracking studies also allow comparisons of the foraging behaviour of individuals within a population (Hatch *et al*., 2010), as well as the differences between males and females (Lewis *et al*., 2005, Quintana *et al*., 2011) and age classes (Votier *et al*., 2011).

The 14 UK Overseas Territories (hereafter ‘UKOTs’) include 13 geographically distinct oceanic islands or archipelagos. These are located in the Caribbean (5), Atlantic Ocean (6), Indian Ocean (1) and Pacific Ocean (1), as well as including the territories of Gibraltar, Cyprus Sovereign Base Areas and the British Antarctic Territory. The UKOTs contain 78 terrestrial Important Bird Areas (IBAs) and support breeding populations of 34 globally threatened bird species and many internationally important populations of seabirds (Sanders 2006).

In the UK, initiatives such as the Seabird Monitoring Programme and the Seabirds at Sea programme (JNCC, 2011), coupled with the demands of the Environmental Impact Assessment (EIA) process prior to marine renewable energy developments, ensure that breeding seabirds in the UK are relatively well monitored and studied. However, seabird populations breeding within the UKOTs receive far less attention, primarily due to financial and logistical constraints. Hilton & Cuthbert (2010) state that “the UKOTs’ biodiversity remains surprisingly obscure in the scientific literature, and according to recent environmental reports of the UK legislature receives rather little attention from the UK Government”. However, the threats facing seabirds breeding on the UKOTs are as great, if not greater than those facing UK seabird populations and include the effects of introduced species such as rats and goats (Hilton and Cuthbert, 2010), habitat degradation (Croxall *et al*., 2012), changes in fishery practice (Bertrand *et al.*, 2012) and climate change (Gremillet and Boulinier, 2009).

In recent years, the utility of identifying IBAs in the marine environment has been recognised to highlight priority areas for seabird conservation, and inform discussions on marine protected areas and marine spatial planning. Capturing the key near-colony feeding areas of breeding seabirds within the IBA network is one obvious approach. BirdLife International has promoted the use of seaward extensions around existing IBA breeding sites for seabirds, based on literature reviews of the known foraging ranges of a species, to capture most of the key foraging habitat required by a colony in a repeatable fashion. This approach uses empirical data on the foraging behaviour of species recorded at one site to estimate or model the foraging behaviour at other sites for the same species (Birdlife International 2010). This approach relies on the foraging data defined for the species being truly representative, which may not be the case if only small sample sizes are used (Soanes *et al*., 2013, Lindberg and Walker, 2007) as such site specific data will always be preferable if possible.

The Island group of the Lesser Antilles in the Caribbean (Fig. 3.1) are of international importance for breeding seabirds (Lowrie *et al*., 2012) with 49 IBAs in this region classified due to the presence of globally or regionally important seabird populations or because they support in excess of 10,000 breeding pairs of seabirds. Seven of these seabird IBAs are located in the UKOT of Anguilla. Marine IBAs (seawards extensions around colonies) have been defined for these sites based on generic foraging radii but have not yet been refined using site specific observations or tracking data.

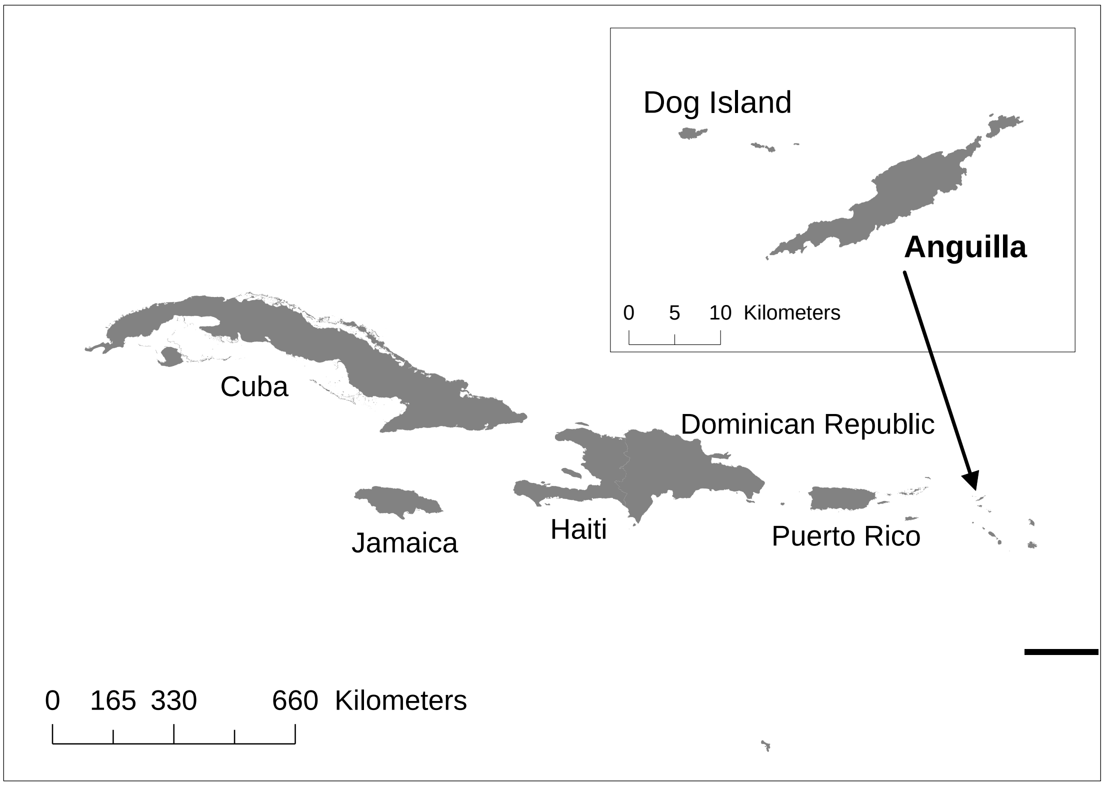


Figure 3.1. Location of Anguilla (Source: ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

This paper presents data from one of the first tracking studies conducted on breeding seabirds in the Lesser Antilles. Work was conducted on Dog Island, a small offshore island of Anguilla that qualifies as an IBA (Birdlife, 2012). Dog Island supports nine breeding seabird species, with globally-significant populations of Sooty tern *Sterna fuscata*, Brown booby *Sula leucogaster* and Laughing gull *Larus artricilla*, and is considered to be the second most important individual island for globally-significant seabird colonies in the eastern Caribbean (Lowrie *et al*., 2012). A marine extension to the Dog Island IBA was designated in 1993 and encompasses an area of 1km extending around the island.

Brown Boobies, breeding on Dog Island, were GPS tracked during their peak chick-rearing period with the aims of:

(1) Providing preliminary information on foraging behaviour.
(2) Assessing differences in the foraging behaviour of males and females.
(3) Identifying how many individuals should be tracked from the colony to reliably define important foraging areas for the chick-rearing period

Methods

Fieldwork was conducted on Dog Island, Anguilla (18°16’N, 63°15’W) from the 27th March- 4th April 2012. Twenty breeding Brown boobies, which had nests containing chicks that were 4-5 weeks old, were captured whilst at their nests, using a crooked pole. GPS data loggers (IgotU G120, Mobile Action, Taiwan) were waterproofed with heat-shrink PVC tubing and attached to the birds’ central 2-3 tail feathers with Tesa ® Extra Power tape (Wilson *et al* 1997). Tags weighed c. 17g which represents 1.5% of the birds’ body weight. Tags were scheduled to record GPS locations every two minutes. Sex was determined using bill colour, with the bill of females having a pink tinge and male bills having a blue tinge (Weimerskirch *et al*., 2009). The data loggers were retrieved 5-7 days later once the batteries were exhausted.

For each foraging trip the total duration (hrs), total distance (km), and maximum distance travelled from the breeding colony (km) were calculated using Arcmap (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). Differences between males and females in these parameters were analysed using GLMM in Minitab (Minitab 16 Statistical Software 2010.) which included ID as a random factor. The circular statistic software Oriana for Windows and the Watsons’ U^2 test (Batschelet, 1981) were used to analyse any differences in the direction travelled between males and females, with direction travelled determined as the bearing of the furthest GPS location from the colony on each foraging trip.

The R package *Trip* (Sumner, 2011), which creates a grid of time spent in pre-defined cells. Grid cells of 2 x 2 km were defined to represent area use, based on the extensive foraging range of this species. The “area of active use” was defined as the total number of 2 x 2 km grid cells used, and the “core foraging areas” were defined as the number of 2 x 2 km grid cells which were most used and included cells where 50% of all time spent when cells were ranked in order of seconds spent in each cell (Worton, 1989; Soanes *et al*. 2013b). We assumed an asymptotic relationship between the numbers of birds’ tracked and total extent of these two areas to evaluate how representative our sample of tracked birds was in estimating the extent of the areas used by the entire colony during the period of the study (Soanes *et al*., 2013b). We used a bootstrapping procedure (BirdLife, 2010), implemented in the R package *Boot* (Canty & Ripley 2007), to randomly resample the foraging areas (the number of

2 x 2 km squares used) of between 2 and 16 individuals included in a sample. Multiple trips were included as this gives more information on the size of a population's foraging area (Soanes *et al.*, 2013b) therefore we restricted the analysis to the first three trips per individual, and to the 16 individuals which made at least three trips. Data (predicted areas of use from each sample of individuals) were re-sampled 10 000 times and 95% confidence limits estimated as the 2.5th and 97.5th percentiles. The number of grid cells used was plotted against the number of individuals in the sample and the best fitting aymptotic non-linear model was fitted to the data using R (R Development Core Team 2008). For this population the most appropriate model based on AIC values was the Michaelis-Menten model (Equation 1). The size of the area used by the entire colony was estimated by extrapolating the non-linear model functions to estimate the whole colony's area of active use and core foraging areas based on a population size of 1231 pairs (Bright and Soanes, 2013), see Soanes *et al.* (2013b) for more detailed methodology.

Equation 1: *Michaelis-Menten model:*

$$y = \frac{ax}{b + x}$$

Where a=the asymptotic value of the y axis, and b=the value of x at which half of the maximum response is attained.

We then plotted the relationship between number of birds and area, with area expressed as a percentage of these extrapolated whole-colony estimates. This enabled us to evaluate how effective our sample was in measuring the extent of the areas used by the entire colony.

The home-range area asymptote prediction derived from the Michelis-Menten model was also compared to the predicted area available to the boobies breeding at Dog island based on the maximum distance travelled by a bird (using the formula: πr^2).

Results

Of 20 loggers deployed, 19 were retrieved. The remaining bird was re-sighted but evaded capture. Females weighed on average 1375 (± 77) g and males 1062 (± 69) g on initial capture. Individuals made between 2-7 foraging trips during the 5-7 day tracking period with 16 birds making at least three foraging trips which were used for the re-sampling analysis (as a compromise between including the most birds and individual foraging trips in the sample). The individual foraging tracks and the core foraging areas (the 2 x 2 km cells where birds spent more than 50% of their time) are shown in Figure 3.2.

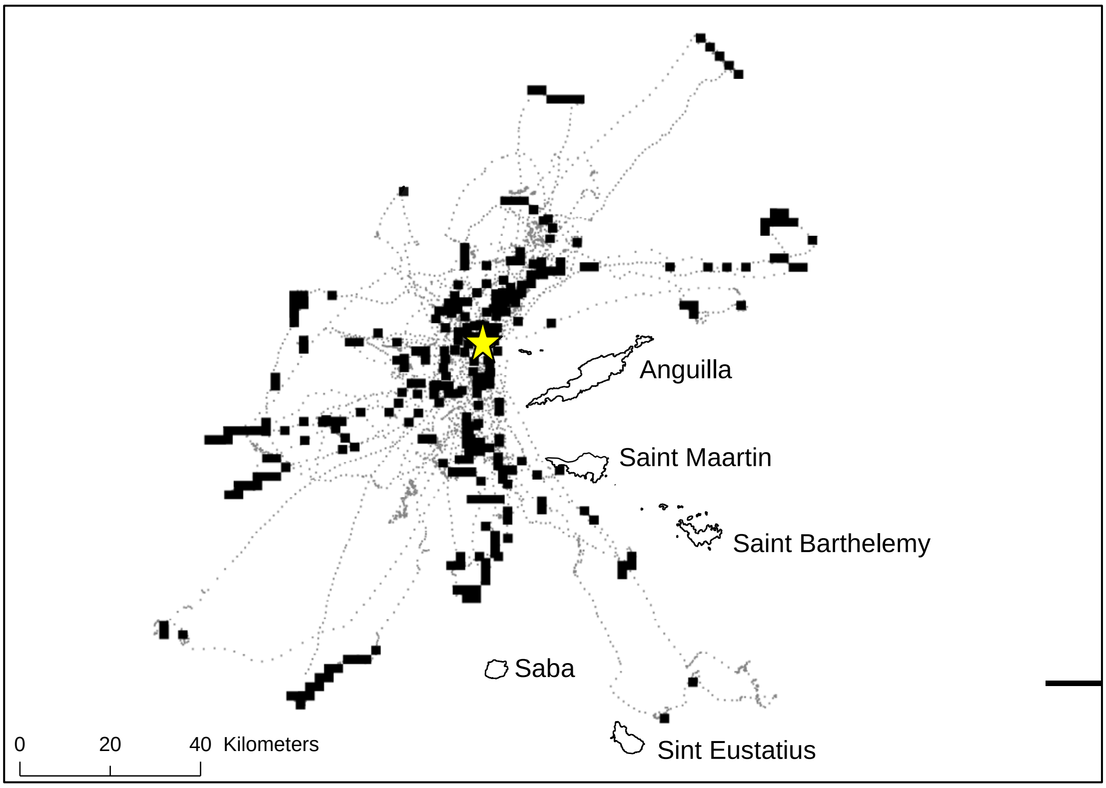


Figure 3.2. Core foraging areas (black squares) of each foraging trip made by 16 Brown boobies breeding on Dog Island. Individual foraging tracks are also shown (grey points). Location of breeding colony indicated by ★

Mean foraging trip distance, and the maximum distance travelled of the 19 birds tracked were found to be longer than the foraging behaviour of this species recorded in a previous study in Mexico for a similar size colony of Brown boobies (Weimerskirch *et al.*, 2009) (Table 3.1).

Table 3.1. Mean (± standard deviation) foraging trip duration, maximum distance from colony and total distance (sample size given in brackets), travelled by Brown boobies on Dog Island and another study colony. *Weimerskirch *et al*.(2009).

	Mean trip duration (hrs)		Mean maximum distance from colony (km)		Mean total distance (km)	
	males	females	males	females	males	females
Isla San Ildefonso, Mexico*	2.0 ± 1.0 (14)	3.0 ± 1.3 (17)	16.6 ± 14.3 (9)	39.2 ± 16.6 (11)	50.9 ± 31.5 (8)	105.6 ± 45.9 (11)
Dog Island	5.8 ± 2.7 (7)	5:4 ± 1.8 (12)	52.9 ± 25.1 (7)	43.8 ± 12.6 (12)	152.1 ± 80 (7)	105.9 ± 2 (12)

Mean foraging trip duration, and the maximum distance travelled from the colony were not significantly different ($F_{(1, 17)}$ = 0.01, p = 0.915 and $F_{(1,17)}$ = 1.45, p = 0.240 respectively) between males and females. However, the trip total distance and direction travelled by males and females was found to be significantly different (F $_{(1,17)}$ = 4.65, p = 0.042 and $U^2_{(21)}$ = 0.174, 30, p > 0.05 respectively). Males had a greater total trip distance than females, with females having a stronger tendency to travel south-west of Dog Island and males north-east of the island (Fig. 3.3 & 3.4).

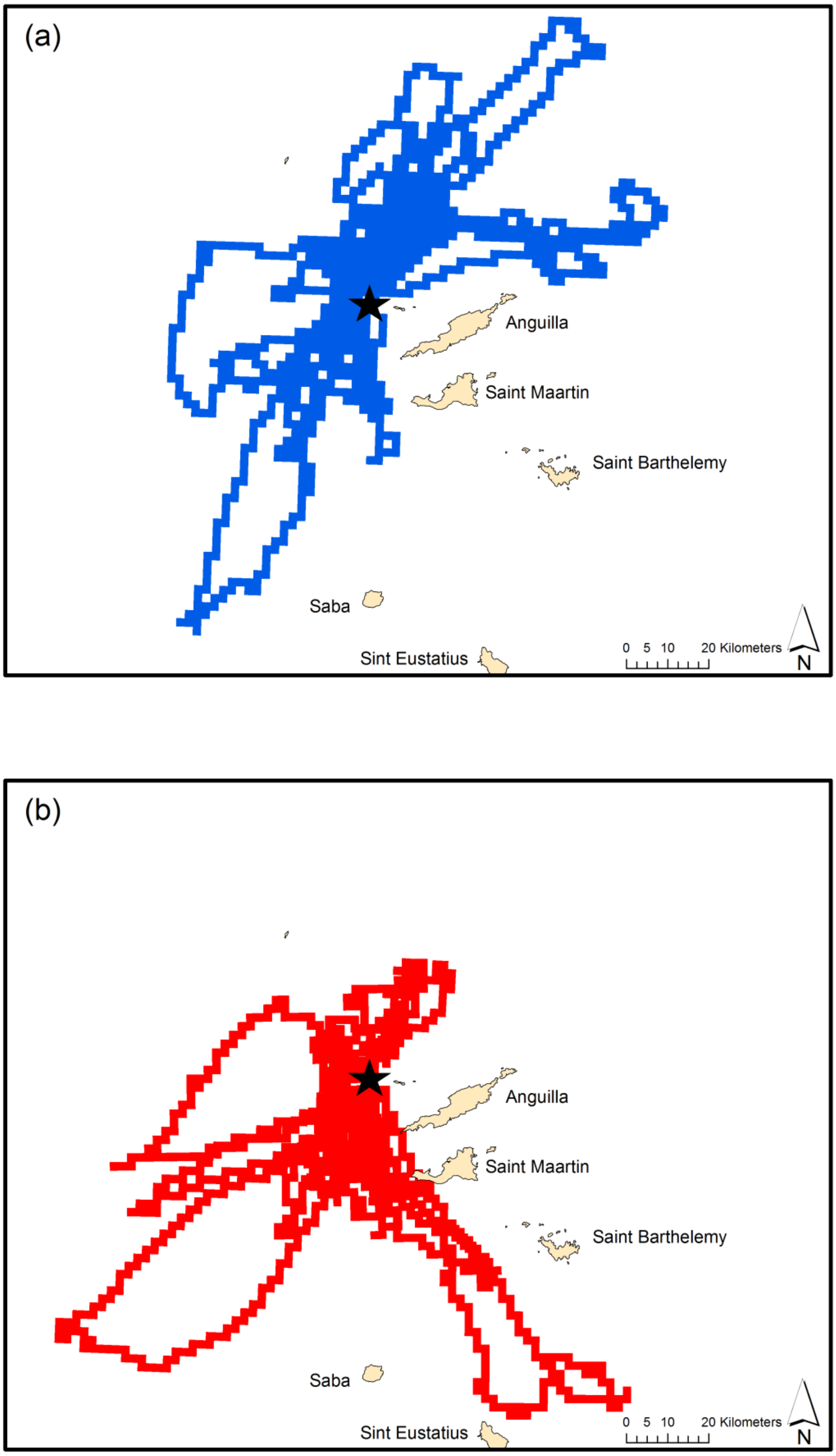


Figure 3.3. Area of active use of (a) the first three trips of seven male Brown boobies (b) the first three trips of nine female Brown boobies. Dog island is indicated by ★

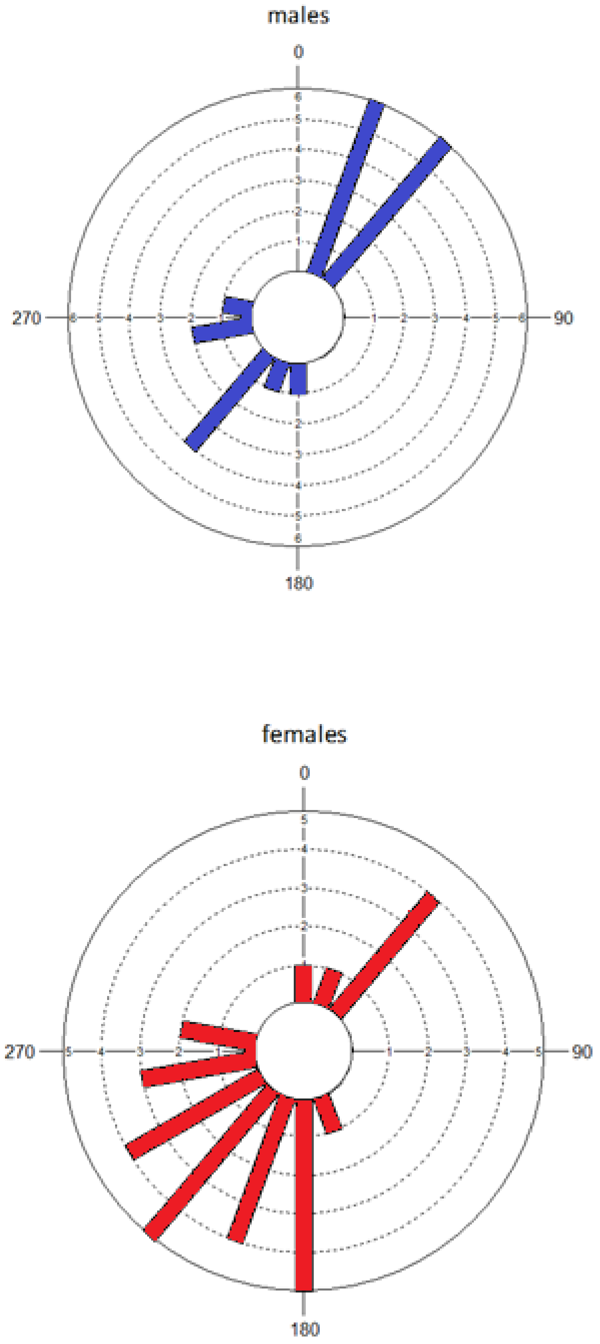


Figure 3.4. The direction travelled on each of the first three foraging trips of seven male Brown boobies and nine female Brown boobies.

The maximum area available to the colony derived from the maximum distance travelled from birds within our tracking sample (max. distance = 100km) was calculated as 31400 km^2. On the basis of the extrapolated predictions of our model, we estimate that the size of the area of active use used by the entire population during the time of our study was 13663 km^2 and the core foraging area was 145 km^2 In other words, the birds spent 50% of their time in just 1 % of the entire area used. To further test the models predictions we used the area prediction to calculate the expected foraging range of birds from the colony by re-arranging the πr^2 equation. This gave an estimated foraging radius of 66 (± 57-81) km from the breeding colony. Which is not dissimilar to the actual foraging ranges recorded (Table 3.1).

We plotted areas of active use and core foraging expressed as a percentage of the estimated areas used by the entire colony as a function of sample size (Fig. 3.5). It is clear from this graph that the modelled asymptotic curve is still rising steeply when up to 16 individuals have been included in the sample. Rearrangement of the Michaelis-Menten equation allows us to predict how many birds should be sampled to assess a greater proportion of the home range area used by the population. Table 3.2 shows that many more birds would be needed to confirm the area of active use and the core foraging area.

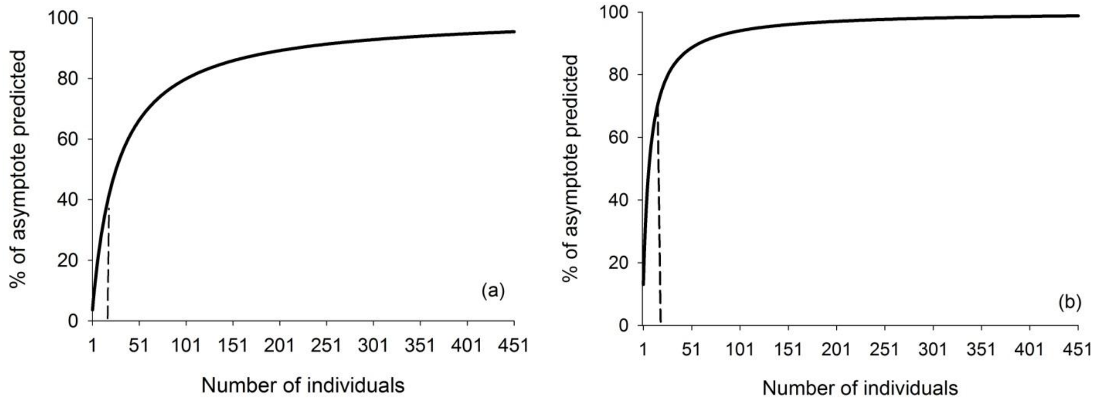


Figure 3.5. The number of individuals from the Brown booby colony required to predict 100% of the asymptotic value of the number of 2 x 2 km^2 cells used for (a) the area of active use and (b) core foraging area. Values before the dashed lines are based on birds tracked (16 individuals); past this point values are extrapolated (based on parameters derived from Equation 1).

Table 3.2. The number of individuals required to predict 50% and 95% of the area of active use and core foraging areas of Brown boobies breeding on Dog Island, based upon a population size of 1231 pairs (Bright and Soanes, 2013) and using the model parameters derived from equation 1. Confidence intervals are shown in brackets.

Number of individuals required to predict:			
Area of active use		Core foraging area	
50%	**95%**	**50%**	**95%**
26 (15-48)	417 (262-672)	7 (3-27)	121 (61-421)

Discussion

Our sample of 19 birds tracked during 2012 provides a good basis for further work on this population. Our data revealed that very few trips were targeted in the same foraging areas suggesting little consistency between and within individuals in their foraging trips. The areas identified from the first three foraging trips of 16 individuals revealed 38% of the colony's area of active use and 64% of the core foraging area used by the colony. To obtain more information on the location of areas of active use and the core foraging areas of the whole colony a greater number of individuals should be tracked, with 417 (CI 267-672), and 121 (CI 61-421) individuals required to accurately predict 95% of the area of active use and the core foraging area respectively. Including a greater number of foraging trips made by each individual in the analysis would likely reduce the number of individuals required to accurately predict the foraging areas of the colony (Soanes *et al.* 2013b). However, the low-cost GPS data loggers commonly used in tracking studies have limited battery life so for far-ranging species such as the Brown booby this may not always be possible. This analysis highlights the need to quantify the limitations of small data sets (a common feature in tracking studies) and not to place too much emphasis on preliminary results without first understanding how representative they may be of the whole population. It should also be emphasised that this tracking study was conducted over 5-7 days of the peak chick-rearing period, but this species is a year-round breeder, therefore concentrations of foraging activity should be examined at different times of the year, covering different life-history stages, to fully evaluate area use.

Males showed a longer track length on their foraging trips than females but did not range further from the colony and their trip duration was not longer. This indicates that males had more circuitous routes than females, which is contrary to the findings of Gilardi (1992) and Weimerskirch *et al.* (2009) who found that females had significantly longer trips than males in both duration and distance; but similar to the findings of Lewis *et al.* (2005) who reported that males made significantly longer trips than females. The direction travelled by males and females was significantly different, perhaps indicating different foraging strategies used by males and females related to sexual dimorphism. Further work should link environmental variables such as bathymetry to the foraging areas of males and females. A larger and more representative sample would also allow us to assess to what extent males and females have distinct foraging areas.

The foraging areas used by this population are varied and are located in the territorial waters not just of Anguilla but also neighbouring islands of Saint Eustatius and Saba (territories of the Netherlands), Saint Barthélemy (territory of France) and Saint Maarten/Saint Martin (territory of France and the Netherlands). Multi-regional protection of the foraging areas of such wide ranging species presents a challenge to governments and environmental organisations but needs to be addressed if successful conservation is to be achieved. Initiatives such as the Nature Conservancy’s “Caribbean Challenge” are trying to tackle marine protection on a multi-national scale in the Caribbean region. This initiative is a large-scale programme advocated by a number of governments and regional and international organizations which aims to protect 20% of the marine and coastal habitats of Caribbean countries associated with the initiative by 2020. The Caribbean’s Large Marine Ecosystem (CLME) project also assists and encourages participating countries from the Wider Caribbean Region to improve the management of their shared Living Marine Resources. The results from this study, and seabird tracking datasets more generally, will be relevant to such multi-regional initiatives.

With the increasing global pressures being placed on our marine ecosystems through activities such as fisheries, and more recently marine renewable energy development, it is vital to understand the foraging behaviour and important foraging areas of breeding seabird populations if negative interactions are to be avoided. Accurate and representative distributional information is essential to either monitoring how foraging behaviour varies over time or to aid species protection via the designation of marine protected areas. Gathering more information on the seabird populations breeding in the UKOTs is particularly important as they remain under-studied in the field of seabird research, despite their global importance.

Acknowledgements

Thanks to Mr Karim Hodge of the Department of Environment and the Government of Anguilla for granting research permissions. Also thanks to the Anguilla National Trust staff and volunteers for logistical support and the Dog Island rat eradication team for making us welcome and supporting our research, in particular Elizabeth ‘Biz’ Bell (Wildlife Management International Ltd.). Thanks also to Steve Holliday, Colin Wilkinson and Steffen Oppel for advice on planning the fieldwork.

References

Batschelet, E. (1981) *Circular statistics in biology,* New York.

Bertrand, S., Rocıo, J., Arbulu Smet, C., Tremblay, Y., Barbraud, C. & Weimerskirch, H. 2012. Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology,* **49:** 1365-2664.

BirdLife International. 2010. Marine Important Bird Areas toolkit: standardised techniques for identifiing priority sites for the conservation of seabirds at sea. (ed. B. International). Cambridge, UK.: Birdlife International.

Birdlife International. 2012. Important Bird Areas in the Caribbean: key sites for conservation. Birdlife International.

Bright, J. & Soanes, L. 2013. Baseline seabird surveys on Dog Island following rat eradication. *Journal of Caribbean Ornithology,* **in press.**

Bugoni, L., D'Alba, L. & Furness, R. W. 2009. Marine habitat use of wintering spectacled petrels Procellaria conspicillata, and overlap with longline fishery. *Marine Ecology-Progress Series,* **374:** 273-285.

Burger, A. E. & Shaffer, S. A. 2008. Application of tracking and data-logging technology in research and conservation of seabirds. *Auk,* **125:** 253-264.

Canty, A. & Ripley, B. (2011). boot: Bootstrap R (S-Plus) Functions. R package version 1.3- 2.

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A. & Taylor, P. 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International,* **22:** 1-34.

Gilardi, J. D. 1992. Sex-specific foraging distributions of Brown Boobies in the Eastern Tropical Pacific. *Colonial Waterbirds,* **15**.

Gremillet, D. & Boulinier, T. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. *Marine Ecology-Progress Series,* **391:** 121-137.

Hamer, K. C., Humphreys, E. M., Garthe, S., Hennicke, J., Peters, G., Gremillet, D., Phillips, R. A., Harris, M. P. & Wanless, S. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology-Progress Series,* **338:** 295-305.

Hatch, S. A., Gill, V. A. & Mulcahy, D. M. 2010. Individual and colony-specific wintering areas of Pacific northern fulmars (Fulmarus glacialis). *Canadian Journal of Fisheries and Aquatic Sciences,* **67:** 386-400.

Hilton, G. M. & Cuthbert, R. J. 2010. The catastrophic impact of invasive mammalian predators on birds of the UK Overseas Territories: a review and synthesis. *Ibis,* **152**.

JNCC. 2011. Seabird Population Trends and Causes of Change: 2011 Report. (http://www.jncc.gov.uk/seabirds2011).

Lewis, S., Schreiber, E. A., Daunt, F., Schenk, G. A., Orr, K., Adams, A., Wanless, S. & Hamer, K. C. 2005. Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis,* **147:** 408-414.

Lewison, R., Oro, D., Godley, B. J., Underhill, L., Bearhop, S., Wilson, R. P., Ainley, D., Arcos, J. M., Boersma, P. D., Borboroglu, P. G., Boulinier, T., Frederiksen, M., Genovart, M., Gonzalez-Solis, J., Green, J. A., Gremillet, D., Hamer, K. C., Hilton, G. M., Hyrenbach, K. D., Martinez-Abrain, A., Montevecchi, W. A., Phillips, R. A., Ryan, P. G., Sagar, P., Sydeman, W. J., Wanless, S., Watanuki, Y., Weimerskirch, H. & Yorio, P. 2012. Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research,* **17:** 93.

Lindberg, M. S. & Walker, J. 2007. Satellite telemetry in avian research and management: Sample size considerations. *Journal of Wildlife Management,* **71:** 1002-1009.

Lowrie, K., Lowrie, D. & Collier, N. 2012. Seabird breeding atlas of the Lesser Antilles. Saint Maartin: Environmental Protection in the Caribbean (EPIC).

McLeay, L. J., Page, B., Goldsworthy, S. D., Paton, D. C., Teixeira, C., Burch, P. & Ward, T. 2010. Foraging behaviour and habitat use of a short-ranging seabird, the crested tern. *Marine Ecology-Progress Series,* **411:** 271-283.

Pichegru, L., Gremillet, D., Crawford, R. J. M. & Ryan, P. G. 2010. Marine no-take zone rapidly benefits endangered penguin. *Biology Letters,* **6:** 498-501.

Quintana, F., Wilson, R., Dell'Arciprete, P., Shepard, E. & Gomez Laich, A. 2011. Women from Venus, men from Mars: inter-sex foraging differences in the imperial cormorant Phalacrocorax atriceps a colonial seabird. *Oikos,* **120:** 350-358.

Sanders, S. *Important Bird Areas in the United Kingdom Overseas Territories: Priority Sites for Conservation*: Royal Society for the Protection of Birds.

Soanes, L., Gauvain, R., Atkinson, P. & Green, J. 2013a. Individual consistency in the foraging behaviour of Northern gannets: implications for interactions with offshore renewable energy developments. *Marine Policy, **38***:505-514

Soanes, L., Arnould, J., Dodd, S., Sumner, M. & Green, J. 2013b. How many seabirds do we need to define important foraging areas. *Journal of Applied Ecology*. **50** (3): 671-679.

Sumner, M.D. (2011). trip: Spatial analysis of animal track data. R package version 1.1-10.

Trebilco, R., Gales, R., Baker, G. B., Terauds, A. & Sumner, M. D. 2008. At sea movement of Macquarie Island giant petrels: Relationships with marine protected areas and Regional Fisheries Management Organisations. *Biological Conservation,* **141:** 2942-2958.

Votier, S. C., Grecian, W. J., Patrick, S. & Newton, J. 2011. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology,* **158:** 355-362.

Wakefield, E. D., Phillips, R. A., Trathan, P. N., Arata, J., Gales, R., Huin, N., Robertson, G., Waugh, S. M., Weimerskirch, H. & Matthiopoulos, J. 2011. Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. *Ecological Monographs,* **81:** 141-167.

Weimerskirch, H., Shaffer, S. A., Tremblay, Y., Costa, D. P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K. & Aurioles, D. 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Marine Ecology-Progress Series,* **391:** 267-278.

Worton, B. J. 1989. Kernel methods for estimating for utilization distribution in home-range studies. *Ecology,* **70:** 164-168.

Chapter 4

Individual consistency in the foraging behaviour of Northern gannets: implications for interactions with offshore renewable energy developments.

Soanes, L.M.[a], Gauvain R.D.[b], Atkinson P.W.[c], Green J.A.[a]

[a] School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP, [b] Alderney Wildlife Trust, St Annes, Channel Islands, UK,[c] British Trust for Ornithology, Thetford, Norfolk, UK.

Published in Marine Policy (2013) *38*:505-514

Photograph taken by Jill Pakenham (BTO)

Author contributions: LMS, JAG devised the project, RDG assisted with logistics, LMS, PWA & RDG conducted fieldwork, LMS wrote the manuscript and analysed data with assistance from JAG.

Abstract

With recent EU directives requiring that Europe must achieve 20% of its energy from renewable sources by 2020 the development of offshore wind, tidal and wave technologies is gaining momentum, increasing pressure on our already vulnerable marine systems and organisms. All EU countries are required to have Environmental Impact Assessment (EIA) guidelines in place for such developments and whilst tracking studies of marine predators have been recommended to aid EIAs, they are as yet not a requirement. This study tracked Northern gannets breeding on Les Etacs, a stack immediately offshore Alderney, Channel Islands, to determine their use of both local and international waters and examine the consistency between an individual's foraging trips. The 15 Northern gannets that made at least two foraging trips foraged in three different territorial waters and their combined home-range area overlapped with nine potential offshore marine renewable energy developments. Repeatability between the first and second foraging trips made by an individual was apparent when considering the direction travelled and the maximum distance travelled from the colony, but not when considering trip duration, or the total trip distance suggesting individuals did not appear to be dependent on specific foraging areas. Our findings highlight the need to consider all important seabird colonies which forage in the range of potential offshore developments and to use tracking technology to determine which colonies may be affected by such developments and the colony's dependence on these areas**.** Tracking studies of birds from important seabird colonies should form an integral part of the EIA process for marine renewable developments.

Introduction

The potential capacity of Europe's offshore wind energy generation is enormous and is expected to play a big part in helping EU countries meet the target set by the European Commission for all member states to achieve 20% of their energy from renewable sources by 2020 (Directive 2001/77/EC). The UK is leading the rest of Europe in offshore renewable energy generation with 517MW capacity in place or to be completed by the end of 2011 and industry experts are forecasting that the UK will achieve up to 23GW capacity by 2020 (RenewableUK 2011). Whilst not yet at the same scale of development as offshore wind technology, tidal and wave energy developments are also gaining momentum (Rourke, Boyle & Reynolds 2010). By January 2010 the UK had 0.85MW of wave energy and 1.55MW of tidal stream installed. Due to the technological support available in the UK and the abundant wave and tidal stream resource it is considered that by 2020 a large share of European marine renewable energy installations (MREIs) will be in UK waters (Willow & Valpy 2011).

Due to the short time scale in which offshore wind farms have been developed and the fact that there are very few sites where the effects of MREIs can be assessed there are few scientific studies on the environmental effects such developments may have (Gill 2005). Potential impacts such as the effect that these developments may have on coastal processes (Lampkin *et al.* 2009), on fish and seabed communities (Linley *et al.* 2008), and with reference to birds; direct mortality (Sugimoto & Matsuda 2011), disturbance of feeding areas and displacement (Kaiser *et al.* 2002; Perrow *et al.* 2011), migration routes (Griffin, Rees & Hughes 2010) and costly avoidance behaviours (Perrow *et al.* 2006; Masden *et al.* 2010), have generally been inferred from existing technologies and developments. Any offshore developments in the EU are subject to environmental monitoring which should be undertaken prior to and post installation of devices (Holmes 1997b). In the UK the Crown Estate has an established research body, the Collaborative Offshore Wind Research into the Environment (COWRIE), to develop and test the guidelines for environmental monitoring for offshore MREIs. COWRIE have set strict standards and guidelines for the boat-based and aerial monitoring of seabirds and cetaceans in potential test site areas based on the methodology of Camphuysen *et al.* (2004) and more recently refined by Maclean *et al.* (2009) Any potential MREI developments in the UK are required to meet these standards before consent for development is granted.

Due to the availability of new and more affordable technologies such as thermal cameras, satellite and GPS data loggers, radar etc. and the increased use of such technology in the monitoring of marine organisms (Johnson *et al.* 2002; Gauthreaux & Livingston 2006; Steer 2010; Langton, Davies & Scott 2011), there has been a greater interest in the application of these technologies to the monitoring of the environmental impacts of MREIs (Carstensen, Henriksen & Teilmann 2006; Zaugg *et al.* 2008; Scheidat *et al.* 2011) particularly with regard to seabirds (Desholm, Fox & Beasley 2005; Desholm *et al.* 2006; Fox *et al.* 2006). Desholm *et al.* (2005) highlighted the advantages that remote techniques can provide in collecting bird data applicable to environmental impact assessments. For example, they can be used during darkness and reduced visibility, across extended time periods, over a larger spatial extent and remotely in offshore regions. Louzao *et al.* (2009) combined vessel-based monitoring and tracking studies to determine the habitat use of Cory's shearwaters *Calonectris diomedea* and concluded that the integration of tracking and vessel-based survey data provided a wider understanding of the predictability of aggregation and the key oceanographic habitats of this species at multiple spatial scales. With vessel-based surveys providing a large-scale perspective of the population level distribution and habitat associations, while tracking data provided more fine-scale and detailed information at the individual level. Inger *et al.* (2009) suggested that to allow for full biodiversity impacts of MREIs to be assessed there exists an urgent need for additional multi- and inter-disciplinary research in this area ranging from engineering to policy. As a result of the increased interest and use of these tracking technologies a further report was published by COWRIE in 2009, advocating the use of remote technologies in the environmental monitoring of MREIs. This concluded that tracking studies, thermal cameras and the use of radar should be complimentary, in certain instances, to existing aerial and boat-based survey methods though this is not yet a requirement (Maclean *et al.* 2009). Another factor to consider in favour of the use of tracking studies is that the foraging ranges of some species have the potential to cross national boundaries and be affected by offshore developments under the control of other governments and therefore subject to a different set of environmental monitoring standards (Holmes 1997b). For example, Pettex *et al.* (2010) found that Northern gannets *Morus bassunus* (from hereon referred to as “gannet”) breeding on Rouzic Island France, foraged in three different territorial waters, the UK, the Channel Islands and France.

The potential adaptability of seabirds to changes or disturbance in their foraging areas will depend on the location of the colony and their habitat preferences (Wakefield, Phillips & Matthiopoulos 2009; Wakefield *et al.* 2011), the physiological constraints of a species (Daunt *et al.* 2002; Shaffer, Costa & Weimerskirch 2003), competition from nearby colonies (Gremillet *et al.* 2004) and individual foraging behaviour. An additional advantage of the use of tracking studies is that they can be used to assess the potential specialisation and/or adaptability of individual birds from within a population, and the implications of this can then be scaled to the population level. Several studies have revealed that individual seabirds do exhibit repeatability in the foraging sites they visit. Irons *et al.* (1998) found that 24 out of 26 Black-legged kittiwakes *Rissa tridactyla* that were tracked remotely at an Atlantic colony over 13 days returned repeatedly, with an average of 19 trips, to the same areas to forage. Likewise a study on gannets breeding on the Bass Rock in Scotland suggested that individuals learnt and remembered the locations of feeding sites and used that knowledge on subsequent foraging trips. By contrast the foraging areas of gannets breeding on Great Saltee (UK), were much less similar, with highly variable distances to destinations, no differences in bearings among individuals and no significant repeatability in distance travelled (Hamer *et al.* 2001).

It may be in an individual bird’s interest to exhibit variable and adaptable foraging behaviour if it relies on mobile prey species. Alternatively individuals that exhibit highly repeatable foraging behaviour may save time and energy in searching for prey and therefore be more able to provide for their offspring and themselves. Tracking studies may help to reveal the plasticity in the behaviour of individuals, colonies and species. Such knowledge can then be applied to assess the potential impacts MREIs may have on particular species, colonies or individuals.

This study focused on the gannet population located in the territorial waters of the Channel Island of Alderney (49.5^{o}N, -4.0^{o}E). This population of approximately 6,900 pairs breed on two islets within Alderney’s territorial waters. This population was one of the reasons that led to the designation of the area under the Ramsar Convention in 2005. In response to proposals for the development of Alderney’s waters as a tidal power site in 2006 and 2007, environmental baseline boat- and land-based surveys were conducted according to COWRIE guidelines to record seabird and cetacean activity (Entec 2008). The EIA report found little foraging activity of gannets in the proposed test site areas. While this may not be surprising, given that this species has a foraging range of up to 440km and foraging trip duration of up 20.5 hours (Votier *et al.* 2011), it may not have been possible to fully evaluate the use of this area with a vessel-based approach. Those that were recorded in these surveys were likely to be breeding in the Channel Islands. However, Alderney's waters are well within the foraging range of the southernmost colony of gannets, on the French islet of Le Rouzic where 11,500 pairs of gannet breed (Siorat & Rocamora 1995). A disadvantage of using only vessel and land-based surveys is that they provide no information on the breeding locations of the gannets recorded. Breeding gannets were GPS-tracked with the aim of determining the main foraging areas of this population and to quantify their use of local waters (within the test site area) as well as waters outside of the Channel Islands legislative control, particularly considering that there are currently 13 MREI development sites located within the potential foraging range of Alderney's gannet colony (ENECO 2009; Eon 2010; La Grenelle Environment 2011). The similarity of foraging trips made by each individual was also examined to allow a preliminary assessment of the repeatability of foraging behaviour of individuals from this colony.

Methods

Data collection

IgotU GT-120 GPS data loggers (Mobile technology, Taiwan) were attached with waterproof tape (Tesa, Extra Power) (Wilson *et al.* 1997) to the tail feathers of 23 chick-rearing gannets breeding on the offshore stack Les Etacs, Alderney, Channel Islands on the 6th June 2011 and recovered 3, 4 or 5 days later. Birds were selected at random and gender was not determined. Loggers were set to record a position every two mins during deployment which was later interpolated to every 10s using the R package "Trip", (as described in Chapter 2).

Home-range analysis

The term "home-range" for the purposes of this study refers to "a minimum area in which an animal has some specified probability of being located" (Worton 1989). Home range estimates were derived from tracking data using the R package "*trip*" (Sumner 2012). The representativeness of this tracking sample of the whole colony was also assessed, (following the methods described in Chapters 2 & 3). The number of 2 x 2 km cells (in a pre-defined grid) that were used by an increasing number of birds included in a sample (1-15 individuals) and the number of 2 x 2 km cells that these birds spent 50% of their time in (when time spent in cells was ranked) were fitted to a Michelis-Menten model. Re-arrangement of the Michaelis-Menten equation allowed predictions of the number of individuals from this colony of 3450 breeding pairs to be determined.

The foraging behaviour of gannets has previously been divided into categories; (1) Out flight, (2) Return flight, with both (1) and (2) usually characterised by high flights speeds and high sinuosity, (3) Diving for prey, (4) Drifting on the sea surface, usually after feeding, and (5) Hunting or search flight (characterised by medium flight speeds) (Mullers *et al.* 2009). Whilst this study does not attempt to define the different foraging behaviour of the gannets tracked, the number of 2 x 2 km cells that the sample spent 50% of its time in is likely to represent core foraging areas based on the rational of Gremillet *et al.* (2004) that a gannet actively exploiting a prey patch will spend more time in a given area than when commuting between feeding patches. The area of active (total number of 2 x 2 km cells visited by the sample) will include all types of foraging behaviour including out and in-bound flight to and from the colony, which can be used to infer important flight paths that may be affected by MREIs. Darkness hours (between 22:00-04:00 BST) were removed from foraging trips to remove fixes where gannets were sat on the sea at night and therefore not actively foraging. Home-range areas predicted when these night time fixes were left in the analysis and when they were removed were compared and very little difference was found in the predicted home range areas but for the purposes of this paper night-time fixes remain removed.

Relationship of foraging areas to offshore renewable energy developments

Using ArcMap 9.3 the core foraging areas and area of active use of the pooled sample of the first two trips made by our tracked gannets and the individual foraging trips made by each gannet were plotted along with the locations of potential offshore wind and tidal power developments at various stages of planning and consent on the South Coast of England (ENECO 2009; Eon 2010) and the Normandy Coast of France (La Grenelle Enviroment 2011). The number of potential offshore developments within the pooled sample's core foraging area and area of active use was determined, and the number of individuals whose foraging areas overlapped with potential development sites was recorded.

Foraging trip characteristics and repeatability

Foraging trip duration, total trip distance and the maximum distance travelled from the colony for the first two trips made by each gannet was calculated using ArcMap 9.3. The value of each of these variables for the second trip was plotted as a function of the value for the first trip and Pearson's correlation was performed in Minitab (Version 15). The Bland and Altman's approach (Bland & Altman 1999) was used to measure agreement in methods (in this case between the first and second foraging trip made by an individual) to analyse our data. In this procedure, the mean of each foraging characteristic (foraging trip duration, total trip distance and maximum distance travelled from colony) for the first and second foraging trips was calculated, as was the difference between them. This calculated difference was then plotted as a function of the mean of that characteristic. Visual comparison of the systematic bias (the overall mean difference) and its limits of agreement (confidence intervals) with the plotted data and zero, within the Brand-Altman plot, revealed whether or not there were consistencies in the foraging characteristics between the first and second foraging trips made by an individual. The difference in direction travelled of the first and second foraging trip made by each individual from the colony to the 2 x 2 km grid cell where it spent most of its time was determined using the circular statistic Watson Williams F-test (Batschelet 1981) in Oriana for Windows 1.06 (Kovach Computing Service, Pentraeth, UK).

Results

Of 23 birds tracked, 17 were recaptured and the loggers retrieved; two others were sighted again at the colony but not recaptured. Access to the birds was limited due to logistical difficulties in accessing the field site and to limit disturbance to the breeding birds. This meant that further re-sighting or recapture opportunities were not available. Individual gannets made between 1-4 foraging trips during the deployment period, with 15 individuals making at least two trips and these data were used in the majority of further analysis. The mean foraging trip duration of all trips undertaken by the 17 birds tracked was 17.6 (± 6.5) hrs (Table 4.1), and mean time spent at the colony between trips was 19.5 (± 2.0) hrs (n = 15).

Table 4.1. Summary of mean (± SD) foraging trip data recorded in this study compared to foraging trip data recorded from chick-rearing gannets at other UK and French colonies.

	Les Etacs, Alderney	Rouzic Island, Brittany[1]	Bass Rock, Scotland[2]	Grassholm, Wales[3]
No.of gannets tracked	17	20	13	23
Foraging trip duration (hours)	17.6 (± 6.5)	17.8 (± 8.6)	21.5 (± 6.7)	25.1 (± 17)
Total trip distance (km)	289 (± 115)	479 (± 206)	440 (± 234)	370 (± 251)
Maximum distance travelled (km)	106 (± 43)	100 (± 35)	155 (± 65)	-

([1]Gremillet et al. 2006, [2]Hamer et al. 2009, [3]Votier et al. 2010)

How representative was the sample?

This sample consisting of the first two trips from 15 individuals predicted only 37 (25-44) % of the area of active use (total number of 2 x 2 km cells used) of this colony and 18 (6-29) % of the core foraging area of this colony. Re-arrangement of the Michalis-Menten equation including colony size predicted that 453 (CI 334-734) individuals would need to be sampled to accurately predict the area of active use of this colony and 1103 (CI 620-2614) would need to be sampled to predict the core foraging areas (Figure 4.1).

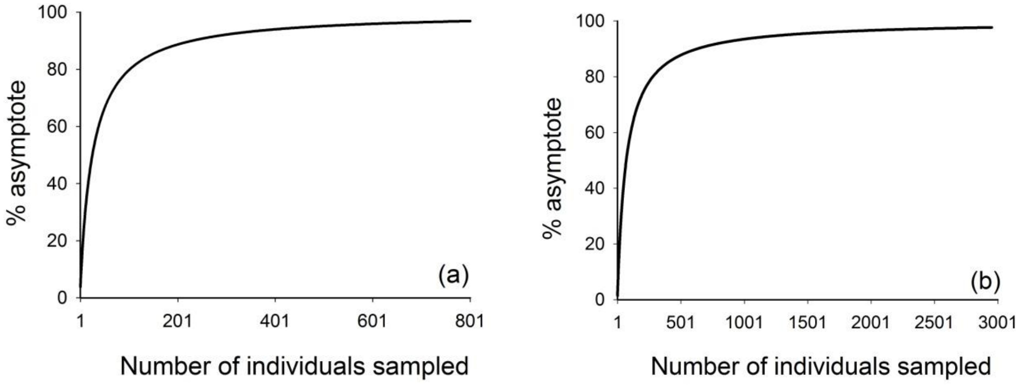


Figure 4.1. Represents the number of individuals from the gannet colony required to predict 100% of the asymptotic value of the number of 2 x 2 km^2 cells used (based on parameters derived from Michelis-Menten equation) for (a) the area of active use and (b) the core foraging area.

Relationship to offshore renewable energy developments

The foraging area of the pooled sample of the first two trips made by 15 gannets overlapped with nine MREI sites (seven in French waters, one in UK waters and the Alderney tidal site) with the foraging trips of 9 out of the 15 individuals tracked overlapping with MREI sites (Figure 4.2). When examining the predicted core foraging areas of the first and second foraging trips made by each individual gannet, eight individuals had a foraging trip that overlapped with a proposed offshore wind development in France and one individual's core foraging area overlapped with a MREI in the UK (Figure 4.3). None of those tracked made a foraging trip with a core foraging area that overlapped with the proposed tidal power development site in Alderney. When examining the area of active use of the 19 foraging trips that overlapped with offshore wind developments 14 also overlapped with Alderney's tidal power development site.

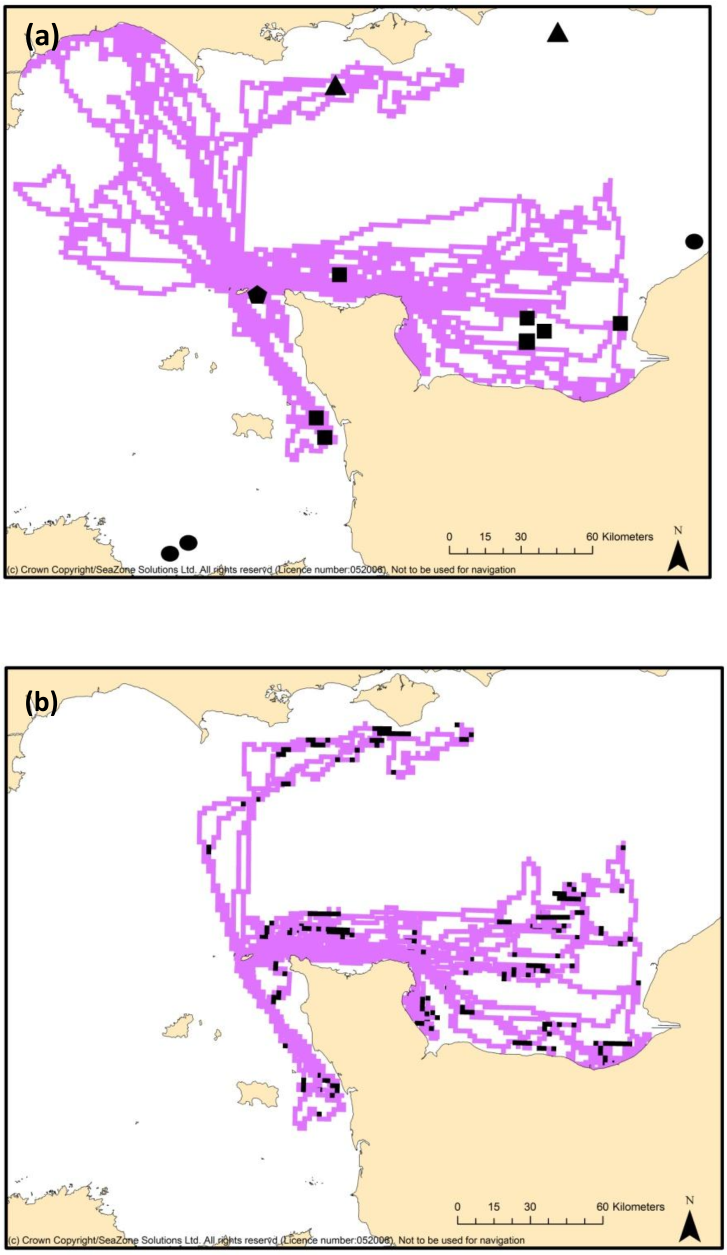


Figure 4.2. **(a)** Home range areas of all gannets and locations of offshore renewable energy developments (pentagon symbol = Alderney tidal power site, square symbol = concept/early planning stage development, triangle symbol = round 3 wind farm, circle symbol=consent application submitted) (b) Areas of active use (pink) and core foraging areas (black) of the foraging trips made by the nine individuals whose core foraging areas overlap with proposed MREI.

Foraging trip characteristics and repeatability

When comparing the foraging characteristics of an individual a significant correlation was found between the first and second foraging trips when considering the maximum distance travelled (R = 0.789, n = 15, $p < 0.001$), indicating repeatability between the first and second foraging trips for the maximum distance travelled by an individual (Figure 4.3d). However, no significant correlations were found between the first and second foraging trips when considering the total distance travelled from the colony, and trip duration (Figure 4.3a & 4.3b). Suggesting little repeatability between the first and second foraging trips when considering these characteristics. However, no significant difference was found in the direction travelled by an individual on its first and second foraging trips (Figure 4.4) indicating significant repeatability between trips in their foraging trip characteristics.

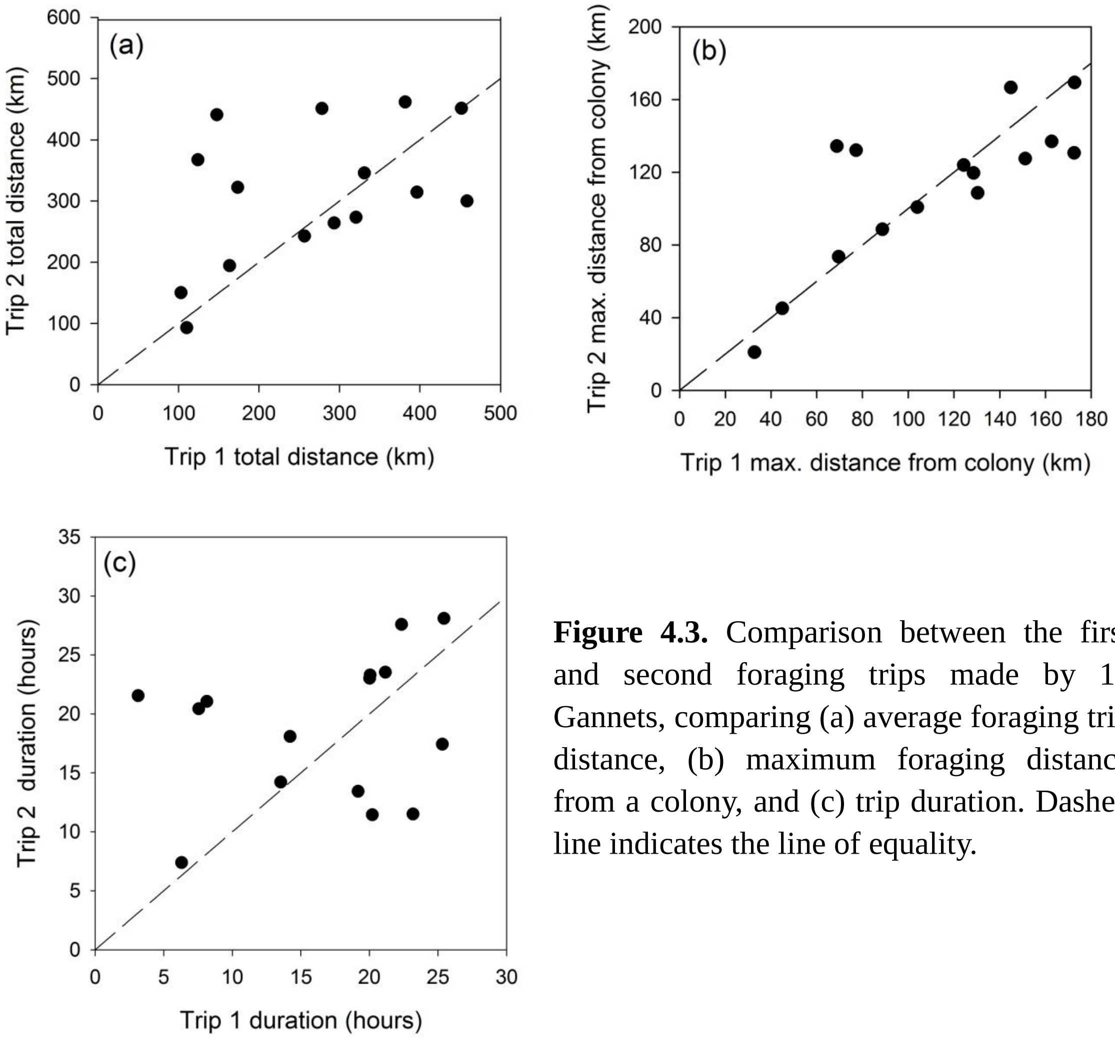
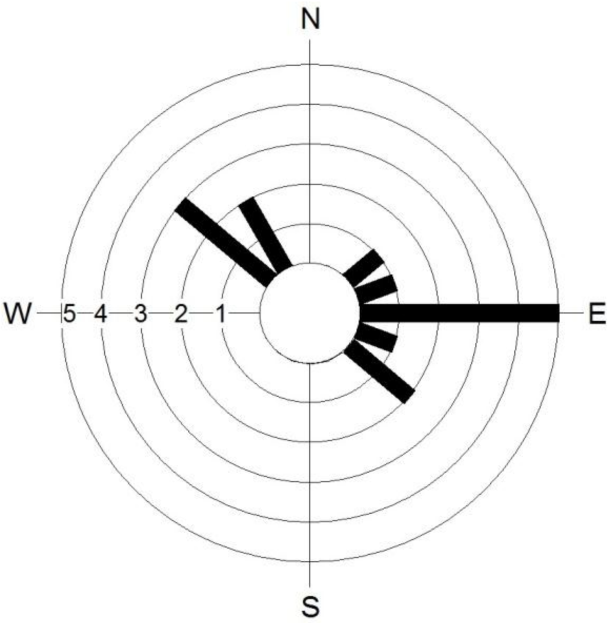


Figure 4.3. Comparison between the first and second foraging trips made by 15 Gannets, comparing (a) average foraging trip distance, (b) maximum foraging distance from a colony, and (c) trip duration. Dashed line indicates the line of equality.

(a)



(b)

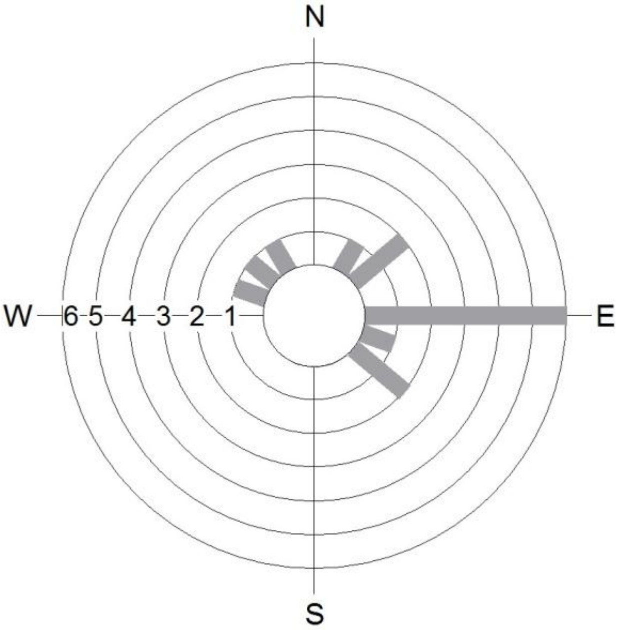


Figure 4.4. The bearings of (a) the first foraging trip (b) the second foraging trip made by 15 gannets. The number of trips made in each direction are represented by the frequency bars.

The Bland-Altman plots plotted to test the agreement between the first and second foraging trips made by an individual revealed that the systematic bias (mean difference expressed as a percentage of the mean value of each foraging characteristic) was close to zero with large limits of agreement (confidence intervals) and large variability in data points for all foraging characteristics; trip duration, and total distance travelled, suggesting low repeatability with the exception of maximum distance travelled from the colony which revealed relatively small limits of agreement (Figure 4.5).

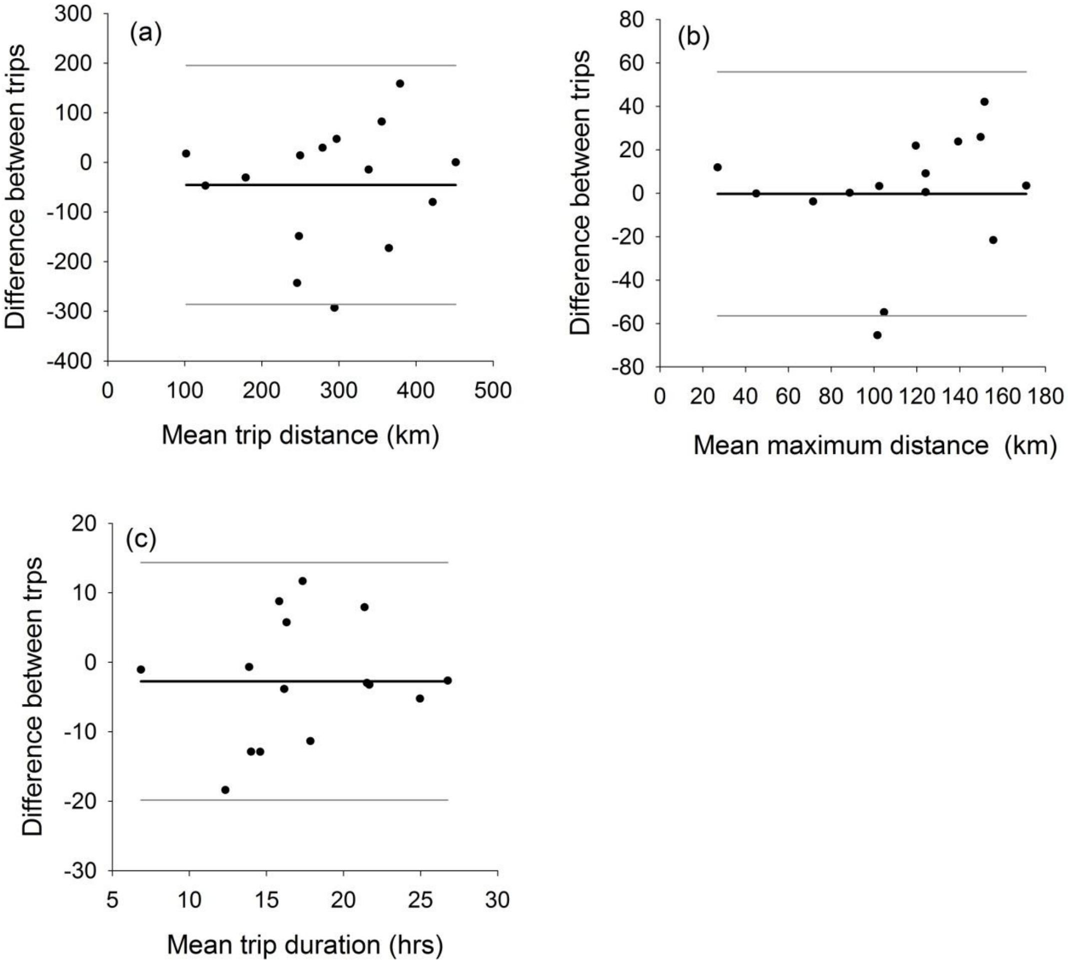


Figure 4.5. Bland-Altman plots of the difference observed in the (a) trip distance, (b) maximum distance travelled and (c) trip duration between the first and second foraging trip made by individual gannets (n = 15), as a function of mean foraging trip distance, maximum distance travelled and trip duration. The black line shows the overall mean difference between trip 1 and trip 2 and the grey lines the overall mean standard error (± 1.96) between trip 1 and trip 2.

Discussion

Foraging trip duration and the maximum distance travelled were comparable to those recorded at other UK and French colonies (Hamer *et al.* 2000; Pettex *et al.* 2010; Votier *et al.* 2011) whilst mean foraging trip distance was lower compared to all other colonies (Table 4.1). The conclusions drawn in this study are based on the tracking data of 15 gannets from a colony of 3450 pairs so we cannot assume that all foraging areas used by the colony were revealed (Figure 4.1), in fact analysis of the representativeness of our sample predicts up to 1103 (CI 620-2614) individuals may be needed to predict core foraging areas, with fewer (453 CI 334-734) required to predict areas of active use for this colony. This indicates a wide range of core foraging areas are being used by this species within its foraging range. However, it is interesting that foraging trips were made in four apparent locations; (1) to the south coast of England, (2) south towards Jersey (3) eastwards around the Cherbourg peninsula and (4) towards the French coast of Le Havre (Figure 4.2).

The pooled area of active use predicted from analysis of the first two trips of 15 gannets revealed that this area overlapped with seven French MREIs at the concept or early planning stage of development, the Alderney tidal power development site and a round 3 wind farm in the UK (Figure 4.2). When examining the core foraging areas of individuals, over half of all birds sampled (9 individuals) had core foraging areas that overlapped with proposed MREI developments (Figure 4.3). Of these nine individuals, eight overlapped with developments in French waters, one in UK waters. None of the 15 individual’s core foraging areas overlapped with the proposed Alderney tidal power development, compared to 8 individuals whose area of active use overlapped with the site. Since the core area represents where the individual spends 50% of its time (Calenge 2007), it represents the most heavily used and most likely foraging areas for the gannet (Gremillet *et al.* 2004). Therefore whilst most gannets breeding on Les Etacs do spend time within the proposed Alderney test site area, they are likely to be using this area as a flight path to and from the colony rather than as an important foraging area. These results highlight the need to look at the “bigger picture” when considering the effects that offshore renewable energy developments may have on seabird populations and for increased collaboration not just nationally, but within Europe when considering the effects of offshore renewable energy developments. This is particularly important as there are wide variations between requirements placed on developers in individual member EU states to fund and prepare environmental impact assessments (Holmes 1997a).

We propose that as part of the integrated monitoring approach as proposed by COWRIE (Walls & Thompson 2009) that tracking studies of seabirds at important colonies within the range of offshore wind farm developments should also be a requirement, to provide valuable information on a colony's use of an area and dependence on particular areas, and that this data should be made freely available to multiple regulatory bodies. Tracking studies can be relatively cheap to conduct with the GPS loggers used in this study costing less than £40 and can provide useful information on the foraging behaviour of a colony in shorter time scales, which can be useful in identifying potentially important foraging areas or for identifying colonies that may be at most risk early on in the EIA process compared to boat-based and aerial monitoring. For example, when analysing the foraging tracks of gannets tracked in this study along with those tracked from the nearby colony of Rouzic (Pettex *et al.* 2010), it seems likely that gannets recorded on the boat-based surveys of Alderney's waters conducted in 2006-07 were gannets breeding on Les Etacs rather than Rouzic island, even though Alderney's waters are well within the foraging range of both colonies. We can only conclude this as tracking data are available for birds from both colonies.

Similarities were found between the first and second trips made by an individual in the maximum distance they travelled and the direction in which individuals travelled but no significant relationship between the first and second foraging trips when considering foraging trip duration and the total trip distance. These results suggest that individual gannets appear not to be particularly dependent on any specific sites and that there is significant variation in the amount of time an individual spends searching for food. At the population level, there is a general consistency in the broad areas that they forage within (Figure 4.2) with four main areas used. The repeatability of an individual's foraging behaviour has been demonstrated in previous studies (Irons 1998; Bearhop *et al.* 2006) whereas others report changes in foraging behaviour. For example, Torres *et al.* (2011) found that the White-capped albatross *Thalassarche steadi* had highly variable and adaptable foraging destinations in response to fisheries. Tracking studies allow us to gauge how much any particular colony, or individual, may depend on certain foraging areas. Our study has revealed that important foraging areas can be relatively easily identified and related to proposed MREIs and we have provided baseline data, prior to any installation, of the foraging behaviour of this colony. It appears that the waters around Alderney are not heavily used foraging areas for the gannets breeding there, with them being more likely to be affected by obstructions to their flight path around the colony rather than underwater installations. This pilot data indicates that the population could potentially be more affected by MREI developments in French waters rather than the Alderney tidal power development. However behaviour may change between years so further years of tracking should be conducted to further support this finding. Few studies have investigated how individuals may adapt to disturbances in their preferred foraging areas as a result of MREIs but tracking studies again can provide an ideal resource to further the understanding in this field using a Before-After-Control-Impact approach (Smith, Orvos & Cairns 1993). The tracking of important seabird colonies that may use the same waters of any proposed MREIs is recommended as an integral part of the EIA, along with more international collaboration on the EIA process.

Acknowledgements

This project was jointly funded by a Doctoral Training Grant from the Natural Environment Research Council and the Alderney Commission for Renewable Energy. We would like to thank Alderney Wildlife Trust volunteers for the assistance with this work, particularly Liz Morgan and our boat skippers Phil Murray, Dave Venn and Darron Machon. Permission to carry out field work was granted by the States of Alderney and the Channel Island Bird Ringing Scheme gave PWA and LMS permission to ring the gannets and attach loggers to the birds.

References

Batschelet, E. (1981) *Circular statistics in biology*. New York.

Bearhop, S., Phillips, R.A., McGill, R., Cherel, Y., Dawson, D.A. & Croxall, J.P. (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Marine Ecology-Progress Series,* **311,** 157-164.

Bland, J.M. & Altman, D.G. (1999) Measuring agreement in method comparison studies. *Statistical Methods in Medical Research,* **8,** 135-160.

Calenge, C. (2007) Exploring habitat selection by wildlife with adehabitat. *Journal of Statistical Software,* **22,** 1-19.

Camphuysen, K.C., Fox, T.A., Leopold, M.M. & Petersen, I.B. (2004) Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K. Royal Netherlands Institute for Sea Research.

Carstensen, J., Henriksen, O.D. & Teilmann, J. (2006) Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Marine Ecology-Progress Series,* **321,** 295-308.

Daunt, F., Benvenuti, S., Harris, M.P., Dall'Antonia, L., Elston, D.A. & Wanless, S. (2002) Foraging strategies of the black-legged kittiwake Rissa tridactyla at a North Sea colony: evidence for a maximum foraging range. *Marine Ecology-Progress Series*, **245,** 239-247.

Desholm, M., Fox, A.D., Beasley, P.D.L. & Kahlert, J. (2006) Remote techniques for counting and estimating the number of bird-wind turbine collisions at sea: a review. *Ibis*, **148,** 76-89.

Desholm, M., Fox, T. & Beasley, P. (2005) Best practice guidance for the use of remote techniques for observing bird behaviour in relation to offshore windfarms. REMTECH-05-2004 Report commissioned by COWRIE ltd.

ENECO (2009) Navitus Bay Wind Park Infrastructure Planning (Environmental Impact Assessment) Regulations 2009. Eneco, Rotterdam.

Entec UK (2008) Seabird and Ceteacen survey for tidal power development in Alderney. Entec Consultancy, UK.

Eon (2010) Rampion Offshore Wind Farm Scoping Report. RSP Group PLC, Helsby.

Fox, A.D., Desholm, M., Kahlert, J., Christensen, T.K. & Petersen, I.K. (2006) Information needs to support environmental impact assessment of the effects of European marine offshore wind farms on birds. *Ibis,* **148,** 129-144.

Gauthreaux, S.A., Jr. & Livingston, J.W. (2006) Monitoring bird migration with a fixed-beam radar and a thermal-imaging camera. *Journal of Field Ornithology,* **77,** 319-328.

Gill, A.B. (2005) Offshore renewable energy: ecological implications of generating electricity in the coastal zone. *Journal of Applied Ecology,* **42,** 605-615.

Gremillet, D., Dell'Omo, G., Ryan, P.G., Peters, G., Ropert-Coudert, Y. & Weeks, S.J. (2004) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Marine Ecology-Progress Series,* **268,** 265-279.

Gremillet, D., Pichegru, L., Siorat, F. & Georges, J.Y. (2006) Conservation implications of the apparent mismatch between population dynamics and foraging effort in French northern gannets from the English Channel. *Marine Ecology-Progress Series,* **319,** 15-25.

Griffin, L., Rees, E. & Hughes, B. (2010) The migration of whooper swans in relation to offshore windfarms. Report prepared by the Wildfowl and Wetland Trust for COWRIE Limited, London.

Hamer, K.C., Humphreys, E.M., Magalhaes, M.C., Garthe, S., Hennicke, J., Peters, G., Gremillet, D., Skov, H. & Wanless, S. (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. *Journal of Animal Ecology,* **78,** 880-889.

Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S. & Wood, A.G. (2001) Contrasting foraging strategies of gannets Morus bassanus at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology-Progress Series,* **224,** 283-290.

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P. & Wood, A.G. (2000) Foraging ranges, diets and feeding locations of gannets Morus bassanus in the North Sea: evidence from satellite telemetry. *Marine Ecology-Progress Series,* **200,** 257-264.

Holmes, S.C. (1997a) Wind energy - Environmental impact assessment: *The UK experience and the EU perspective*.

Inger, R., Attrill, M.J., Bearhop, S., Broderick, A.C., Grecian, W.J., Hodgson, D.J., Mills, C., Sheehan, E., Votier, S.C., Witt, M.J. & Godley, B.J. (2009) Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *Journal of Applied Ecology,* **46,** 1145-1153.

Irons, D.B. (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology,* **79,** 647-655.

Johnson, G.D., Erickson, W.P., Strickland, M.D., Shepherd, M.F., Shepherd, D.A. & Sarappo, S.A. (2002) Collision mortality of local and migrant birds at a large-scale wind-power development on Buffalo Ridge, Minnesota. *Wildlife Society Bulletin,* **30,** 879-887.

Kaiser, M.J., Elliott, A., Galandi, M., Rees, E.I.S., Caldow, R., Stillman, R., Sutherland, W. & Showler, D. (2002) Predicting the displacement of common scoter *Melanitta nigra* from benthic feeding areas due to offshore windfarms. COWRIE Limited, London.

Lampkin, D.O., Harris, J.M., Cooper, W.S. & Coates, T. (2009) Coastal process modelling for offshore wind farm environmental impact assessment: best paractice guide. COWRIE Limited, London.

Langton, R., Davies, I.M. & Scott, B.E. (2011) Seabird conservation and tidal stream and wave power generation: Information needs for predicting and managing potential impacts. *Marine Policy,* **35,** 623-630.

Le Grenelle Environment. (2011) Dossier de Presse: Installation de 3000MW d'eoliennes en mer. La Grenelle Environment, France.

Linley, E.S.A., Wilding, T.A., Black, K., Hawkins, A.J.S. & Mangi, S. (2008) Review of reef effects of offshore windfarm structures and their potential enhancement and mitigation. Scotland.

Louzao, M., Becares, J., Rodriguez, B., Hyrenbach, K.D., Ruiz, A. & Arcos, J.M. (2009) Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. *Marine Ecology-Progress Series,* **391,** 183-197.

Maclean, I.M.D., Wright, L.J., Showler, D.A. & Rehfish, M.M. (2009) A review of assessment methodologies for offshore windfarms. (ed. B.T.f.O. Report). British Trust Ornithology Report commissoned by COWRIE ltd.

Masden, E.A., Haydon, D.T., Fox, A.D. & Furness, R.W. (2010) Barriers to movement: Modelling energetic costs of avoiding marine wind farms amongst breeding seabirds. *Marine Pollution Bulletin,* **60,** 1085-1091.

Mullers, R.H.E., Navarro, R.A., Daan, S., Tinbergen, J.M. & Meijer, H.A.J. (2009)

Energetic costs of foraging in breeding Cape gannets Morus capensis. *Marine Ecology-Progress Series,* **393,** 161-171.

Perrow, M.R., Gilroy, J.J., Skeate, E.R. & Tomlinson, M.L. (2011) Effects of the construction of Scroby Sands offshore wind farm on the prey base of Little tern Sternula albifrons at its most important UK colony. *Marine Pollution Bulletin,* **62,** 1661-1670.

Perrow, M.R., Skeate, E.R., Lines, P., Brown, D. & Tomlinson, M.L. (2006) Radio telemetry as a tool for impact assessment of wind farms: the case of Little Terns Sterna albifrons at Scroby Sands, Norfolk, UK. *Ibis,* **148,** 57-75.

Pettex, E., Bonadonna, F., Enstipp, M.R., Siorat, F. & Gremillet, D. (2010) Northern gannets anticipate the spatio-temporal occurrence of their prey. *Journal of Experimental Biology,* **213,** 2365-2371.

RenewableUK (2011) State of the industry report Onshore and offshore wind: progress update. RenewableUK, UK.

Rourke, F.O., Boyle, F. & Reynolds, A. (2010) Tidal energy update 2009. *Applied Energy,* **87,** 398-409.

Scheidat, M., Tougaard, J., Brasseur, S., Carstensen, J., Petel, T.V., Teilmann, J. & Reijnders, P. (2011) Harbour porpoises (Phocoena phocoena) and wind farms: a case study in the Dutch North Sea. *Environmental Research Letters,* **6,** 10.

Shaffer, S.A., Costa, D.P. & Weimerskirch, H. (2003) Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Functional Ecology,* **17,** 66-74.

Siorat, F. & Rocamora, G. (1995) Changes in numbers and distribution of the Northern Gannet (Morus bassanus) on Rouzic Island, (Reserve naturelle des Sept-Iles, Bretagne), France 1939-1994. *Colonial Waterbirds,* **18,** 172-178.

Smith, E.P., Orvos, D.R. & Cairns, J. (1993) Impact assessment using the before-after-control-impact (BACL) model - Concerns and comments. *Canadian Journal of Fisheries and Aquatic Sciences,* **50,** 627-637.

Steer, J. (2010) Bioacoustic monitoring of New Zealand birds. *Notornis,* **57,** 75-80.

Sugimoto, H. & Matsuda, H. (2011) Collision risk of White-fronted Geese with wind turbines. *Ornithological Science,* **10,** 61-71.

Sumner, M.D. (2011). trip: Spatial analysis of animal track data. R package version 1.1-10.

Torres, L.G., Thompson, D.R., Bearhop, S., Votier, S., Taylor, G.A., Sagar, P.M. &

Robertson, B.C. (2011) White-capped albatrosses alter fine-scale foraging behavior patterns when associated with fishing vessels. *Marine Ecology-Progress Series,* **428,** 289-301.

Votier, S.C., Bearhop, S., Witt, M.J., Inger, R., Thompson, D. & Newton, J. (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology,* **47,** 487-497.

Votier, S.C., Grecian, W.J., Patrick, S. & Newton, J. (2011) Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology,* **158,** 355-362.

Wakefield, E.D., Phillips, R.A. & Matthiopoulos, J. (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology-Progress Series,* **391,** 165-182.

Wakefield, E.D., Phillips, R.A., Trathan, P.N., Arata, J., Gales, R., Huin, N., Robertson, G., Waugh, S.M., Weimerskirch, H. & Matthiopoulos, J. (2011) Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. *Ecological Monographs,* **81,** 141-167.

Walls, R.J., Pendlebury, C.J., Budgey, R., Brookes, K. & Thompson, P. (2009) Revised best practice guidance for the use of remote techniques for ornithological monitoring at offshore windfarms. Cowrie, Cowrie.

Willow, C. & Valpy, B. (2011) Wave and Tidal Energy in the UK, State of the Industry report. RenewableUK, UK.

Wilson, R.P., Putz, K., Peters, G., Culik, B., Scolaro, J.A., Charrassin, J.B. & RopertCoudert, Y. (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin,* **25,** 101-106.

Worton, B.J. (1989) Kernel methods for estimating for utilization distribution in home-range studies. *Ecology,* **70,** 164-168.

Zaugg, S., Saporta, G., Van Loon, E., Schmaljohann, H. & Liechti, F. (2008) Automatic identification of bird targets with radar via patterns produced by wing flapping. *Journal of the Royal Society Interface,* **5,** 1041-1053.

Chapter 5

Factors affecting the foraging behaviour of the European Shag;

Implications for seabird tracking studies.

Soanes, L.M.[a], Arnould, J.P.Y[b], Dodd, S.G.[c], Milligan, G.[a], Green, J.A.[a]

[a] School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP. [b] School of Life and Environmental Sciences, Deakin University, Burwood, 3215, Australia. [c] Royal Society for the Protection of Birds, North Wales Office, Bangor, LL57 4FD.

Photograph by Johann Bourgeois 2012

Author Contributions: LMS and JAG conceived and designed the study. LMS and SGD conducted fieldwork. JPYA provided financial assistance, LMS & GM analysed the data. LMS wrote the manuscript; with editorial advice from other authors.

Abstract

Seabird tracking has become an ever more popular tool to aid environmental processes such as the designation of marine protected areas and environmental impact assessments. However, samples used are usually small and little consideration is given to experimental design and sampling protocol. European shag *Phalacrocorax aristotelis* were tracked using GPS technology over three breeding seasons and the following foraging trip characteristics: trip duration, trip distance, maximum distance travelled from the colony, size of area used and direction travelled from colony were determined for each foraging trip. The effect of sex, year of study, breeding site, number and age of chicks and the timing of tracking on foraging behaviour were investigated using a General Estimation Equation model. A range of sampling scenarios reflecting likely field sampling, were also tested to compare how foraging behaviour differed depending on composition of the sample of birds tracked. Trip distance, maximum distance travelled from the colony, direction travelled and the area used by individuals were most significantly affected by the breeding site of an individual; whist trip duration was most affected by the year of study. The importance of sampling regime and the influence that year, sex, age and number of chicks and breeding site have on the foraging trip characteristics have been demonstrated for this coastal feeding seabird. Given the logistical and financial constraints in tracking large numbers of individuals, this study highlights the need for researchers to consider the composition of their study sample to ensure any identified foraging areas are as representative as possible of the whole colony's foraging area.

Introduction

In recent years, the number of seabird tracking studies using Global Positioning System data loggers, satellite transmitters and geolocators has increased substantially due to the availability of cheaper and smaller technologies, adding greatly to our understanding of seabird behaviour and ecology (Burger and Shaffer, 2008). A range of seabird species have now been tracked ranging from the 150 gram Thin-billed prion *Pachyptila belcheri* (Quillfeldt *et al.*, 2012) to the 12 kg Wandering albatross *Diomedea exulans* (Shaffer *et al.*, 2005, Gremilliet et al., 2012). These studies have been used to inform the designation of and to determine the effectiveness of marine protected areas (e.g. BirdLife, 2010, Harris *et al.*, 2007, Hyrenbach *et al.*, 2006), to provide data for environmental impact assessments (e.g. Perrow *et al.*, 2006, Soanes *et al.*, 2013), to examine the effects of environmental change (e.g. Durant *et al.*, 2009, Wanless *et al.*, 2007, Wilson *et al.*, 2002) and to assess changes in fishery practices (e.g Bugoni *et al.*, 2009, Copello and Quintana, 2009) (Table 5.1). However, the logistical and financial constraints of working at seabird colonies often means that samples of individuals used in tracking studies may fail to properly represent the traits of the population. A review of recent literature (Table 5.1) revealed seabird tracking studies used a mean sample size of 29 individuals in each year of study (range = 4-124, median = 23, n = 33). Sample size in these studies were found to represent a mean of only 1.4 % of the total colony size (range 0.001-25 %, n=30 colonies), which is somewhat biased by the study of Stenhouse *et al.* (2012) who tracked 30 individuals from a colony of 65 pairs. If this study is excluded from the sample we find that the sample size used at the remaining colonies represented only 0.7 % (range 0.001 – 6.6 %, n=29 colonies) of the study colony. Birds were tracked for more than one field season in just two out of the 25 of the studies.

Table 5.1: A summary of the published papers returned, between Nov 2011-Nov 2012, when the term “seabird tracking” was entered into the search engine Web of Knowledge^{SM} (Thomson Reuters, USA). Colony size was reported in only half of the publications, for those which did not report colony size it was found (when available) through the Birdlife International database (www.birdlife.org/datazone).

Species (Latin name)	**Focus of study**	**Number of individuals deployed**	**Size of colony (pairs)**	**Reference**
Fregata magnificens	Environmental variability	16	1200	De Monte *et al* 2012
Sula variegata	Fisheries	26	172 480	Bertrand *et al* 2012
Morus bassunus	Sex specific foraging	(3 years) 36, 42, 27	40 000	Stauss *et al* 2012
Morus bassunus	Renewable energy	23	4500	Soanes *et al* 2012
Morus bassunus	Pollution risk	46 adults, 18 juv.	4 unspecified islands	Montevecchi *et al* 2012
Morus capensis	Foraging areas at 2 sites	21, 25	32 000, 84 000	Moseley *et al* 2012
Phalacrocorax bougainvillii *& Sula variegata*	Comparison between species	20 51	240 000 41 000	Weimerskirch *et al* 2012
Thalassarche melanophrys	Habitat use	49	74 000	Wakefield *et al* 2012
Calonectris diomedea	Trophic level specialisation	23, 29	30 000, 850	Alonso *et al* 2012
Puffinus mauretanicus	Year round foraging areas	6	-	Loazou *et al* 2012
Puffinus mauretanicus	Year round foraging areas	26	200	Guilford *et al* 2012
Calonectris diomedea	Fisheries & climate change	100	29 540	Ramos *et al* 2012
Rissa tridactyla	Wintering areas at 18 sites	10-16	-	Frederiksen *et al* 2012
Fratercula arctica	Renewable energy	7	40 000	Harris *et al* 2012
Alle alle	Wintering areas	124	3 500 000	Fort *et al* 2012
Alle alle	Breeding foraging areas	13	-	Jakubas *et al* 2012
Spheniscus magellanicus	Comparison of six colonies	12 , 18, 4, 15, 4,7	56 737, 128 000, 32 337 20 287, 56 792, 2000	Sala *et al* 2012
Eudyptes chrysocome	Comparison of 3 colonies	22, 20, 20	120 000, 150 000, 50 000	Thiebot *et al* 2012
Larus atlanticus	Breeding foraging areas	(2 years) 10, 12	91	Suarez *et al* 2010
Ichthyaetus audounii	Breeding foraging areas	8	12 000	Christel *et al* 2012
Stercorarius skua	Foraging areas	7,11,4	n/a, n/a, 2170	Magnusdottir *et al* 2012

These limited sampling regimes are likely to fail to adequately represent population-level characteristics. Due, in part, to the known variability in seabird foraging behaviour due to effects such as inter-individual differences caused by underlying physiology (Biro and Stamps, 2010), sex related differences (Weimerskirch *et al*., 2009, Pinet *et al*., 2012), age and experience (Daunt *et al*., 2007), environmental factors (Chivers *et al*., 2012), location of breeding site (Hipfner *et al*., 2007), stage of breeding and clutch size. Soanes *et al*. (2013b) highlight the need for researchers to explore and accept the limitations of their data sets before drawing conclusions on the location and extent of a whole colony's important foraging areas by considering the number of individuals and foraging trips included in a sample. Therefore, while it may not be possible to sample a large number of individuals from any particular colony, we should ensure that the individuals that are sampled are as representative as possible of the whole study population.

In this study, we examined the effect of a range of factors on the foraging behaviour of European shags *Phalacrocorax aristotelis* (Linnaeus, 1761) breeding at a single colony (484 breeding pairs). The effects of year, sex, age of chicks, timing of tracking and the breeding site on foraging trip distance, duration, maximum distance travelled from the colony and the size of the area used were tested with the aim of determining which, if any, are the most important factors to consider when planning and undertaking a seabird tracking study. We then simulated different realistic sampling regimes to evaluate how sample selection can influence conclusions on apparent foraging characteristics.

Methods

Field methods

European Shags (from here on referred to as "shags"), breeding on Puffin Island, Wales, (53.3ºN, 4.0ºW) were tracked using IgotU GT-120 GPS data loggers (Mobile Action, Taiwan) over three consecutive breeding seasons (2010-2012). A total of 28, 31 and 25 individuals were instrumented in 2010, 2011 and 2012 respectively. Loggers were deployed between the 9th May and 18th June of each year and samples represented males and females, individuals breeding at three different sites, with different numbers of chicks (one - three) at the time of tracking and with varying ages of chicks (from 1-35 days) (Table 5.2). Loggers were attached to the back feathers with waterproof Tesa ® Extra power tape (Wilson *et al.*, 1997). Loggers weighed 15 g when packaged, which equates to less than 1% of a shags body weight.

Table 5.2. Sample sizes used for each explanatory variable included in the General Estimation Equation model.

	Sample size	**Number of foraging trips**
Sex		
Males	28	302
Females	29	261
Site		
Ledge	32	293
North side	17	197
Beach	8	73
Year		
2010	20	174
2011	16	161
2012	21	228
Number of chicks		
1 chick	7	59
2 chicks	20	191
3 chicks	30	313
Total	57	563

Regular visits to nests before, during and after tracking allowed us to estimate the age of the chicks. The number of chicks that reached approximately 30-35 days old per nest was recorded (this is the age when they become mobile and were difficult to assign to individual nests) as an estimate of the productivity of each nest.

Tracking data

The GPS devices did not always record a position every 120 s as programmed to do so, in part due to the diving activity of shags. This may provide a biased sample of the spatial distribution of foraging activity (McLeay *et al.*, 2010), and so GPS fixes were interpolated to every 10 seconds using the software R (R Development Core Team 2008) with the package "*Trip*" (Sumner 2011). This package was also used to calculate the area covered on each foraging trip by calculating the time spent in a pre-defined grid of 1 x 1 km cells surrounding the breeding colony. The number of cells used on each trip was used to represent the size of the area (km^2) covered on each foraging trip. Total trip distance (km), trip duration (min), and the maximum distance travelled from the colony (km) were also calculated for each trip.

Statistical Methods

We tested the effects of a range of categorical and continuous explanatory variables including: (1) sex of the bird, (2) number of chicks, (3) age of chicks at the time of tracking, (4) location of nest on the island, (5) date that tracking was undertaken and (6) year of tracking on the four foraging trip response variables described above. Our aim was to determine which, if any, might account for the variation in foraging behaviour that was observed between individuals. Total trip distance, trip duration, and the maximum trip distance were *ln*-transformed. Generalised Estimation Equations (GEE) (Liang and Zeger, 1986) were used in the analysis; this allowed for compound correlation structures to be specified for each individual, in order to account for within-individual correlation, they also are more suitable for understanding population effects rather than individual specific effects. The models were implemented in the "*geepack*" version 1.1-6 package (Højsgaard *et al.*, 2012) in the R software environment (R Development Core Team 2011). All models incorporated the same terms consisting of sex, number of chicks year of study and location of site as fixed factors and the numeric factors of age of chicks at time of tracking and number of days into the tracking season that tracking was undertaken (days from 1st April each year). The model outputs were analysed using one-way ANOVAs, and significant terms at $p < 0.05$ level were then submitted to *post-hoc* Tukey comparison tests to ascertain within-factor differences. In addition to the main model the circular statistic software Oriana (Kovack Computing Services, UK) for windows and the Watson-Williams F-Test (Batschelet, 1981) were also used to analyse any differences in the direction travelled in relation to the explanatory variables. In all analyses a significance level of $p < 0.05$ was applied.

Maps of time spent in predefined grid cells of 1 x 1 km were plotted to compare use of space by shags around the colony for the explanatory variables that were found to be significant after the GEE model was run (those with a p-value < 0.05). Home-range areas were represented as the actual time spent in a pre-defined grid of 1 x 1 km cells surrounding the breeding colony (Page *et al*., 2006). The number of 1 x 1 km cells that the animals spent 100% of their time was used to represent their area of active use and the number of cells that the animals spent 50% of their time (after ranking for frequency of use was) used to represent their core-foraging areas (Casper *et al.*, 2010, Soanes *et al*., 2013b).

A range of sampling scenarios to represent commonly implemented field sampling campaigns were also simulated and compared. Likely scenarios were selected by reviewing the literature for tracking studies of the European shag and other closely related species. For example Cook *et al.* (2012) tracked samples of 8, 5 and 16 chick-rearing Cape cormorants *Phalacrocorax capensis* (from 3 colonies) representing both sexes over a 7 week period, Quintana *et al.* (2011) tracked 27 male and 26 female Imperial cormorants *Phalacrocorax atriceps* over three breeding seasons but only during the first two weeks of chick rearing, Kotzerka *et al.* (2011) tracked 14 chick-rearing male Cape cormorant *Phalacrocorax pelagicus* over a 6 week period and Watanabe *et al.* (2011) tracked 26 (20 males and 6 female) Kerguelen cormorants *Phalacrocorax verrucosus* which were rearing one or two chicks only. Eight sampling scenarios were devised; (A1) shags tracked between the 1st-14th May 2010 versus (A2) shags tracked between the 15th May-14th June 2010; (B1) shags breeding at the ledge site in 2010 versus (B2) shags breeding at the North side and beach sites in 2010; (C1) shags with chicks under 14 days old in 2011 versus (C2) shags with chicks over 14 days old in 2011 and finally (D1) all shags tracked in 2011 compared to (D2) all shags tracked in 2012. These samples included 6 - 11 individuals (29-181 foraging trips) reflecting commonly used field sample sizes.

Results

Each year, 18-21 loggers (20 in 2010, 18 in 2011 and 21 in 2012) were retrieved from shags breeding on Puffin Island. Two loggers in 2011 were retrieved waterlogged and all others were lost by the birds before they could be recaptured. Data from a mean of 9.7 (± 0.6 SEM) foraging trips were obtained per individual (range 2-20 trips). Mean total trip distance for all birds sampled over all years was 12.1 (± 0.8) km, mean trip duration was 95 (± 6) min, maximum distance travelled from the colony 6.1 (± 0.5) km and mean area used on each trip was 12.0 (± 0.7) km^2.

Total trip distance was found to differ significantly between the sexes ($p < 0.001$), with males travelling shorter distances (8.4 ± 0.5 km) than females (11.1 ± 0.5 km). Significant differences ($p = 0.022$) were also observed in total trip distance between individuals raising one chick (9.0 ± 0.8 km) and individuals raising three chicks (10.7 ± 0.5 km) (Table 5.3). Significant differences between all breeding sites were also observed ($p < 0.05$) with shags breeding at the ledge site exhibiting the greatest trip distance (11.6 ± 0.6 km) compared to those breeding at the North site (9.4 ± 0.6 km) and those breeding at the beach site (4.4 ± 0.6 km) (Fig. 5A).

Trip duration was most sensitive to the year of study with significant differences ($p < 0.02$) observed in trip duration between 2010 (90 ± 5 mins) and 2011 (76 ± 3 min), and between 2011 and 2012 (96 ± 5 min) (Fig. 5B). Sex also significantly affected trip duration ($p = 0.04$), with females having a shorter trip duration (72.5 ± 3 min) than males (94.6 ± 5 min). Individuals raising one chick at the time of tracking had significantly ($p = 0.0004$) shorter trip durations (75 ± 5 min) than those raising three chicks (95 ± 4 min). The age of chicks also significantly increased trip duration ($p = 0.049$) (Table 5.3).

Table 5.3: Summary of mean estimates (± SEM) by response variable and explanatory factor. P-values indicate significance of anova test of the variables stated in the contrast column. Highlighted cells = significant p-values.

	Trip distance			Trip duration			Maximum distance			Area used		
	Mean	*Contrast*	*p-value*	***Mean***	*Contrast*	*p-value*	***Mean***	*Contrast*	*p-value*	***Mean***	*Contrast*	*p-value*
Sex												
Female	11.1 ± 0.5	M:F	**<0.001**	94.6 ± 4.6	M:F	**0.04**	4.6 ± 0.2	M:F	**0.001**	12.6 ± 0.60	M:F	0.09
Male	8.4 ± 0.5			75.2 ± 2.9			3.6 ± 0.2			11.3 ± 0.5		
Chicks												
One	9.0 ± 0.8	1:2	0.44	75.2 ± 5.1	1:2	0.10	3.7 ± 0.3	1:2	0.323	10.7 ± 0.8	1:2	0.23
Two	8.1 ± 0.6	1:3	**0.02**	85.6 ± 4.2	1:3	**0.004**	3.5 ± 0.3	1:3	**0.016**	10.8 ± 0.6	1:3	**0.01**
Three	10.7 ± 0.5	2:3	0.10	94.6 ± 3.8	2:3	0.26	4.5 ± 0.2	2:3	0.162	12.9 ± 0.6	2:3	0.15
Site												
Beach	4.4 ± 0.6	L:B	**<0.001**	78.3 ± 6.0	L:B	0.11	1.8 ± 0.3	L:B	**<0.001**	7.28 ± 0.9	L:B	**<0.001**
Ledge	11.6 ± 0.6	N:B	**<0.001**	93.7 ± 3.7	N:B	0.92	4.9 ± 0.2	N:B	**<0.001**	13.5 ± 0.6	N:B	**0.02**
North side	9.4 ± 0.6	B:N	**0.003**	84.8 ± 4.1	B:N	**0.08**	4.1 ± 0.08	B:N	**0.0010**	11.1 ± 0.6	B:N	**0.005**
Year												
2010	8.0 ± 0.6	2010:2011	0.91	90.0 ± 5.2	2010:2011	**0.02**	3.2 ± 0.2	2010:2011	0.370	10.6 ± 0.6	2010:2011	0.76
2011	10.1 ± 0.7	2010:2012	0.38	77.5 ± 3.0	2010:2012	0.97	4.4 ± 0.3	2010:2012	0.072	12.4 ± 0.9	2010:2012	0.72
2012	10.2 ± 0.6	2011:2012	0.67	95.6 ± 4.7	2011:2012	**0.02**	4.4 ± 0.3	2011:2012	0.754	12.3 ± 0.6	2011:2012	1
	Slope						***Slope***			***Slope***		
Days	-0.009		0.03	-0.27		0.054	-0.013		0.361	-0.12		0.40
Age	-0.007		0.67	0.003		**0.049**	-0.01		0.052	-0.11		0.99

Maximum distance travelled was also found to be significantly different between the sexes ($p = 0.001$) with females travelling further (4.6 ± 0.2 km) than males (3.6 ± 0.2 km) (Fig. 5C). Significant differences ($p = 0.016$) were also observed in the maximum distance travelled between individuals raising one chick (3.7 ± 0.3 km) compared to individuals raising three chicks (4.5 ± 0.2 km) and between all breeding sites ($p < 0.001$) with shags breeding at the ledge site exhibiting the greatest maximum distance travelled (4.9 ± 0.2 km) compared to those breeding at the North site (4.1 ± 0.08 km) and those breeding at the beach site (1.8 ± 0.3 km) (Table 5.3).

The area used (km^2) on each foraging trip was most sensitive to breeding site with significant differences found between all sites (< 0.05) (Table 5.3). Those breeding at the beach site foraged over a smaller area (7.3 ± 0.9 km^2) compared to those breeding at the North site (11.1 ± 0.6 km^2) and the ledge site (13.5 ± 0.6 km^2) (Fig. 5). Significant differences in foraging area were also observed between shags rearing one chick (10.7 ± 0.8 km^2) compared to those rearing three chicks (12.9 ± 0.6 km^2) (Fig. 5.1D). Maps of time spent in 1 km^2 cells revealed different areas of use for shags rearing one chick compared to those rearing three chicks and for shags breeding at the three different sites (Fig. 5.2 & 5.3).

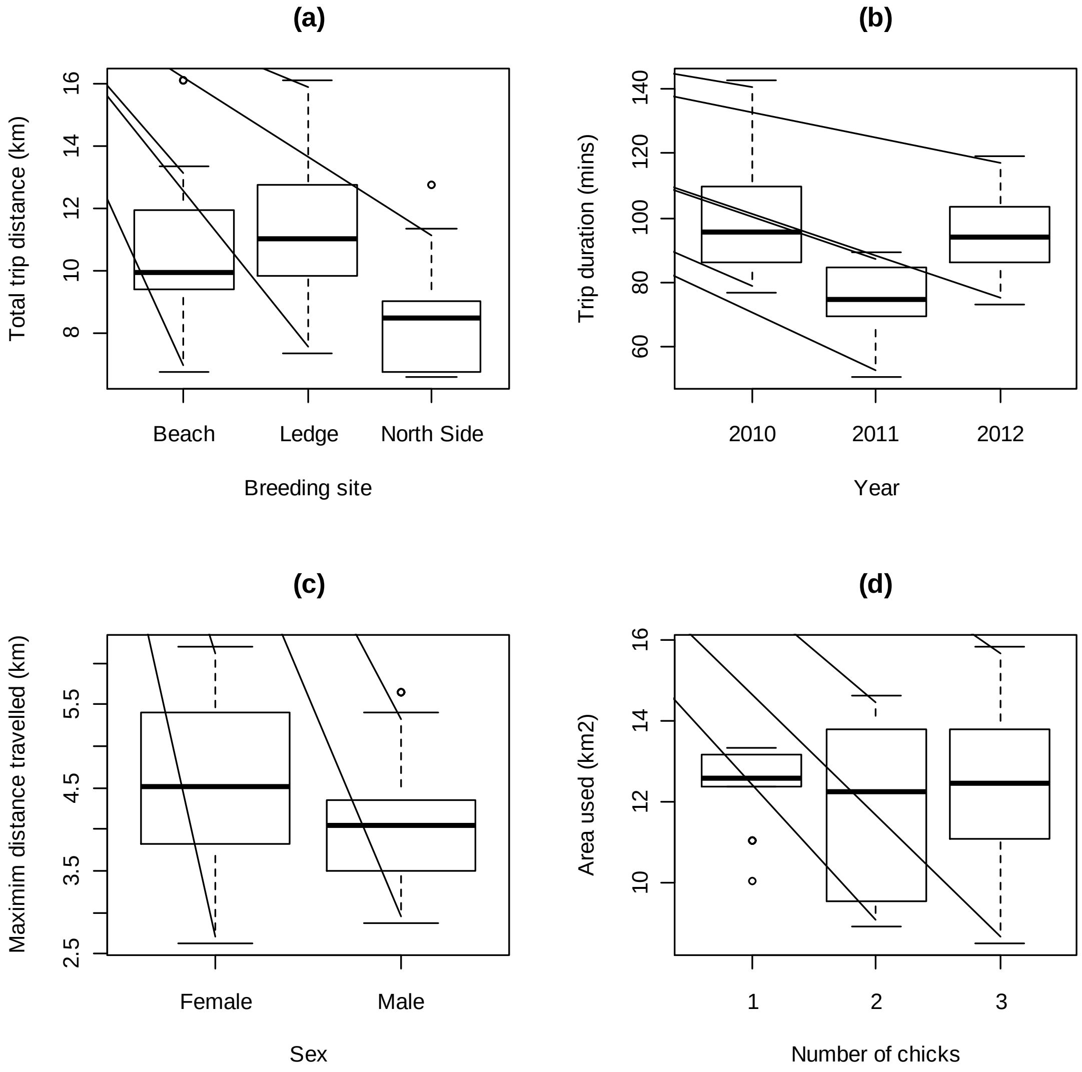
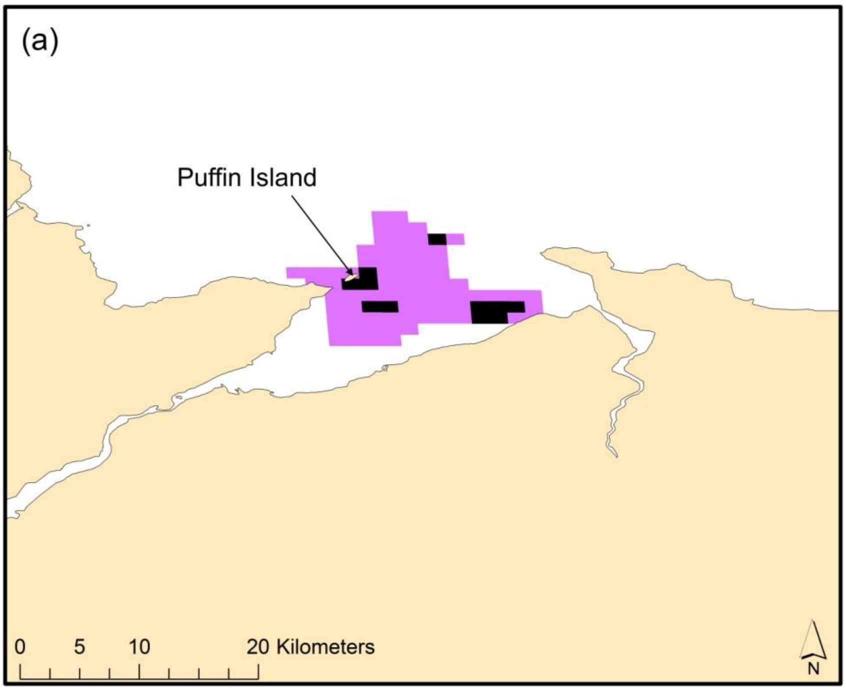


Figure 5.1. Examples of the mean differences in the foraging trip response variables significantly affected by the explanatory variables



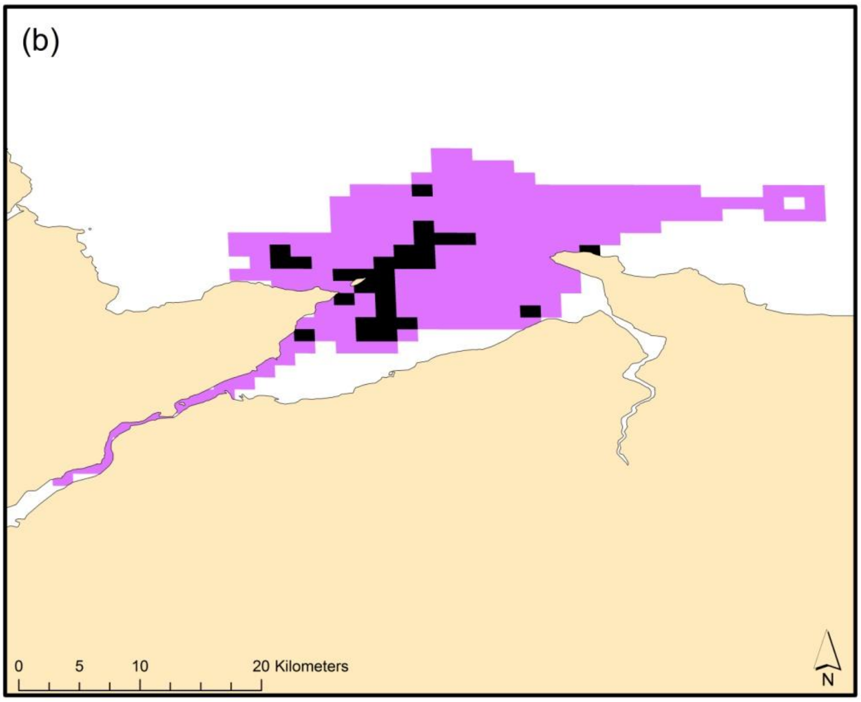


Figure 5.2. Time spent in pre-defined 1 x 1 km cells for (a) shags with one chick and (b) shags with three chicks. Black squares indicate where 50% of all time was spent, pink squares indicate where 100% of time was spent.

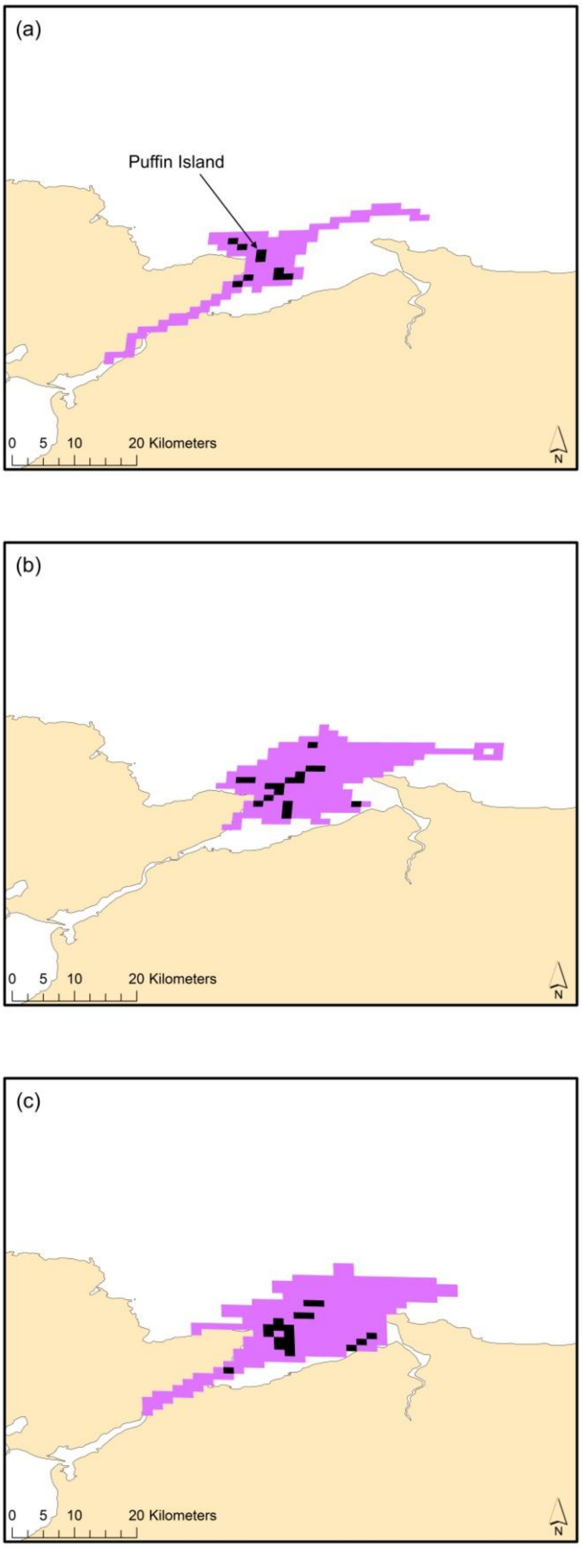


Figure 5.3. Time spent in pre-defined 1 x 1 km cells for (a) shags breeding at the beach site and (b) shags breeding at the North site and (c) shags breeding at the ledge. Black squares indicate where 50% of all time was spent; pink squares indicate where 100% of time was spent.

For direction travelled, significant differences were found between sites ($F_{2,\ 520}$= 78.551, $p < 0.001$). Pair-wise comparisons revealed significant differences between the beach & North site (F_{250}=139.7, $p < 0.001$); beach and ledge (F_{342} = 140.6, $p < 0.001$) and ledge and North site (F_{448} =17.0, $p < 0.001$). Trips originating from the beach site travelled a mean bearing of 22.6.^{0} (SD 73.3^0), from the North side site 70.32^0 (SD 80.8^0) and from the ledge site 100.5^0 (SD 53.8^0) (Fig. 5.4). Significant differences ($p < 0.05$) were not observed in the direction travelled between males and females, between years or between individuals which were raising one, two or three chicks at the time of tracking.

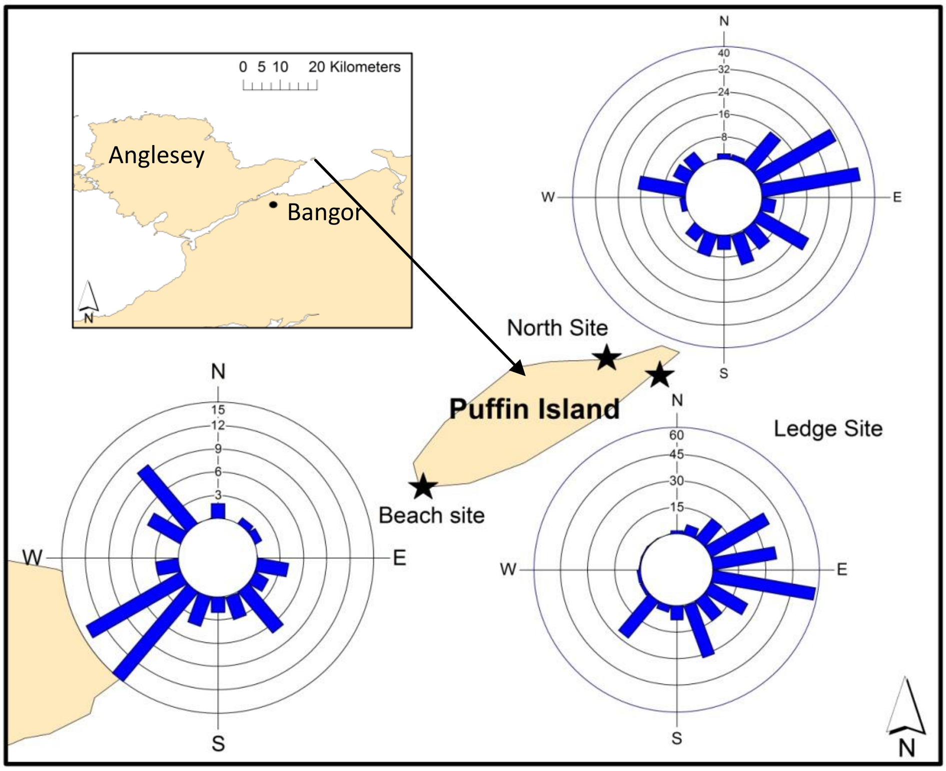
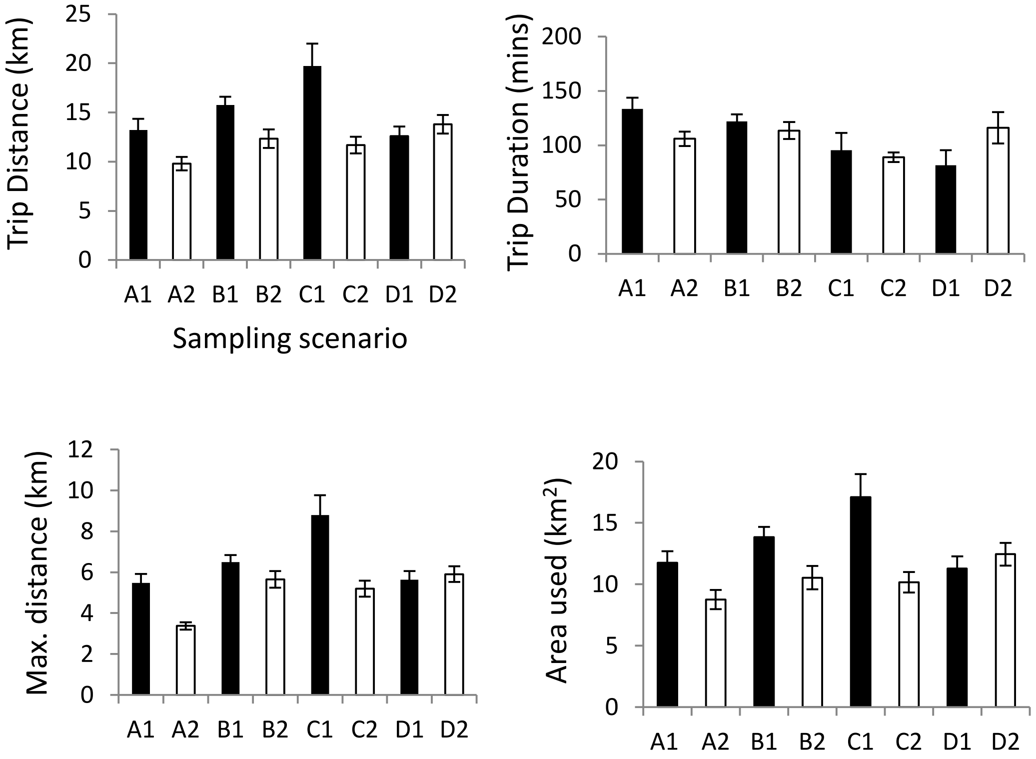


Figure 5.4. The direction travelled on each foraging trip made at the three sites on the island (beach, ledge and North side). Insert map shows the location of Puffin Island (53.3^{o}N, 4.0^{o}W) in relation to the Isle of Anglesey and the North Coast of Wales.

Different sampling regimes produced different estimates for all foraging trip response variables (Fig. 5.5), in some cases predicting a difference in up to 50% for the foraging trip parameters. For example, using a sample from 2010 tracked over a three week period between mid May to the first week of June produced a foraging trip distance of 9.8 (standard error ± 0.7) km compared to 13.2 (± 1.1) km for a sample tracked in the same year but earlier in the season (Fig. 5.5, A1 versus. A2). Tracking individuals breeding at the ledge site in 2010 produced a foraging area estimate of 13.8 (± 0.8) km^2 compared to 10.5 (± 0.95) km^2 when sampling individuals only from the North and beach sites (Fig. 5.5. B1 versus B2). Similarly a sample tracked in 2011 with chicks under 14 days old produced a maximum foraging trip distance of 8.8 (± 0.97) km compared to 5.1 (± 0.38) km from a sample of individuals tracked in the same year but that was composed only of individuals with chicks over 14 days old (Fig. 5.5. C1 versus C2). Trip duration was found to be greater by 26 minutes in 2012 (116 ± 15) mins compared to trip duration in 2011 (82 ± 14 min) (Fig. 5.5. D1 versus D2).



A1 = 1st-14th May 2010
A2 = 15th May – 14th June 2010

B1 = Ledge 2010
B2 = North side & beach sites 2010

C1 = Chicks under 14 days 2011
C2 = Chicks over 14 days 2011

D1 = 2011
D2 = 2012

Figure 5.5. Different sampling scenarios and the effect on average foraging trip distance, trip duration, maximum distance travelled from the colony and the area used (± standard error).

Discussion

The European shag is widespread throughout north-western and southern Europe where more than 75% of the global population is found. In the UK, this species breeds on coastal sites, mainly in the north and west, where over half their population is found at fewer than 10 sites, making them an Amber listed species (Eaton *et al*., 2009). This is the first published study reporting the foraging behaviour of the European shag determined using GPS technology. Previous studies on this species have used observations at sea and radio telemetry techniques (Wanless *et al*., 1991, Wanless *et al*., 1998, Elkins and Williams, 1974). Understanding the foraging behaviour of the European shag is important, particularly with the anticipated rise in offshore marine renewable developments occurring in UK waters (RenewableUK, 2011), as given the coastal nature of this species, it is likely to be more susceptible to offshore marine developments (Langton *et al*., 2011).

Intraspecific variation in foraging ecology has previously been observed for other central place foragers. For example, Austin *et al.* (2003) found wide variation in the foraging ecology of individual Grey seals *Halichoerus grypus*, and warned that the practice of examining average responses over populations obscures variability in behavioural ecology. Bonadonna *et al.* (2001) found that Antarctic fur seals *Arctocephalus gazella* exhibited two foraging tactics which were repeatable within an individual. Bolnick *et al.* (2002) stated the degree of individual specialisation varies widely within a population as a result of the diverse array of physiological, behavioural and ecological mechanisms that can act upon an individual. This study conducted over three consecutive field seasons revealed that all five of the foraging trip response variables examined (foraging trip distance, foraging trip duration, maximum distance travelled from the colony, area used and the direction travelled from the colony) can all be influenced by the explanatory factors included in the GEE model (sex, age of chicks, number of chicks, breeding site, day of season and year of study).

The most important of the explanatory factors tested on trip duration, the maximum distance travelled from the colony and the area used was the breeding site, with those breeding at the beach site having a reduced foraging trip duration, maximum distance and area compared to those breeding at the North site and the ledge. The direction travelled between these sites was also found to be significantly different (Fig. 5.2). This is an important finding as the logistics of seabird tracking work often means only sub-colonies from any site can or are sampled. Puffin Island is only 1.4 km long and 0.5 km at its widest point, but even at this relatively small colony, significant differences in the foraging parameters of shags breeding at different sub-colonies were observed. Similarly Hipfner *et al*. (2007) found that small-scale distribution influenced the parental foraging effort of the Tufted puffins *Fratercula cirrhata* breeding at two sub-colonies only 1.5 km apart on a single island based on stable isotope analysis. At a larger geographic scale Lescroel and Bost (2005) found that the foraging behaviour of Gentoo penguins *Pygoscelis papua* breeding at different sites within the Kerguelen archaelopeligo were more variable that the foraging behaviour observed across the rest of its southern hemisphere range. Individuals breeding at different sites may represent birds of different status (e.g. younger, inexperienced breeders). For example, Aebischer and Couslon (1990) reported that survival of Black-legged kittiwake *Rissa tridactyla* was greater for those nesting in the middle of a colony compared to those on the outskirts, probably related to intrinsically fit and less fit individuals. However, European shags have been reported as either selecting nesting sites randomly or that low quality birds nest preferentially closer to higher quality individuals (Velando and Freire, 2001). The number of chicks reaching 30-35 days old in each nest in our study was compared between each breeding site using a Kruskal Wallis one-way analysis on ranks. No significant differences were found in the number of chicks raised between the sites ($H_{df=2} = 2.971$, $p = 0.226$) therefore factors other than individual quality may explain differences in the foraging behaviour at these breeding sites such as bathymetric or oceanographic features around the island (Wienecke and Robertson, 2006).

Foraging trip total distance, trip duration, the maximum distance travelled from the colony and the area used were all significantly affected by the number of chicks an individual was raising with those raising three chicks making significantly longer trips than those raising one chick. No previously reported studies have related foraging trip characteristics to the number of chicks a seabird is rearing. However, studies have examined parental effort in relation to brood size, for example Gonzales-Medina *et al.* (2010) found the number of feeding sessions was significantly greater for Laughing gull *Leucophaeus atricilla* rearing three chicks compared to one chick. Similarly, Robinson *et al.* (2001) suggested that common terns, that generally raise three chicks, exhibited a higher rate of food delivery than Arctic terns *Sterna paradisaea*, which generally raise two chicks, (despite the adults birds being of similar size and morphology), thus indicating that having more chicks results in shorter foraging trips. This study found individuals raising three chicks made longer foraging trips, perhaps indicating more favourable foraging grounds further from the colony or that higher quality individuals had the ability to exploit these better resources and therefore provision for more chicks (Lescroel *et al*., 2009, Lescroel *et al*., 2010).

Total trip distance, trip duration and the maximum distance travelled were also significantly affected by sex, with females travelling on average for longer than males. Differences in foraging behaviour between sexes has been widely reported for many seabird species. Weimerskirch *et al*. (2009) found that female Brown boobies *Sula leucogaster* and Blue-footed boobies *Sula nebouxii* tended to have longer foraging trips, foraged farther from the colony, flew greater distances and had larger zones of area-restricted search than males. Quintana *et al.* (2011) reported that male and female Imperial cormorants *Phalacrocorax atriceps* travelled away from their colony using routes virtually perpendicular to each other so that their foraging areas were distinctly different, with females foraging close to the coast while males foraged offshore in deeper water. These studies and the present study represent sexually dimorphic seabirds which could explain the differences observed although studies where males and females are monomorphic have also been reported. Paredes *et al.* (2008) found that female Brunichs guillemot *Uria lomvia* more commonly foraged during twilight periods and dived shallower than males which foraged primarily during daylight hours and Pinet *et al*. (2012) studied the Barau’s petrel *Pterodroma baraui* throughout the breeding period and found sexual differences in foraging habitats and activities. For the sexually dimorphic shag in our study, the smaller females tended on average to travel further and use a larger foraging area than males perhaps reflecting their ability to dive to different depths to exploit prey resources (Quillfeldt *et al.,* 2011, Cook *et al.,* 2007) or could result from competitive exclusion (Phillips *et al.,* 2011).

The year of study was an important factor influencing the trip duration but not the other response variables. When comparing 2011 with 2010 and 2012, birds in 2010 travelled the same distance from the colony and the same total distance as the other years but spent longer on foraging trips. The effect of year of study on foraging strategy is predictable given the variability in climatic and weather patterns in any year, which directly relate to sea surface temperature and chlorophyll a abundance which will in turn affect the productivity of the ocean. Inter- annual variance in the foraging behaviour of seabirds has often been reported (Chivers *et al.*, 2012, Garthe *et al.*, 2011). However, only 2 out of the 25 studies published between November 2011-November 2012 (Table 5.1) tracked seabirds for more than one breeding season. Whilst this may not be necessary for the objectives of some studies, for those aiming to identify important foraging ranges and foraging areas, it should be important to consider inter-annual variation given the range of environmental factors that could potentially influence the year of study.

The different hypothetical sampling regimes analysed in this study produced quite different estimates for the foraging trip variables. This study highlights the problem of using small sample sizes coupled with a failure to consider the effects of behavioural, environmental and ecological effects on an individual's foraging behaviour. Drawing inferences to the population as a whole from small samples representing a limited spatial, temporal or behavioural scale are unlikely to fully represent the population (Lindberg and Walker, 2007).

Including a larger number of individuals and foraging trips in a sample in any single year will help reduce the influence of variability in foraging trip characteristics caused by factors such as sex, breeding site etc. (Soanes *et al.*, 2013b). However as highlighted, samples used in tracking studies are often small. The European shag is a localised coastal feeder, the average distance travelled from the colony on Puffin Island was 5.6 km (range 0.2-19.9 km). Yet even for this relatively short distance forager, the impacts of the explanatory variables were significant on foraging response variable predictions. It is likely that seabirds which have a larger foraging radius may exhibit even greater differences in their foraging behaviour in relation to the explanatory variables tested. Therefore the selection of individuals and timing of tracking for inclusion in tracking studies of any central-place forager are important factors to consider to ensure that the limited samples often used in such studies most accurately predict the colony's foraging characteristics.

Acknowledgements

This project was funded by a Doctoral Training Grant from the Natural Environment Research Council, with support from the RSPB's FAME project. We would like to thank Dr. Charles Bishop, Ashley Tweedale, Dr. Rachel Taylor (Bangor University), and volunteers from both the University of Liverpool and Bangor University for assistance with planning and fieldwork. Data collection on Puffin Island would not have been possible without permission to carryout fieldwork from Sir Richard Williams-Bulkeley. Permission was granted by the Countryside Council for Wales to conduct bird capture and tagging work on Puffin Island

References

Aebischer, N.J. & Coulson, J.C. (1990) Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *Journal of Animal Ecology,* **59,** 1063-1071.

Alonso H, Granadeiro JP, Paiva VH, Dias AS, Ramos JA, Catry P (2012) Parent-offspring dietary segregation of Cory's shearwaters breeding in contrasting environments. *Marine Biology* **159** 1197-1207

Austin, D., Bowen, W.D. & McMillan, J.I. (2004) Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos,* **105,** 15-30.

Bates, D., Maechler, M. & Bolker, B. (2011) R Package "lme4": Linear mixed-effects models using S4 classes. http://cran.r-project.org.

Batschelet, E. (1981) *Circular statistics in biology*. New York.

BirdLife International (2010) Marine Important Bird Areas toolkit: standardised techniques for identifiing priority sites for the conservation of seabirds at sea. (ed. B. International). Birdlife International, Cambridge, UK.

Biro, P.A. & Stamps, J.A. (2010) Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology & Evolution,* **25,** 653-659.

Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003) The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist,* **161,** 1-28.

Bonadonna, F., Lea, M.A., Dehorter, O. & Guinet, C. (2001) Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal *Arctocephalus gazella*. *Marine Ecology-Progress Series,* **223,** 287-297.

Bugoni, L., D'Alba, L. & Furness, R.W. (2009) Marine habitat use of wintering spectacled petrels Procellaria conspicillata, and overlap with longline fishery. *Marine Ecology-Progress Series,* **374,** 273-285.

Burger, A.E. & Shaffer, S.A. (2008) Application of tracking and data-logging technology in research and conservation of seabirds. *Auk,* **125,** 253-264.

Casper, R.M., Sumner, M.D., Hindell, M.A., Gales, N.J., Staniland, I.J. & Goldsworthy, S.D. (2010) The influence of diet on foraging habitat models: a case study using nursing Antarctic fur seals. *Ecography,* **33,** 748-749.

Chivers, L.S., Lundy, M.G., Colhoun, K., Newton, S.F., Houghton, J.D.R. & Reid, N. (2012) Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. *Marine Ecology-Progress Series,* **456,** 269-267.

Christel, I., Navarro, J., del Castillo, M., Cama, A. & Ferrer, X. (2012) Foraging movements of Audouin's gull (Larus audo*uinii) in the E*bro Delta, NW Mediterranean: A preliminary satellite-tracking study. *Estuarine Coastal and Shelf Science,* **96,** 257-261.

Cook, T.R., Cherel, Y., Bost, C.-A. & Tremblayz, M. (2007) Chick-rearing Crozet shags (*Phalacrocorax melanogenis*) display sex-specific foraging behaviour. *Antarctic Science,* **19,** 55-63.

Copello, S. & Quintana, F. (2009) Spatio-temporal overlap between the at-sea distribution of Southern Giant Petrels and fisheries at the Patagonian Shelf. *Polar Biology,* **32,** 1211-1220.

Daunt, F., Wanless, S., Harris, M.P., Money, L. & Monaghan, P. (2007) Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology,* **21,** 561-567.

Durant, J.M., Hjermann, D.O., Frederiksen, M., Charrassin, J.B., Le Maho, Y., Sabarros, P.S., Crawford, R.J.M. & Stenseth, N.C. (2009) Pros and cons of using seabirds as ecological indicators. *Climate Research,* **39,** 115-129.

De Monte, S., Cotte, C., d'Ovidio, F., Levy, M., Le Corre, M. & Weimerskirch, H. (2012) Frigatebird behaviour at the ocean-atmosphere interface: integrating animal behaviour with multi-satellite data. *Journal of the Royal Society Interface,* **9,** 3351-3358.

Eaton, M., Brown, A., Noble, D., Musgrove, A., Hearn, R., Aebischer, N., Gibbons, D., Evans, A. & Gregory, R. (2009) Birds of Conservation Concern 3: the population status of birds in the United Kingdom, Channel Islands and the Isle of Man. *British Birds,* **102,** 296-341.

Elkins, N. & Williams, M.R. (1974) Shag movements in North-East Scotland. *Bird Study,* **21,** 149-151.

Ford, R.G. (1979) The analysis of Space use Patterns. *Journal of Theroetical Biology***,** 125-155.

Fort, J., Beaugrand, G., Gremillet, D. & Phillips, R.A. (2012) Biologging, Remotely-Sensed Oceanography and the Continuous Plankton Recorder Reveal the Environmental Determinants of a Seabird Wintering Hotspot. *Plos One,* **7**.

Garthe, S., Montevecchi, W.A. & Davoren, G.K. (2011) Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnology and Oceanography,* **56,** 802-812.

Gonzalez-Medina, E., Castillo-Guerrero, J.A. & Mellink, E. (2010) Parental and chick responses of Laughing Gulls (*Leucophaeus atricilla*) to increase of flight costs and brood size. *Journal of Ornithology,* **151,** 687-694.

Gremillet, D., Prudor, A., le Maho, Y. & Weimerskirch, H. (2012) Vultures of the seas: hyperacidic stomachs in wandering albatrosses as an adaptation to dispersed food resources, including fishery wastes. *PloS one,* **7**.

Guilford, T., Wynn, R., McMinn, M., Rodriguez, A., Fayet, A., Maurice, L., Jones, A. & Meier, R. (2012) Geolocators Reveal Migration and Pre-Breeding Behaviour of the Critically Endangered Balearic Shearwater Puffinus mauretanicus. *Plos One,* **7**.

Harris, J., Haward, M., Jabour, J. & Woehler, E.J. (2007) A new approach to selecting Marine Protected Areas (MPAs) in the Southern Ocean. *Antarctic Science,* **19,** 189-194.

Harris, M.P., Bogdanova, M.I., Daunt, F. & Wanless, S. (2012) Using GPS technology to assess feeding areas of Atlantic Puffins *Fratercula arctica*. *Ringing & Migration,* **27,** 43-49.

Hedd, A., Montevecchi, W.A., Otley, H., Phillips, R.A. & Fifield, D.A. (2012) Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. *Marine Ecology-Progress Series,* **449,** 277-290.

Hipfner, J.M., Charette, M.R. & Blackburn, G.S. (2007) Subcolony variation in breeding success in the tufted puffin (*Fratercula cirrhata*): Association with foraging ecology and implications. *Auk,* **124,** 1149-1157.

Hyrenbach, K.D., Keiper, C., Allen, S.G., Ainley, D.G. & Anderson, D.J. (2006) Use of marine sanctuaries by far-ranging predators: commuting flights to the California Current System by breeding Hawaiian albatrosses. *Fisheries Oceanography,* **15,** 95-103.

Højsgaard, S., Halekoh, U. & Yan, J. (2012) The R package geepack for Generalised Estimating Equations. *Journal of Statistical Software,* **15,** 1-11.

Jakubas, D., Iliszko, L., Wojczulanis-Jakubas, K. & Stempniewicz, L. (2012) Foraging by little auks in the distant marginal sea ice zone during the chick-rearing period. *Polar Biology,* **35,** 73-81.

Kotzerka, J., Hatch, S.A. & Garthe, S. (2011) Evidence for foraging-site fidelity and individual foraging behaviour of pelagic cormorants rearing chicks in the Gulf of Alsaka *Condor,* **113,** 80-88.

Langton, R., Davies, I.M. & Scott, B.E. (2011) Seabird conservation and tidal stream and wave power generation: Information needs for predicting and managing potential impacts. *Marine Policy,* **35,** 623-630.

Lescroel, A., Ballard, G., Toniolo, V., Barton, K.J., Wilson, P.R., Lyver, P.O. & Ainley, D.G. (2010) Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology,* **91,** 2044-2055.

Lescroel, A. & Bost, C.A. (2005) Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Marine Ecology-Progress Series,* **302,** 245:261.

Liang, K.Y. & Zeger, S.L. (1986) Longitudinal data-analysis using generalized linear models. *Biometrika,* **73,** 13-22.

Lindberg, M.S. & Walker, J. (2007) Satellite telemetry in avian research and management: Sample size considerations. *Journal of Wildlife Management,* **71,** 1002-1009.

Louzao, M., Delord, K., Garcia, D., Boue, A. & Weimerskirch, H. (2012) Protecting Persistent Dynamic Oceanographic Features: Transboundary Conservation Efforts Are Needed for the Critically Endangered Balearic Shearwater. *Plos One,* **7**.

Magnusdottir, E., Leat, E.H.K., Bourgeon, S., Strom, H., Petersen, A., Phillips, R.A., Hanssen, S.A., Bustnes, J.O., Hersteinsson, P. & Furness, R.W. (2012) Wintering areas of Great Skuas Stercorarius skua breeding in Scotland, Iceland and Norway. *Bird Study,* **59**.

McLeay, L.J., Page, B., Goldsworthy, S.D., Paton, D.C., Teixeira, C., Burch, P. & Ward, T. (2010) Foraging behaviour and habitat use of a short-ranging seabird, the crested tern. *Marine Ecology-Progress Series,* **411,** 271-283.

Montevecchi, W., Fifield, D., Burke, C., Garthe, S., Hedd, A., Rail, J.-F. & Robertson, G. (2012) Tracking long-distance migration to assess marine pollution impact. *Biology Letters,* **8,** 218-221.

Moseley, C., Gremillet, D., Connan, M., Ryan, P.G., Mullers, R.H.E., van der Lingen, C.D., Miller, T.W., Coetzee, J.C., Crawford, R.J.M., Sabarros, P., McQuaid, C.D. & Pichegru, L. (2012) Foraging ecology and ecophysiology of Cape gannets from colonies in contrasting feeding environments. *Journal of Experimental Marine Biology and Ecology,* **422**.

Page, B., McKenzie, J., Sumner, M.D., Coyne, M. & Goldsworthy, S.D. (2006) Spatial separation of foraging habitats among New Zealand fur seals. *Marine Ecology-Progress Series,* **323,** 263-279.

Paredes, R., Jones, I.L., Boness, D.J., Tremblay, Y. & Renner, M. (2008) Sex-specific differences in diving behaviour of two sympatric Alcini species: thick-billed murres and razorbills. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* **86,** 610-622.

Perrow, M.R., Skeate, E.R., Lines, P., Brown, D. & Tomlinson, M.L. (2006) Radio telemetry as a tool for impact assessment of wind farms: the case of Little Terns *Sterna albifrons* at Scroby Sands, Norfolk, UK. *Ibis,* **148,** 57-75.

Peron, C., Weimerskirch, H. & Bost, C.-A. (2012) Projected poleward shift of king penguins' (Aptenodytes patagonicus) foraging range at the Crozet Islands, southern Indian Ocean. *Proceedings of the Royal Society B-Biological Sciences,* **279**.

Phillips, R.A., McGill, R.A.R., Dawson, D.A. & Bearhop, S. (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Marine Biology,* **158,** 2199-2208.

Pinet, P., Jaquemet, S., Phillips, R.A. & Le Corre, M. (2012) Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Animal Behaviour,* **83,** 979-989.

Quillfeldt, P., McGill, R.A.R., Furness, R.W., Moestl, E., Ludynia, K. & Masello, J.F. (2012) Impact of miniature geolocation loggers on a small petrel, the thin-billed prion *Pachyptila belcheri*. *Marine Biology,* **159,** 1809-1816.

Quintana, F., Wilson, R., Dell'Arciprete, P., Shepard, E. & Gomez Laich, A. (2011) Women from Venus, men from Mars: inter-sex foraging differences in the imperial cormorant *Phalacrocorax atriceps* a colonial seabird. *Oikos,* **120,** 350-358.

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramos, R., Granadeiro, J.P., Nevoux, M., Mougin, J.-L., Dias, M.P. & Catry, P. (2012) Combined spatio-temporal impacts of climate and longline fisheries on the survival of a trans-equatorial marine migrant. *PloS one,* **7**.

RenewableUK (2011) State of the industry report Onshore and offshore wind: progress update. RenewableUK, UK.

Robinson, J.A., Hamer, K.C. & Chivers, L.S. (2001) Contrasting brood sizes in Common and Arctic Terns: The roles of food provisioning rates and parental brooding. *Condor,* **103,** 108-117.

Sala, J.E., Wilson, R.P., Frere, E. & Quintana, F. (2012) Foraging effort in Magellanic penguins in coastal Patagonia, Argentina. *Marine Ecology-Progress Series,* **464,** 273-287.

Shaffer, S.A., Tremblay, Y., Awkerman, J.A., Henry, R.W., Teo, S.L.H., Anderson, D.J., Croll, D.A., Block, B.A. & Costa, D.P. (2005) Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology,* **147,** 833-843.

Soanes, L., Gauvain, R., Atkinson, P. & Green, J. (2013a) Individual consistency in the foraging behaviour of Northern gannets: implications for interactions with offshore renewable energy developments. *Marine Policy,* ***38,*** 505-514.

Soanes, L., Arnould, J., Dodd, S., Sumner, M. & Green, J. (2012b) How many seabirds do we need to define important foraging areas. *Journal of Applied Ecology,* **50** (3) 671-679.

Stauss, C., Bearhop, S., Bodey, T.W., Garthe, S., Gunn, C., Grecian, W.J., Inger, R., Knight, M.E., Newton, J., Patrick, S.C., Phillips, R.A., Waggitt, J.J. & Votier, S.C. (2012) Sex-specific foraging behaviour in northern gannets Morus bassanus: incidence and implications. *Marine Ecology Progress Series,* **457,** 151-162.

Stenhouse, I.J., Egevang, C. & Phillips, R.A. (2012) Trans-equatorial migration, staging sites and wintering area of Sabine's Gulls *Larus sabini* in the Atlantic Ocean. *Ibis,* **154,** 42051.

Suarez, N., Retana, M.V. & Yorio, P. (2012) Spatial patterns in the use of foraging areas and its relationship with prey resources in the threatened Olrog's Gull (Larus atlanticus). *Journal of Ornithology,* **153,** 861-871.

Sumner, M. (2012) Package "Trip". CRAN.r.project.org.

Team., R.D.C. (2012) R: A language and environment for statistical. R Foundation for Statistical Computing, Vienna, Austria.

Thaxter, C., Lascelles, B., Sugar, K., Cook, A., Roos, S., Bolton, M., Langston, R. &

Burton, N. (2012) Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation,* **156,** 53-61.

Thiebot, J.-B., Cherel, Y., Trathan, P.N. & Bost, C.-A. (2012) Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. *Ecology,* **93**.

Velando, A. & Freire, J. (2001) How general is the central-periphery distribution among seabird colonies? Nest spatial pattern in the European Shag. *Condor,* **103,** 544-554.

Wakefield, E.D., Phillips, R.A. & Belchier, M. (2012) Foraging black-browed albatrosses target waters overlaying moraine banks - a consequence of upward benthic-pelagic coupling? *Antarctic Science,* **24**.

Wanless, S., Frederiksen, M., Daunt, F., Scott, B.E. & Harris, M.P. (2007) Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. *Progress in Oceanography,* **72,** 30-38.

Wanless, S., Gremillet, D. & Harris, M.P. (1998) Foraging activity and performance of Shags Phalacrocorax aristotelis in relation to environmental characteristics. *Journal of Avian Biology,* **29,** 49-54.

Wanless, S., Harris, M.P. & Morris, J.A. (1991) foraging range and feeding locations of shags *Phalacrocorax-aristotelis* during chick rearing. *Ibis,* **133,** 30-36.

Watanabe, Y.Y., Takahashi, A., Sato, K., Viviant, M. & Bost, C.A. (2011) Poor flight performance in deep-diving cormorants. *Journal of Experimental Biology,* **214,** 412-421.

Weimerskirch, H., Shaffer, S.A., Tremblay, Y., Costa, D.P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K. & Aurioles, D. (2009) Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Marine Ecology-Progress Series,* **391,** 267-278.

Weimerskirch, H., Bertrand, S., Silva, J., Bost, C. & Peraltilla, S. (2012) Foraging in Guanay cormorant and Peruvian booby, the major guano-producing seabirds in the Humboldt Current System. *Marine Ecology-Progress Series,* **458,** 231-145.

Wienecke, B. & Robertson, G. (2006) Comparison of foraging strategies of incubating king penguins Aptenodytes patagonicus from Macquarie and Heard islands. *Polar Biology,* **29,** 424-438.

Wilson, R.P., Gremillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., Schafer-Neth, C., Scolaro, J.A., Bost, C.A., Plotz, J. & Nel, D. (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology-Progress Series,* **228,** 241-261.

Wilson, R.P., Putz, K., Peters, G., Culik, B., Scolaro, J.A., Charrassin, J.B. & RopertCoudert, Y. (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin,* **25,** 101-106.

Chapter 6

Foraging behaviour of the Black-legged kittiwake: The role of ecological and environmental factors.

Soanes, L.M.[a], Arnould, J.P.Y [b], Dodd, S.D.[c], Green, J.A.[a]

[a] School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP.[b] School of Life and Environmental Sciences, Deakin University, Burwood, 3215, Australia.[c] Royal Society for the Protection of Birds, North Wales Office, Bangor, LL57 4FD.

Photograph by Johann Bourgeois 2012

Author contributions: LMS & JAG designed the study, LMS & SGD conducted fieldwork, JPYA provided financial support for the research. LMS analysed and wrote this manuscript with support from JAG,

Abstract

The Black-legged kittiwake *Rissa tridactyla* has been well studied throughout its breeding range and, as such, we have a good understanding of this species' life history characteristics and population dynamics. The abundance of the Black-legged kittiwake and its relatively limited capacity to switch prey sources, has meant this species has often been advocated as a suitable "bio-indicator" of the marine environment, and tracking studies have been employed for this purpose. Here we examine how ecological (sex, stage of breeding and number of chicks an individual is rearing) and environmental (year of study, timing of tracking and wind speed) factors influence the foraging trip characteristics of this species, and find that stage of breeding (incubating or chick-rearing), significantly affects the foraging trip characteristics as does year of study. These findings were put into the context of marine spatial planning and used to examine foraging area overlap with the Irish Sea offshore wind development zone. It was found that 31% of the chick-rearing individuals tracked over three years had foraging trips that overlapped with the proposed wind farm area compared to 58% of incubating individuals tracked over the same three years. Thus, highlighting the importance of sampling at a range of temporal and spatial scales to gain the most representative data from any study colony, before conclusions on identifying important foraging areas can be made.

Introduction

The Black-legged kittiwake *Rissa tridactyla* (Linnaeus 1758) (from here on referred to as "kittiwake") is the most abundant gull species in the world, with about 9,000,000 adults distributed through the Northern hemisphere (Coulson 2011). In the UK, which supports 8% of its global population, a 25% decline was reported between 1988 and 2002. This change in numbers has been attributed to declines in the abundance of their prey related to climate change, and the presence of large sandeel fisheries in the North Sea (Frederiksen *et al.* 2004). In some years productivity has been so poor, that no chicks fledge from colonies; in 2008 only one chick on average was fledged from every four nests, compared with close to one per nest between 1986 and 1995 (Mitchell & Dunn 2004). However, breeding success for this species does vary widely between years, for example in 2011 productivity had increased to 0.7 chicks per pair. Kittiwakes, as surface-feeders, are particularly susceptible to changes in their food source, therefore have a limited capacity to switch to alternate prey sources (Furness & Tasker 2000).

Because of the kittiwakes' dependence on limited prey sources, this species has often been recommended as being an appropriate "bio-indicator" of changes in the oceanic habitat. For example, Iversen *et al.* (2007) suggested that kittiwakes are effective samplers of prey populations, and their diets can provide valuable information about lower trophic levels. Piatt *et al.* (2007) reported that kittiwake breeding success was strongly influenced by food supply, and Frederiksen *et al.* (2007) found that both regional and annual variation in kittiwake breeding performance was related to sea surface temperature. As well as relating changes in the marine environment to kittiwake breeding parameters, the availability of smaller and more affordable tracking technologies has enabled researchers to examine how kittiwakes may alter or adapt their foraging behaviour to account for changes in their marine environment. For example, using radio telemetry and examination of diet Suryan *et al.* (2000) demonstrated that kittiwakes exhibited prey switching and a considerable increase in foraging range in response to an apparent decrease in 1-year old herring. Similarly Hamer *et al.* (1993) radio-tracked individuals in two years; one of which where sandeel abundance was measured to be 10 times higher, in the low abundance year no chicks fledged and foraging trips recorded were approximately three times longer with individuals flying more than 40 km from the colony, compared to 68% fledging success in the high abundance year, when individuals were recorded flying on average 5 km from the colony. Thus, the observable changes in the breeding success and foraging behaviour of kittiwakes can be related to environmental parameters, making this species a suitable candidate for monitoring environmental change and potentially for assessing the effects of man-made disturbance to its marine environment such as offshore renewable energy developments.

The use of seabirds as bio-indicators has its pros and cons (Durant *et al.* 2009). One factor that should be considered is individuals within a seabird colony do not all behave in the same way and may vary in terms of life history characteristics such as phenology, feeding and wintering areas, productivity, survival and foraging behaviour (Hamer & Hill 1993, Wendeln & Becker 1999, Suryan *et al.* 2000, Kotzerka *et al*. 2011, Chivers *et al*. 2012). Using kittiwakes as ecological indicators to monitor environmental conditions has its advantages (Piatt *et al*. 2007, Parsons et al. 2008, Durant *et al.* 2009). However, the samples used in such monitoring should be large enough to account for individual variability and the potential effects of environmental and ecological factors on any individuals foraging behaviour (Soanes *et al*. 2013a).

In this study we compare the foraging behaviour of kittiwakes breeding on the Special Protected Area (SPA) of Puffin Island (Wales) between three breeding seasons and examine the effect that year, sex, stage of breeding, timing of tracking and wind speed may have on the foraging areas identified. With particular emphasis on assessing if the foraging areas of this regionally important population overlap with the Irish Sea Offshore Development Zone (ISZ), one of nine zones within UK waters identified by the Crown Estates in 2009 as a "*favourable area of opportunity for the development of large scale commercial offshore wind energy development*" (Crown Estates 2010).

Methods

Field methods

Black-legged kittiwakes, breeding on Puffin Island, Wales, (53.3ºN, 4.0ºW) were tracked using IgotU GT-120 GPS data loggers (Mobile Action, Taiwan) over three consecutive breeding seasons (2010-2012). A total of 31, 41 and 45 individuals were instrumented in 2010, 2011 and 2012 respectively. Loggers were deployed between the 9th June and 6th July of each year and samples represented males and females, and those incubating eggs and rearing chicks. Loggers were attached to the back feathers with waterproof Tesa ® Extra power tape (Wilson *et al.*, 1997). Loggers weighed 15 g when packaged which equates to approximately 3% of a kittiwakes body weight. Head and bill measurements were taken to allow sex to be determined following the methods of Coulson *et al.* (2009).

Productivity of a sample of control nests was recorded every year according to the standard methods for monitoring UK seabirds (Walsh *et al.* 1995). These estimates were compared to the productivity of nests where adult birds were tracked to assess any detrimental effect of logger deployment. A chi^2 test was performed to determine any significant differences in productivity between the two.

Tracking data

The GPS devices were set to record a position every 120 s but sometimes the device failed to find a signal. This may provide a biased sample of the spatial distribution of foraging activity (McLeay *et al.*, 2010). As such, GPS fixes were interpolated to every 10 seconds using the statistical software R (R Development Core Team 2011) with the package "*Trip*" (Sumner 2011). This package was also used to calculate the area covered on each foraging trip by calculating the time spent in a pre-defined grid of 1 x 1 km cells surrounding the breeding colony (Page *et al.*, 2006). The total number of 1 x 1 km cells that the birds spent their time within was used to represent their area of active use and the number of cells that the birds spent 50% of their time (after ranking for frequency of use) was used to represent their core-foraging areas (Casper *et al*., 2010, Soanes *et al*., 2013a). The number of cells used on each trip was used to represent the total size of the foraging area (km^2). Total trip distance (km), trip duration (min), and the maximum distance travelled from the colony (km) were also calculated for each foraging trip.

Weather data

Wind speed data was provided by the UK Met office (Met Office 2013) for the months of May, June and July (to represent the main incubation and chick rearing periods of kittiwakes breeding on Puffin Island) of 2010, 2011, and 2012 from the closest marine buoy (53.2ºN, 3.5ºW), which lies approximately 35 km west of Puffin Island. Wind speed at this buoy was recorded 10-64 times a day. We calculated a mean wind speed for each 24 hour period.

Statistical Methods

The effects of a range of categorical and continuous explanatory variables including: (1) sex of the bird, (2) stage of breeding (eggs versus chicks), (3) date that tracking was undertaken (4) year of tracking and (5) wind speed on the four foraging trip response variables described above were investigated. Our aim was to determine which, if any, might account for the variation in foraging behaviour observed between individuals. Total trip distance, trip duration, and the maximum trip distance were *ln*-transformed. Generalised Estimation Equations (GEE) (Liang and Zeger, 1986) were used in the analyses; this allowed for compound correlation structures to be specified for each individual, in order to account for within-individual correlation. The models were implemented in the "*geepack*" version 1.1-6 package (Højsgaard *et al*., 2012) in the R software environment. All models incorporated the same terms consisting of sex, stage of breeding (eggs or chicks), days into tracking season that tracking was undertaken (days from 1st April each year), the year the tracking was conducted and average wind speed on the date each foraging trip was undertaken. The model outputs were analysed using one-way ANOVAs, and significant terms at $P < 0.05$ level were then submitted to *post-hoc* Tukey comparison tests to ascertain within-factor differences.

Maps of time spent in predefined grid cells of 1 x 1 km were plotted to compare use of space by kittiwakes around the colony for the explanatory variables that were found to be significant after the GEE model was run (those with a p-value < 0.05).

Results

Each year, 15-29 loggers (15 in 2010, 29 in 2011 and 23 in 2012) were retrieved from kittiwakes breeding on Puffin Island all others were lost by the birds before they could be recaptured. No significant differences in the productivity of control nests versus nests from which an adult had been tracked was found ($p < 0.05$) in any year. Productivity of the colony varied between years with 2010 being the most productive year with 1.56 chicks per pair compared to 2012 where productivity was only 0.77 chicks per pair (Figure 6.1).

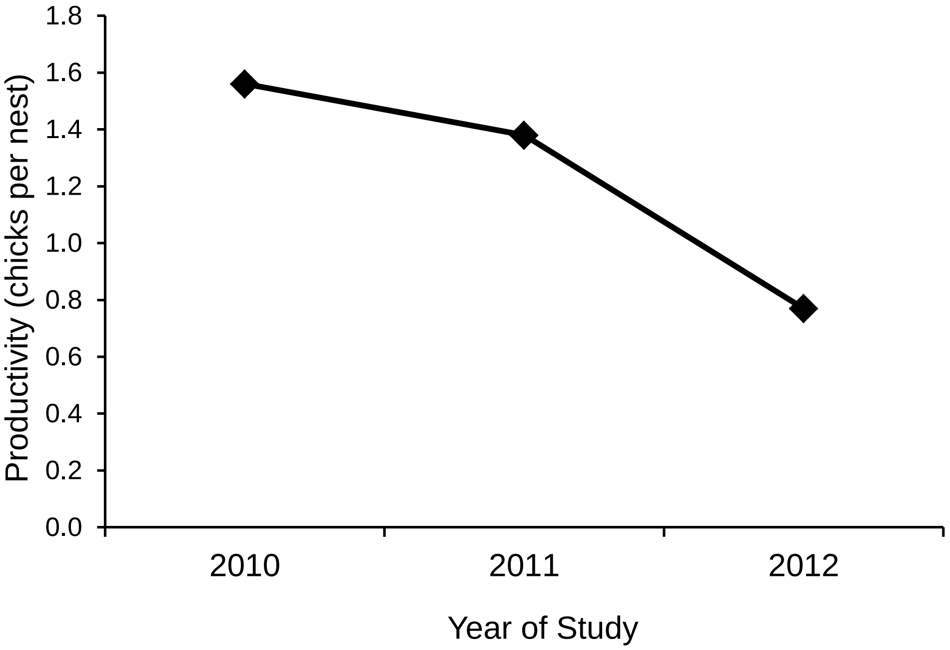


Figure 6.1. Productivity of kittiwakes in the years of study. n = 68 (2010), 60 (2011), and 61 (2012).

Data from a mean of 3.4 (± 0.3 SEM) foraging trips were obtained per individual (range 1-12 trips). The loggers could not be deployed for the full life of the batteries (approximately 5 days) as after around 72 hours of deployment the loggers would have fallen off the bird. Mean total trip distance for all birds sampled over all years was 55.9 (± 3.2) km, mean trip duration was 307 (± 19) mins, maximum distance travelled from the colony 19.0 (± 1.0) km and the mean area used on each trip was 75.4 (± 5.3) km^2 with 6.8 (± 0.4) km^2 being used as core foraging areas, where birds spent 50% of their total foraging trip time.

Trip distance, trip duration, the maximum distance travelled from the colony area of active use and core foraging area used on each foraging trip were not significantly affected by the sex of the bird, the date of tracking or the wind speed ($p > 0.005$) (Table 6.1). The foraging trip characteristics were however significantly affected by the stage of breeding, with individuals incubating eggs travelling on average further, for longer and covering a greater distance than those rearing chicks (Figure 6.2- 6.5). The year of study also revealed significant differences with individuals in 2012 travelling further, for longer and covering a greater distance compared to 2011 and 2010 (Figure 6.2, 3 & 5).

Table 6.1: Summary of mean estimates (± SEM) by response variable and explanatory factor. P-values indicate significance of anova test of the variables stated in the contrast column. Highlighted cells = significant p-values.

	Trip distance			Trip duration			Max distance			100 % cells			50 % cells		
	Mean	**contrast**	**p value**	**Mean**	**contrast**	**p value**	**Mean**	**contrast**	**p value**	**Mean**	**contrast**	**p value**	**Mean**	**contrast**	**p value**
Sex															
M	33.9 (30.6-37.5)	M:F	0.993	179.5 (179.5-196.4)	M:F	0.65	11.2 (10.2-12.4)	M:F	0.565	56.5 (51.1-61.9)	M:F	0.32	6.4 (5.8-6.9)	M:F	0.79
F	31.3 (28.4-34.4)			175.9 175.9-192.5)			10.48 (9.6-11.5)			64.1 (57.5-70.7)			7.1 (6.5-7.6)		
Chicks															
1	24.5 (22.2-27.7)	1.2	0.10	148.4 (148.4-162.4)	1.2	0.62	8.6 (7.7-9.6)	1.2	0.181	47.4 (42.3-52.7)	1.2	0.698	5.4 (4.9-5.6)	1.2	0.247
2	33.8 (30.9-36.9)	eggs:1	< 0.001	165.7 (149.9-183.1)	eggs:1	<0.001	11.6 (10.5-12.7)	eggs:1	0.002	54.7 (49.2-60.1)	eggs:1	<0.001	6.7 (6.1-7.3)	eggs:1	<0.001
eggs	49.9 (45.6-54.5)	eggs:2	0.02	317.3 (265.1-379.9)	eggs:2	<0.001	16.8 (14.0-20-0)	eggs:2	0.171	113.7 (108.8-131.6)	eggs:2	<0.001	11.3 (10.4-12.1)	eggs:2	0.001
Year															
2010	16.8 (15.0-18.7)	2010:2011	0.001	104.6 (94.6-115.6)	2010:2011	0.006	5.7 (5.1-6.4)	2010:2011	> 0.001	24.6 (21.9-27.3)	2010:2011	0.082	3.9 (3.5-4.2)	2010:2011	0.33
2011	37.7 (34.8-40.8)	2010:2012	<0.001	212.7 (194.4-232.8)	2010:2012	<0.001	12.4 (11.3-13.6)	2010:2012	> 0.001	56.4 (51.4-61.8)	2010:2012	<0.001	6.3 (5.8-6.8)	2010:2012	<0.001
2012	58.6 (51.4-66.7)	2011:2012	0.04	262.4 (230.4-298.8)	2011:2012	0.662	19.5 (17.1-22.2)	2011:2012	0.012	112.8 (100.8-124.9)	2011:2012	<0.001	11.3 (10.2-12.4)	2011:2012	<0.001
Days			0.75			0.43			0.88			0.82			0.99
Wind			0.21			0.71			0.50			0.84			0.616

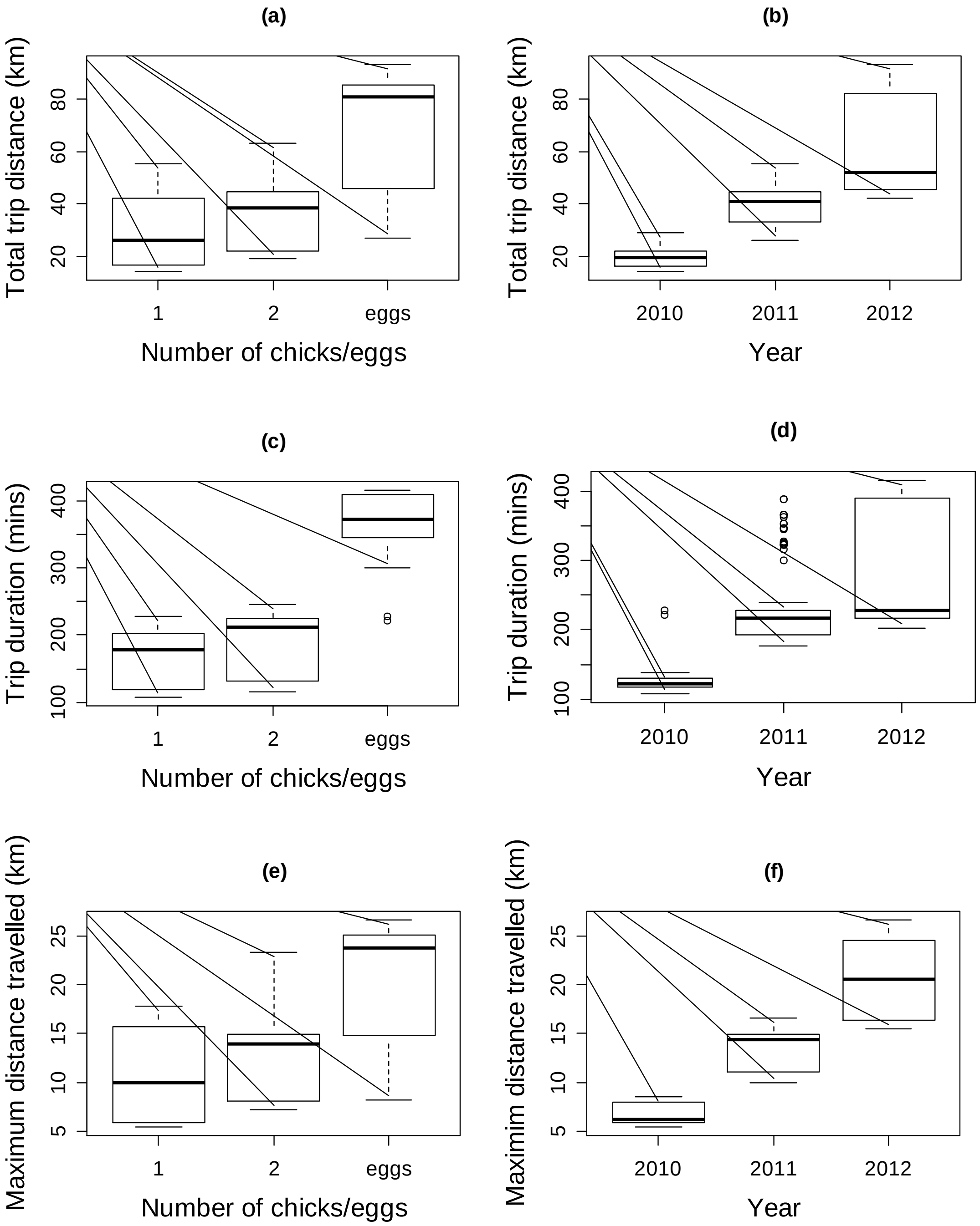


Figure 6.2. The effect of stage of breeding, number of chicks and year on total trip distance (a & b), trip duration (c & d) and the maximum distance travelled from the colony (e & f).

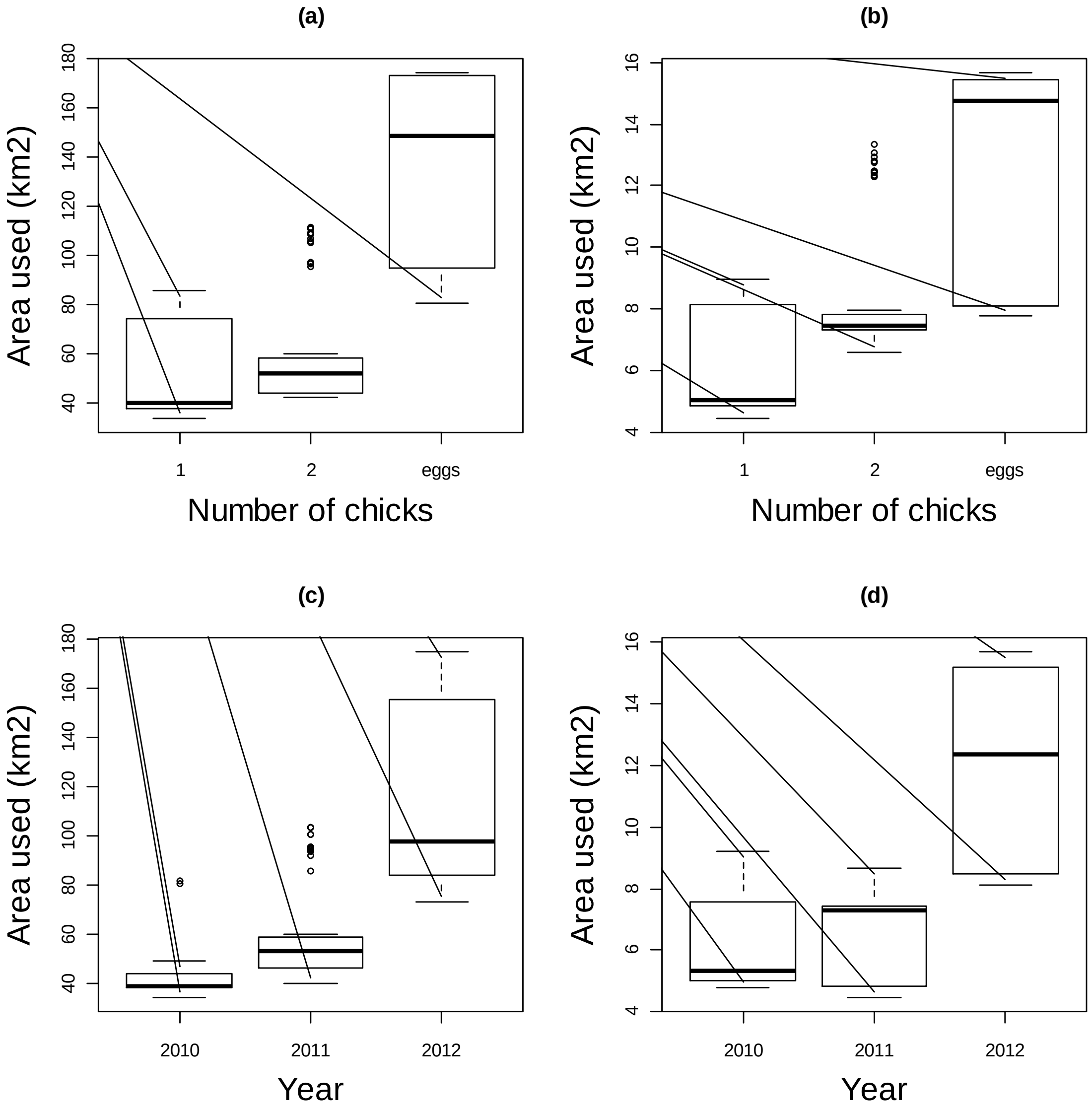


Figure 6.3. The area of active use (a) and core foraging areas (b) used by kittiwakes that were incubating or rearing one or two chicks and the area of active use (c) and core foraging areas (d) of kittiwakes in 2010, 2011 and 2012.

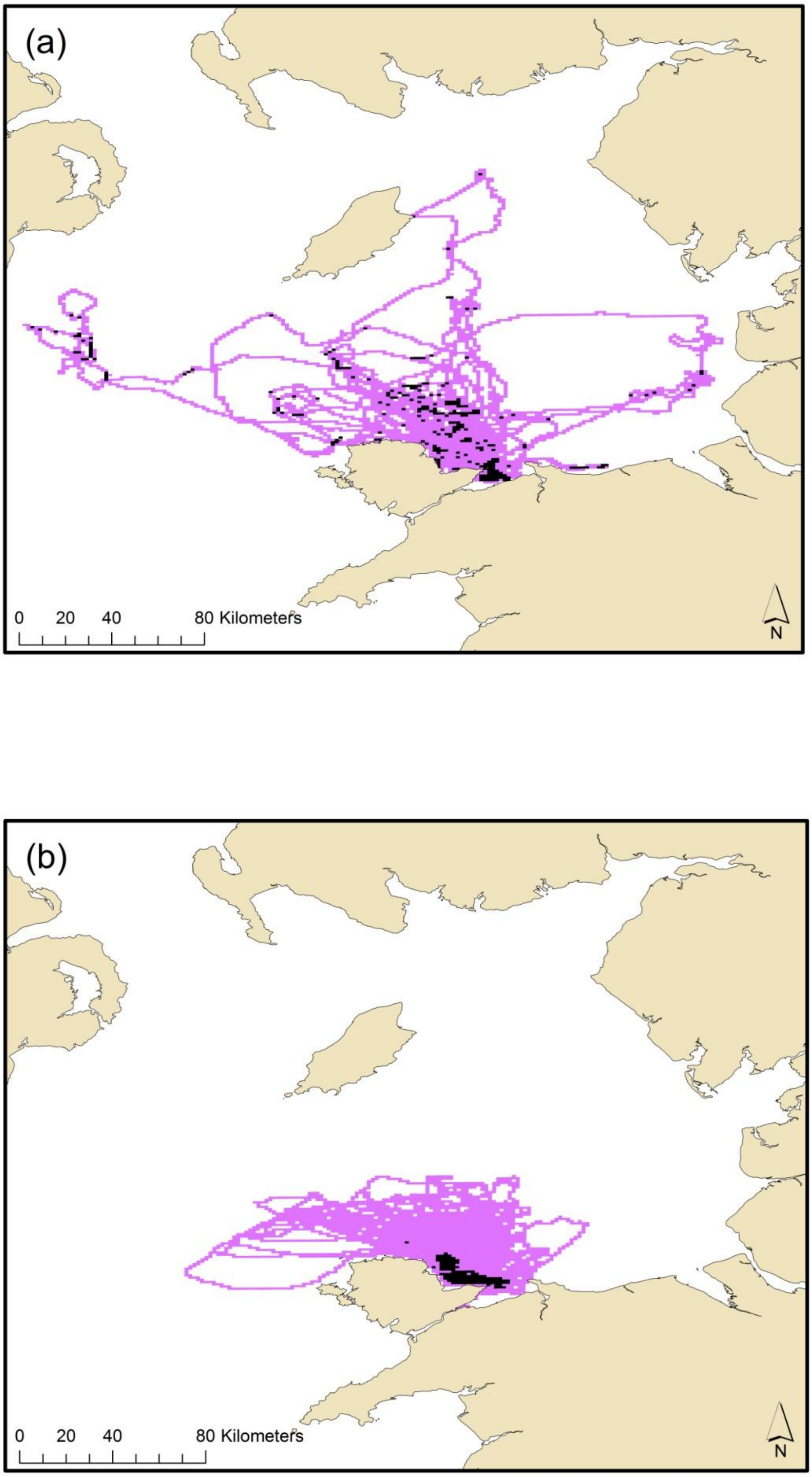


Figure 6.4. (a) The areas of active use (pink) and core foraging areas (black) of incubating kittiwakes and (b) of chick-rearing kittiwakes

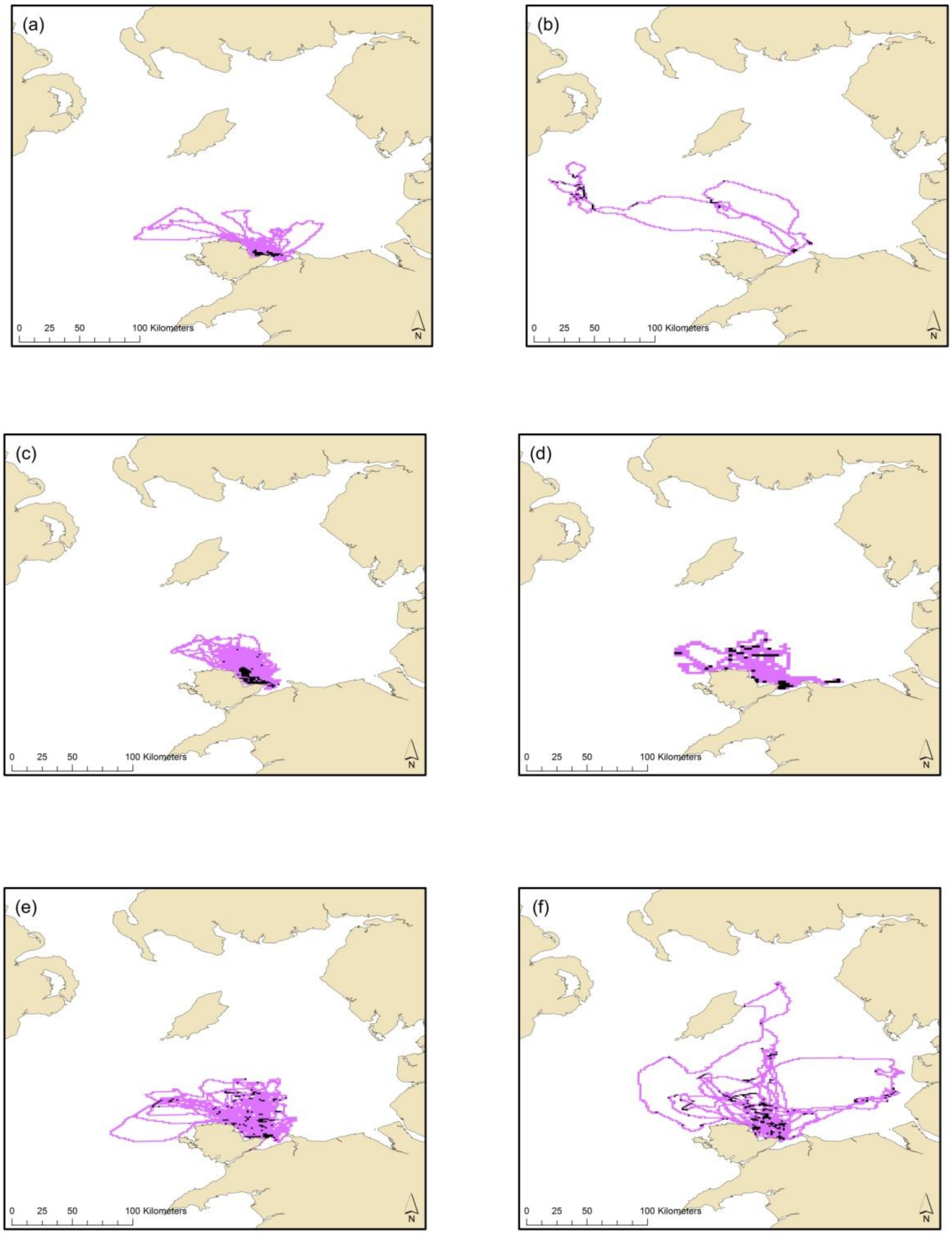


Figure 6.5. The areas of active use (pink) and core foraging areas (black) of chick-rearing kittiwakes in (a) 2010, (c) 2011, (e) 2012, and of incubating kittiwakes in (b) 2010, (d) 2011 and (f) 2012.

The percentage of individual kittiwakes whose foraging trips overlapped with the ISZ varied between years, with more overlap observed in 2012, and with individuals that were incubating compared to those that were chick-rearing (Table 6.2). Figure 6.6 shows the foraging tracks of all 28 individuals whose foraging trips overlapped with the ISZ.

Table 6.2. The number of individual kittiwakes whose foraging trips overlapped with the Irish Sea Offshore Wind Development Zone, comparing year of tracking and individuals that were either incubating of chick-rearing at the time of tracking.

	No. of birds tracked	No. of birds that overlapped with ICZ	% of birds that overlapped with ICZ
2010	15	2	13%
2011	29	8	28%
2012	23	18	74%
Incubating	26	15	58%
Chick-rearing	41	13	31%

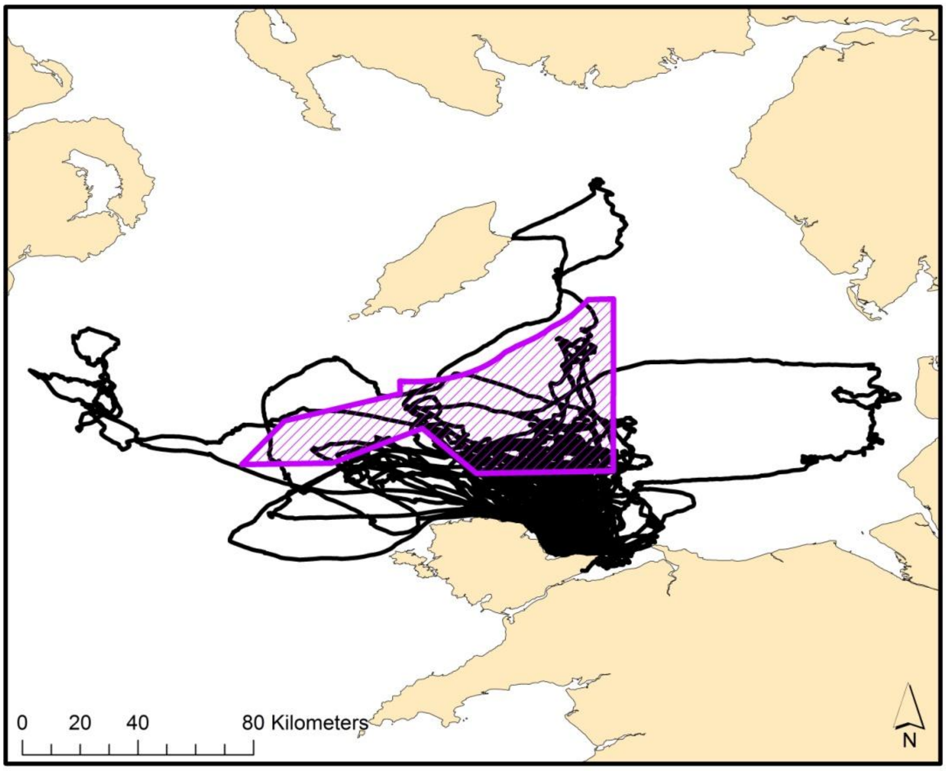


Figure 6.6. Foraging trips of the 28 individual kittiwakes whose foraging trips overlapped with the Irish Sea offshore wind development zone (ISZ) (shaded in pink). *Shapefile of ISZ provided by Centrica Energy (2012).*

Discussion

The total trip distance, trip duration, maximum distance travelled from the colony and the foraging areas of the Black-legged kittiwake breeding on Puffin Island were significantly different depending on whether the individuals were incubating or chick-rearing at the time of tracking and also between the three years of study. Whilst our results should be interpreted carefully (based on small sample sizes, Soanes *et al.* 2013a) the finding of significant differences in foraging strategy within a breeding season and also between consecutive years are interesting and should be considered in further seabird tracking studies.

Soanes *et al.* (2013b) advocate the use of tracking studies to provide data for the Environmental Impact Assessment (EIA) process to allow the identification of important foraging areas related to offshore marine renewable energy developments.

There are studies that have reported potential effects of renewable energy developments based on the tracking of individual seabirds (Perrow *et al.* 2006, Harris *et al.* 2012). However, in general, tracking studies are usually conducted on a short temporal and spatial scale so likely to include individuals that are at a particular stage of breeding (incubating or chick rearing) rather than incorporating individuals from all stages of breeding. Our results from the tracking of 67 kittiwakes over three years on Puffin Island suggest that 31% of individuals overlap with the ISZ if only chick rearing individuals are assessed compared to 58% of individuals exhibiting overlap if only incubating birds are examined. Considering the different energetic requirements of adult birds during incubation, where they only have to incubate their eggs and protect them against predators and adverse weather compared to chick-rearing, where adults have the extra cost of obtaining food for their chicks in addition to their own energy needs and are constrained by having to feed chicks at regular intervals it is not surprising that the exhibit different foraging strategies throughout the breeding cycle (Humphreys *et al.* 2006).

The effect of year of study on the foraging behaviour of seabirds has been previously reported and has been related to environmental conditions. For example, Chivers *et al.* (2012) reported that during periods of low food availability kittiwakes modified their foraging strategy by increasing their foraging range to include more profitable food patches, and suggest that the reason for this is that the metabolic costs of attempting to catch prey are high for kittiwakes compared with other activities and may explain why foraging range was extended rather than foraging intensity increased. Lescroel *et al.* (2010) related the foraging performance of Adélie penguins *Pygoscelis adeliae* to breeding success at the population level, and demonstrated the importance of weather conditions on their foraging behaviour and individual quality. In this study kittiwakes foraged furthest in 2012 and 2011 compared to 2010, suggesting poorer conditions for foraging or a shift in prey distribution between years. Interestingly the years with greater foraging trip distance, and duration were also the years where the lowest productivity was recorded (Figure 6.6).

Wind speed, during the days of tracking was not significantly related to foraging behaviour in this study. Although, wind direction and sea state could also play a part in determining foraging strategy, but data on these weather conditions were not available for the study area. The sex of bird was also not found to be a significant factor influencing the foraging trip characteristics of this population, although a systematic bias in assigning sex to tracked birds may exist as sex was determined by comparing head and bill measurements to birds recorded at a different colony and measured by a different researcher (Hamer & Furness 1991; Coulson *et al.,* 2009), for more accurate sexing of individuals blood and feather samples should be analysed.

Applying tracking data to the EIA process can be a useful tool, however the difference in foraging behaviour and the observed overlap in foraging area with the ISZ observed between years and between individuals that were either incubating or chick-rearing highlights the importance of collecting tracking data over more than one breeding season and more than one stage of breeding to fully identify any potential effect of offshore renewable energy developments.

This study highlights the differences in foraging behaviour and foraging areas predicted by kittiwakes at different times of the breeding season and between consecutive years, again reiterating the need for researchers to carefully consider the conclusions they draw from tracking studies conducted over a limited temporal scale. This study also identified a potential relationship between foraging behaviour related to productivity in each year, with productivity being lower in years when foraging effort was increased.

Acknowledgements

This project was funded by a Doctoral Training Grant from the Natural Environment Research Council, with support from the RSPB's FAME project. We would like to thank Dr. Charles Bishop, Ashley Tweedale, Dr. Rachel Taylor (Bangor University), and volunteers from both the University of Liverpool and Bangor University for assistance with planning and fieldwork. Data collection on Puffin Island would not have been possible without permission to carryout fieldwork from Sir Richard Williams-Bulkeley. Permission was granted by the Countryside Council for Wales to conduct bird capture and tagging work on Puffin Island.

References

Chivers, L.S., Lundy, M.G., Colhoun, K., Newton, S.F., Houghton, J.D.R. & Reid, N. (2012) Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. *Marine Ecology-Progress Series,* **456,** 269-267.

Coulson, J. (2011) *The Kittiwake*. T & AD Poyser, London.

Coulson, J.C. (2009) Sexing Black-legged Kittiwakes by measurement. *Ringing & Migration*, **24,** 233-239.

Durant, J.M., Hjermann, D.O., Frederiksen, M., Charrassin, J.B., Le Maho, Y., Sabarros, P.S., Crawford, R.J.M. & Stenseth, N.C. (2009) Pros and cons of using seabirds as ecological indicators. *Climate Research*, **39,** 115-129.

Crown Estates. (2010) Wind report 2010. www.thecrownestate.co.uk.

Frederiksen, M., Edwards, M., Mavor, R.A. & Wanless, S. (2007) Regional and annual variation in black-legged kittiwake breeding productivity is related to sea surface temperature. *Marine Ecology Progress Series*, **350,** 137-143.

Frederiksen, M., Wanless, S., Harris, M.P., Rothery, P. & Wilson, L.J. (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology,* **41,** 1129-1139.

Furness, R.W. & Tasker, M.L. (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series*, **202,** 253-264.

Hamer, K,C & Furness, R.W. (1991) Sexing great skuas *Catharacta skua* by discriminant analysis using external measurements. *Ringing & Migration* **12**: 16-22.

Hamer, K.C. & Hill, J.K. (1993) Variation and regulation of meal size in corys shearwater *Calonetris diomedea*. *Journal of Animal Ecology,* **62,** 441-450.

Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P. & Burns, M.D. (1993) The influence of food-supply on the breeding ecology of kittiwakes *Rissa-Tridactyla* in Shetland. *Ibis,* **135,** 255-263.

Harris, M.P., Bogdanova, M.I., Daunt, F. & Wanless, S. (2012) Using GPS technology to assess feeding areas of Atlantic Puffins *Fratercula arctica*. *Ringing & Migration*, **27,** 43-49.

Humphreys, E.M., Wanless, S. & Bryant, D.M. (2006) Stage-dependent foraging in breeding black-legged kittiwakes Rissa tridactyla: distinguishing behavioural responses to intrinsic and extrinsic factors. *Journal of Avian Biology,* **37,** 436-446.

Iverson, S.J., Springer, A.M. & Kitaysky, A.S. (2007) Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. *Marine Ecology Progress Series,* **352,** 235-244.

Kotzerka, J., Hatch, S.A. & Garthe, S. (2011) Evidence for foraging-site fidelity and individual foraging behaviour of pelagic cormorants rearing chicks in the Gulf of Alsaka *Condor,* **113,** 80-88.

Lescroel, A., Ballard, G., Toniolo, V., Barton, K.J., Wilson, P.R., Lyver, P.O. & Ainley, D.G. (2010) Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology,* **91,** 2044-2055.

Met Office (2013). www.metoffice.gov.uk. (c) Crown Copyright.

Mitchell, P.I., Newton, S. F., Ratcliffe, N. & Dunn, T.E. (2004) *Seabird Populations of Britain and Ireland*. T & AD Poyser, London.

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S. & Reid, J.B. (2008) Seabirds as indicators of the marine environment. *Ices Journal of Marine Science,* **65,** 1520-1526.

Perrow, M.R., Skeate, E.R., Lines, P., Brown, D. & Tomlinson, M.L. (2006) Radio telemetry as a tool for impact assessment of wind farms: the case of Little Terns *Sterna albifrons* at Scroby Sands, Norfolk, UK. *Ibis,* **148,** 57-75.

Piatt, J.F., Harding, A.M.A., Shultz, M., Speckman, S.G., van Pelt, T.I., Drew, G.S. & Kettle, A.B. (2007) Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series,* **352,** 221-234.

Soanes, L.M., Arnould, J.P.Y, Dodd, S.G., Sumner, M.D. & Green, J.A (2013a) How many seabirds do we need to define important foraging areas. *Journal of Applied Ecology,* **50** (3), 671-679

Soanes, L.M., Gauvain, R.D., Atkinson, P.W. & Green, J.A. (2013b) Individual consistency in the foraging behaviour of Northern gannets: implications for interactions with offshore renewable energy developments. *Marine Policy,* **38**:505-514.

Suryan, R.M., Irons, D.B. & Benson, J. (2000) Prey switching and variable foraging strategies of Black-legged Kittiwakes and the effect on reproductive success. *Condor,* **102,** 374-384.

Walsh, P., Halley, D., Harris, M., del Nevo, A., Sim, L. & Tasker, M. (1995) *Seabird monitoring handbook for Britain and Ireland: a compilation of methods for survey and monitoring of breeding seabirds*. JNCC / RSPB /ITE / Seabird Group, Peterborough.

Wendeln, H. & Becker, P.H. (1999) Effects of parental quality and effort on the reproduction of common terns. *Journal of Animal Ecology*, **68,** 205-214.

Chapter 7

General Discussion

Photo Johann Bourgeois 2012

7.1 General Discussion

Seabirds are a diverse group adapted to a wide range of environments. As such, this group exhibits diverse life history characteristics from the Emperor penguin *Aptenodytes forsteri* which spend 115 days fasting during the breeding season in freezing temperatures (Pinshow & Welch 1980) to the Marbled murrelet *Brachyramphus marmoratus* which flies up to 75 km to breed in old growth trees in coniferous forests (Whitworth *et al*. 2000).

The study of seabird behaviour at sea has gained momentum in recent years with advances in tracking technology allowing the production of smaller and more affordable devices which has allowed a greater range of seabird species to be tracked at sea and their foraging behaviours assessed (Burger & Shaffer 2008). Interest in seabirds at sea began initially in the 1970's to determine and assess the possible effects that offshore oil and gas energy developments may have on seabird populations. In the last ten years a shift in focus has occurred, with seabird at-sea data being used to inform marine spatial planning, through the designation of marine protected areas and for assessing the impacts of offshore marine renewable energy developments. The study of seabirds at sea has also revealed interesting differences in the foraging, migration and wintering areas of many species (Bugoni, D'Alba & Furness 2009; Guilford *et al.* 2009; Freeman *et al.* 2010), as well as identifying different foraging strategies between species, colonies, sexes and age groups (Weimerskirch *et al.* 1993; Hamer *et al.* 2001; Weimerskirch *et al.* 2009).

The overall aim of this study was to investigate and identify the important foraging areas of seabirds related to marine spatial planning and offshore renewable energy developments. However, it became clear during the background research for this project that there were methodological issues in tracking studies that should be addressed before extrapolated conclusions are made on the important foraging areas of seabird colonies based on relatively small sample sizes. Lindberg & Walker (2007) acknowledge that some studies using relatively small sample sizes have led to some important observations, but they question the inference of these observations to the populations of interest *"biologists that mark a non-representative sample of individuals run the risk of being very confident in unreliable results, and this is highlighted when a small sample of individuals is marked over a limited spatial range"*.

In response to the issue that small sample sizes are often used in seabird tracking research (Table 5.1), **Chapter 2** introduces an analytical approach to determine how representative any tracking sample may be of the colony in question. This approach was applied to the datasets collected from all species in this study, and found that for a relatively localised coastal feeder such as the European shag, relatively few individuals from the study population may be required to accurately predict foraging areas, whilst for longer distance foragers such as the Northern gannet and Brown booby larger sample sizes may be required. Whilst it may not be logistically or financially feasible to track such large numbers of birds, this study advocates that researchers make it clear in their resulting outputs how representative their tracking data may be of the colony in question.

Chapters 3 and **4** introduce two studies which highlight the use of tracking studies to aid in the conservation of seabirds, and find that the foraging trips of seabirds breeding on the study islands cross into different territorial waters. Thus highlighting the need for collaboration between countries and territories in protecting seabirds at sea. **Chapter 3** attempts to identify important foraging areas of the Brown booby breeding on the Important Bird Area (IBA) of Dog Island, Anguilla and finds that marine spatial planning in a single territory would not fully protect or represent the areas used by this far-ranging species. **Chapter 4** relates the foraging areas of Northern gannets breeding in the Channel Islands to potential offshore renewable energy developments. It was found that the foraging range of the sample tracked overlapped with nine proposed offshore marine renewable energy development sites in three different territorial waters, and also identified that foraging behaviour was not consistent within an individual. With the first foraging trip not being particularly similar (distance and duration) to the second foraging trip made by any bird, suggesting that this species breeding at this colony will have the ability to adapt/alter its foraging areas in response to changes in some areas of its marine environment.

Chapters 5 and **6** examine how environmental and ecological factors can affect the foraging areas and foraging behaviour predicted from the limited sample sizes often used in tracking studies. **Chapter 5** revealed that even for the European shag, which is a relatively short distance forager, the effects of sex, year of study, number of chicks, age of chicks and most importantly breeding site all had significant effects on foraging trip distance, duration, maximum distance travelled from the colony and the area used. A range of sampling scenarios likely to reflect actual field sampling were tested, differences of up to 50% in the size of the predicted foraging area were observed, depending on the composition of the sample. **Chapter 6** related the foraging behaviour of Black-legged kittiwake to ecological factors (year of study, timing of tracking and whether the bird was incubating or chick-rearing at the time of tracking) and also to environmental factors (wind strength). This study highlighted that the tracking of individuals at only a particular time of the breeding season could lead researchers to draw entirely different conclusions on the impact that marine renewable developments may have on a population. For example, the foraging areas of 28% of chick-rearing kittiwakes overlapped with the Irish Sea Renewable energy development zone (ICZ) compared to 67% of incubating kittiwakes. This highlights the need for tracking studies to be performed at different stages of the breeding season to fully examine the foraging areas of the colony.

It is important that the information being drawn from tracking studies accurately predicts the colony's foraging habitats or otherwise, the researcher accepts the limitations of their data and makes it clear in their publications and reports that the foraging areas predicted from small samples may not always identify all important foraging areas and may actually over-emphasise the importance of others (BirdLife International 2004). This thesis has identified some basic methodological considerations and analytical problems to which many tracking studies succumb to. Our approach helps to highlight the pitfalls and suggests improvements to current methodologies and analysis. The tracking of seabirds and other marine central-place foragers has the potential to provide valuable information to help in protecting our marine resources through marine spatial planning and feeding into EIA's as well as providing information on climatic processes and fisheries management. It is therefore important for anybody conducting tracking studies to ensure the most appropriate data is collected.

However, given the logistical and financial constraints of tracking a large number of individuals, it is likely that the results from small tracking datasets will continue to be used to aid in the designation of or to evaluate the effectiveness of MPZ, to assess the impact of developments and for assessing changes in oceanic conditions or fishery practices (Ancel *et al.* 1992; Weimerskirch *et al.* 1995; Durant *et al.* 2009). Whilst these practices may, in theory, hold promise as being useful to marine spatial planners and conservationists, this research has identified that the use of seabird tracking datasets as they generally stand using small sample sizes may not be as useful as they have been advocated simply because of the variability in individual behaviour and the effects that environmental and ecological effects such as weather and climatic conditions can have on foraging behaviour. Researchers should carefully consider if the findings of any tracking study are actually worth the investment of time, money and inconvenience to birds, and if not, to consider how their objective could otherwise be achieved, most likely by the formation of larger scale collaborative projects tracking birds over longer spatial and temporal scales. For example Arcos *et al.* (2012) combined seabird tracking data, at-sea surveys, habitat data and species distribution modelling to identify marine IBA's in Spain. Similarly whilst Chapter 3 advocates the usefulness of seabird tracking for the EIA process for offshore developments, tracking data alone is unlikely to provide sufficient information on the possible impacts such developments may have on seabird populations, but when combined with at sea-surveys and some knowledge of the energetics of a species could provide valuable information.

7.2 Further work

This thesis has used a time-based approach for identifying areas where birds spend most of their time. Further development of this work could focus on the ecological interpretation of the distribution of the study species. For example, by analysing the area-restricted searching pattern of birds, and linking this to habitat variables and larger-scale remotely-sensed data such as sea-surface temperature and chlorophyll a abundance (De Monte *et al.* 2012; Renner *et al.* 2013; Tancell *et al.* 2013; Thiebault & Tremblay 2013). This approach would not only add greatly to our understanding of the species ecology and behaviour, but may also enable the prediction of foraging areas of seabirds at other important colonies. For example, Birdlife International (2010) advocate a foraging radius approach to delineate foraging areas around important seabird colonies based on foraging trip characteristics and habitat requirements determined from tracking data of the same species breeding elsewhere. Modelling approaches which incorporate tracking data can also aid in the prediction of potential foraging areas and in delineation of IBA's and marine protected areas for a range of species. To date, few studies have used tracking data to model/predict seabird distribution, although recent work by Oppel *et al.* (2012) tested a range of modelling techniques to predict the winter distribution of the endangered Balearic shearwater by combining at-sea survey data with 13 environmental variables (such as sea surface temperature, chlorophyll a abundance and distance from coast). This ecological niche modelling approach is an established method for determining the distribution of terrestrial species and has great promise for seabird conservation allowing wildlife managers and governmental organisations to incorporate important seabird areas into marine spatial planning. An understanding of the environmental variables that govern seabird distribution will also allow predictions to be made on the possible effects of climate change, offshore marine renewable energy developments or changes in fishery practices.

7.3 Conclusions

Seabird tracking has and will continue to be an important tool in seabird conservation and marine spatial planning, particularly with the greater research emphasis now being placed on understanding the distribution of seabirds in relation to environmental variables. Whilst researchers are currently trialing various techniques of analysis, interpretation and presentation of data, it is important to evaluate the likely representativeness of any data set before far-reaching broad conclusion are drawn on the foraging behaviour of a species or important foraging areas when based on small sample sizes. However, tracking technology is likely to continue to improve, which in turn will allow more affordable loggers to be deployed for longer periods of time whilst still reducing the impact on the bird, with these advancements we are likely to see a lot more representative and useful tracking data being used to aid in management practices.

References

Ancel, L., Kooyman, G.L., Ponganis, P.J., Gendner, J.P., Lignon, J., Mestre, X., Huin, N., Thorson, P.H., Robisson, P. & Le Maho, Y. (1992) Foraging behaviour of emperor penguins as a resource detector in winter and summer. *Nature (London),* **360,** 336-339.

Benoit-Bird, K.J., Battaile, B.C., Heppell, S.A., Hoover, B., Irons, D., Jones, N., Kuletz, K.J., Nordstrom, C.A., Paredes, R., Suryan, R.M., Waluk, C.M. & Trites, A.W. (2013) Prey Patch Patterns Predict Habitat Use by Top Marine Predators with Diverse Foraging Strategies. *Plos One,* **8,** 12.

BirdLife Internatinal (2010) Marine Important Bird Areas toolkit: standardised techniques for identifiing priority sites for the conservation of seabirds at sea. (ed. B. International). Birdlife International, Cambridge, UK.

BirdLife International (2004) Tracking ocean wanderers: the global distribution of albatrosses and petrels. Results from the Global Procellariiform Tracking Workshop, 1–5. South Africa. Birdlife International, Cambridge.

Bugoni, L., D'Alba, L. & Furness, R.W. (2009) Marine habitat use of wintering spectacled petrels Procellaria conspicillata, and overlap with longline fishery. *Marine Ecology-Progress Series,* **374,** 273-285.

Burger, A.E. & Shaffer, S.A. (2008) Application of tracking and data-logging technology in research and conservation of seabirds. *Auk,* **125,** 253-264.

De Monte, S., Cotte, C., d'Ovidio, F., Levy, M., Le Corre, M. & Weimerskirch, H. (2012) Frigatebird behaviour at the ocean-atmosphere interface: integrating animal behaviour with multi-satellite data. *Journal of the Royal Society, Interface / the Royal Society,* **9**.

Durant, J.M., Hjermann, D.O., Frederiksen, M., Charrassin, J.B., Le Maho, Y., Sabarros, P.S., Crawford, R.J.M. & Stenseth, N.C. (2009) Pros and cons of using seabirds as ecological indicators. *Climate Research,* **39,** 115-129.

Freeman, R., Dennis, T., Landers, T., Thompson, D., Bell, E., Walker, M. & Guilford, T. (2010) Black Petrels (Procellaria parkinsoni) Patrol the Ocean Shelf-Break: GPS Tracking of a Vulnerable Procellariiform Seabird. *Plos One,* **5,** 11.

Guilford, T., Meade, J., Willis, J., Phillips, R.A., Boyle, D., Roberts, S., Collett, M., Freeman, R. & Perrins, C.M. (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society B-Biological Sciences,* **276,** 1215-1223.

Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S. & Wood, A.G. (2001) Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology-Progress Series,* **224,** 283-290.

Lindberg, M.S. & Walker, J. (2007) Satellite telemetry in avian research and management: Sample size considerations. *Journal of Wildlife Management,* **71,** 1002-1009.

Arcos, J., Becares, J., Villero, D., Brotons, L., Rodriguez, B. & Ruiz, A. (2012) Assessing the location and stability of foraging hotspots for pelagic seabirds: An approach to identify marine Important Bird Areas (IBAs) in Spain. *Biological Conservation,* **156,** 30-42.

Oppel, S., Meirinho, A., Ramirez, I., Gardner, B., O'Connell, A.F., Miller, P.I. & Louzao, M. (2012) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biological Conservation,* **156,** 94-104.

Pinshow, B. & Welch, W.R. (1980) Winter breeding in emperor penguins – a consequence of summer heat. *Condor,* **82,** 159-163.

Renner, M., Parrish, J.K., Piatt, J.F., Kuletz, K.J., Edwards, A.E. & Hunt, G.L. (2013) Modeled distribution and abundance of a pelagic seabird reveal trends in relation to fisheries. *Marine Ecology Progress Series,* **484,** 259-277.

Suryan, R.M., Santora, J.A. & Sydeman, W.J. (2012) New approach for using remotely sensed chlorophyll a to identify seabird hotspots. *Marine Ecology Progress Series,* **451,** 213-225.

Tancell, C., Phillips, R.A., Xavier, J.C., Tarling, G.A. & Sutherland, W.J. (2013) Comparison of methods for determining key marine areas from tracking data. *Marine Biology,* **160,** 15-26.

Thiebault, A. & Tremblay, Y. (2013) Splitting animal trajectories into fine-scale behaviorally consistent movement units: breaking points relate to external stimuli in a foraging seabird. *Behavioral Ecology and Sociobiology,* **67,** 1013-1026.

Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. (1993) Foraging strategy of Wandering albatross through the breeding season – A study using satelitte telemetry. *Auk,* **110,** 325-342.

Weimerskirch, H., Shaffer, S.A., Tremblay, Y., Costa, D.P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K. & Aurioles, D. (2009) Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Marine Ecology-Progress Series*, **391,** 267-278.

Weimerskirch, H., Wilson, R.P., Guinet, C. & Koudil, M. (1995) Use of seabirds to monitor sea-surface temperatures and to validate satellite remote sensing measurments in the Southern-Ocean. *Marine Ecology-Progress Series,* **126,** 299-303.

Whitworth, D.L., Nelson, S.K., Newman, S.H., Van Vliet, G.B. & Smith, W.P. (2000) Foraging distances of radio-marked Marbled Murrelets from inland areas in southeast Alaska. *Condor,* **102,** 452-456.