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# The influence of seabird-derived nutrients on island food-webs

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## Declaration

I declare that the work described in this thesis is of my own composition and has been carried out entirely by myself unless otherwise cited or acknowledged. No part of this thesis has been submitted for any other degree or qualification.

The following chapter has been published in co-authorship with my supervisor and others:

Chapter 6: published as Cross, A. D. P., Hentati-Sundberg, J., Osterblom, H., McGill, R. A. R. and Furness, R. W., 2014. Isotopic analysis of island House Martins *Delichon urbica* indicates marine provenance of nutrients. *Ibis*, 156, 676 – 681.

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# Abstract

There is an increasing understanding of the influence seabirds have on island food webs globally, which often arises from the trans-boundary input of nutrients. Seabird-derived nutrients, primarily in the form of guano, can have significant effects on island communities by increasing primary productivity and then indirectly influencing other species. However, there are few studies looking at how the influence of seabirds permeates island food webs to higher trophic levels, in particular within the United Kingdom, which holds globally significant populations of seabirds. To understand the extent to which seabirds influence islands, the size of the seabird population must be first reliably determined. With an increasing seabird population size and density the effects of seabirds on land increases concomitantly.

The Atlantic puffin *Fratercula arctica* is a difficult species to reliably monitor, given its underground presence from the use of burrows and its notoriously erratic attendance at colonies. This study looks firstly at a novel method to monitor the Atlantic puffin using time-lapse photography. Time-lapse photography provides a way to derive an estimate of population size from counts of individuals, by repeated photographs across a period of time with relatively low cost and from areas normally considered inaccessible. The results showed there was a significant and positive relationship between the maximum numbers of Atlantic puffins observed and the size of the population; further work is required though to reduce the error associated with population size estimates. Data from high temporal resolution time-lapse photography shows how the attendance of Atlantic puffins at the colony varies over different temporal scales. Given the variability in sampling intensity the study stresses the need for standardised sampling intensity with the use of photography to monitor Atlantic puffins.

Secondly, this study showed how the presence of two seabird species, the Atlantic puffin and the great skua *Stercorarius skua,* alters island food webs. These seabird species are likely to change plant community diversity, relative to areas without seabirds. The chemical concentration of grasses inside seabird colonies was also altered: grasses had significantly higher concentrations of nitrogen and also had higher values of $\delta^{15}N$, relative to areas without seabirds. These chemical alterations suggest that nutrients from seabirds are incorporated into local vegetation. Furthermore, samples of hair from rabbits and sheep found within puffin colonies also had significantly higher values of $\delta^{15}N$, suggesting that nutrients travel from seabirds into secondary consumers, via ornithogenic forage. An

additional study on the transfer of nutrients within island food webs showed how ornithogenic nutrients deposited on an island in the Baltic Sea were incorporated into house martins, via aquatic insects.

These studies, along with an understanding of seabird population size, suggest that the impact of seabirds on island food webs may be considerable and have large consequences for island conservation and management.

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# Chapter 1

# Introduction

The study of island ecology has been the focus of scientific research since the time of Darwin and Wallace (Darwin 1859, Wallace 1881, Simberloff 1970). Islands have provided a natural system for insights into speciation, evolution, competition and ecology in general (MacArthur and Wilson 1967, Vitousek *et al.* 1996, Mulder *et al.* 2011). These developments have led to the practice of conservation and furthered public concern governing environmental matters and awareness (Whittaker and Fernández-Palacios 2007).

A growing concern over the loss of biodiversity (Donald *et al.* 2001, Brooks *et al.* 2002) has been met with an increased understanding of the importance of islands in maintaining biodiversity, but there are many other aspects of island ecology that need to be understood (Mulder *et al.* 2011). Islands frequently contain endemic species or populations of species that have persisted and/or evolved in isolation from mainland populations (Bellingham *et al.* 2010, Jones 2010). Seabirds are one group of species which are found on islands around the world and are considered to be more threatened than any other group of birds with similar numbers of species (Mulder *et al.* 2011, Croxall *et al.* 2012). The decline in seabird populations and eradication of whole island colonies has provided ecologists an understanding of how island ecosystems are both connected and dependent upon the presence of seabirds.

## 1.1 The influence of seabirds on island ecology

Globally, there is an increasing understanding of the influence seabirds have on the island habitats they typically occupy. More often than not, this influence only becomes evident with their removal (Jones 1992, Croll *et al.* 2005, Maron *et al.* 2006, Grant-Hoffman *et al.* 2010) which often arises from the introduction of invasive predators (Towns *et al.* 1990, Bellingham *et al.* 2010). Removal of seabirds or a decline in their population can result in a shift of ecosystem structure and function (Maron *et al.* 2006). The influence of seabirds on land is however also evident without their extermination by the noticeable signs of an active seabird colony: the presence of burrows and nests, altered vegetation, and often most noticeably from guano (Ellis 2005).

Seabird colonies often influence the ecological communities surrounding them and these changes are well documented in the literature (Mulder *et al.* 2011). Whilst most studies document an immediate and direct influence to surrounding vegetation (Norton *et al.* 1997, Stapp *et al.* 1999, Polis *et al.* 2004, Ellis 2005, Grant-Hoffman *et al.* 2010), there are fewer studies which document indirect influence to other organisms and trophic levels. The following sections therefore detail firstly the direct influence which seabirds have on islands from three main processes: nutrient input, physical disturbance and seed dispersal. Secondly, a summary of the indirect influences which seabirds have on island communities is reported.

### 1.1.1 Nutrient input

Seabirds, as central-place foragers during the breeding season (Fagan *et al.* 2007), will forage at sea then return to their breeding island. These return journeys result in the transportation of nutrients from the marine environment to land, which can have significant effects upon the recipient community (Mulder *et al.* 2011).

In general, trans-boundary movement of predators, prey and nutrients has been shown to strongly affect local population dynamics and community structure (Polis *et al.* 1997). Seabirds have been studied for their role in acting as a vector of spatial subsidies from marine to insular systems and the corresponding effect on plant and animal populations (Gillham 1956, Polis and Hurd 1996, Anderson and Polis 1999, Sanchez-Piñero and Polis 2000, Croll *et al.* 2005, Ellis 2005, Caut *et al.* 2012). Seabirds act as vectors through their capacity to introduce, often through guano, large quantities of marine-derived nutrients, such as forms of organic carbon, phosphorous *e.g.* $PO_4^{3-}$, and nitrogen *e.g.* $NO_3^-$ and $NH_4^+$ (Ellis 2005). Nutrients are further input through eggs (Siegfried *et al.* 1978), feathers (Williams and Berruti 1978, Smith 2008), carrion (Williams *et al.* 1978, Ellis 2005), drip from the nasal salt glands (Sobey and Kenworthy 1979), and from pellets and carcasses of chicks and adults (Williams *et al.* 1978). This represents a significant transfer of chemical elements of marine origin into the terrestrial environment.

Within studies on trans-boundary input nitrogen (N) and phosphorous (P) are the most commonly studied elements, due to the confounding production of autochthonous organic carbon from vegetation (Mizutani *et al.* 1991). N and P are often deposited in such large quantities that a comparison from studies on nutrient input (Allaway and Ashford 1984, Anderson and Polis 1999) show deposition by seabirds far outweighs agricultural fertiliser application in the northern hemisphere (Pearson and Stewart 1993, Rajakaruna *et al.* 2009).

It is important to note that although seabirds mediate change in soils (Heine and Speir 1989, Jakubas *et al.* 2008, Schaeffer *et al.* 2008, Wright *et al.* 2010), they also affect other systems within insular ecosystems indirectly. For example, excess ammonia and nitrates within soils under the right conditions can lead to ammonia volatilisation (Pearson and Stewart 1993). Volatilised ammonia can then enter the atmosphere in vast concentrations and be subsequently deposited back onto land through wet and dry N deposition (Wright *et al.* 2010), leading to further acidification, eutrophication and impacts on nearby soils and plant communities (Fangmeier *et al.* 1994, Wilson *et al.* 2004b).

The transfer of nutrients by seabirds onto land generally increases primary productivity, although this is dependent upon the nutrient's concentration and chemical composition (Polis *et al.* 1997, Smith 2008, Rajakaruna *et al.* 2009). A comparison between areas affected by birds and those unaffected can show floral composition to differ slightly or even be drastically changed as a result of guano deposition (Wait *et al.* 2005). Furthermore, the provision of nutrients from seabird carcasses or prey remains can support scavenging organisms (López-Victoria *et al.* 2009).

### 1.1.2 Physical disturbance

Physical disturbance of soil by animals can influence ecosystem structure and function (Butler 1995, Whitford and Kay 1999, Bancroft *et al.* 2005a) but studies showing such effects from seabirds on island systems remain scarce (Butler 1995). Bancroft *et al.* (2005b) suggest that soil processes on island systems are of particular ecological concern given that islands typically have soils of poor aggregation and nutrient composition, high water infiltration rate, harsh environmental conditions, and communities, which exist in an unstable state of equilibrium.

In general physical disturbance arises during the breeding season, through the processes of nest building and the actions of scratching, pecking and also trampling of plants and soils (Sobey and Kenworthy 1979, Mulder *et al.* 2011). The exact influence of nest building varies with each seabird species, dependent on nest type, *e.g.* tree, burrow, crevice or surface nests. The variables often found to be influenced by physical disturbance commonly include physical soil characteristics *e.g.* temperature, bulk density, water content, water repellency, infiltration and soil strength (Bancroft et al. 2005b). Chemical characteristics of soil influenced by physical disturbance include altered nutrient concentrations, soil pH and conductivity (Garcia *et al.* 2002, Bancroft *et al.* 2005b). Overall though, there are relatively few studies which have demonstrated the negative impacts of disturbance by non-herbivorous vertebrates (Maesako 1999).

Between seabird species, it is considered that burrow nesting species could have one of the largest effects on land through physical disturbance (Mulder *et al.* 2011), although the degree of influence depends upon nesting density, the age of the colony and the burrowing species (Mulder *et al.* 2011). In general, burrowing species typically of the order Procellariidae, *e.g.* shearwaters and petrels, and Charadriiformes of the family Alcidae, *e.g.* puffins, are known to burrow extensively. Burrowing reduces the stability of the top soil (Boag and Alexander 1996) and alters physical and chemical properties of soils, which can alter species richness and seedling growth (Roberts *et al.* 2007, Grant-Hoffman *et al.* 2010). The impacts of burrowing and trampling further affect communities through the exposure of roots and from initiating retrogressive succession (Maesako 1991, 1999).

By comparison surface nesters can have a relatively small impact on islands, although this is again dependent upon each species and their nesting density (Mulder *et al.* 2011, Kolb *et al.* 2012). Sobey and Kenworthy (1979) showed that treading and sitting by herring gulls *Larus argentatus* caused mechanical damage to plants and suppressed vegetation in regularly frequented areas. Boundary clashes between birds may also result in indiscriminate disturbance through pecking and pulling of both dead and alive plant material (Mulder *et al.* 2011). The impact of tree nesters varies with each species. Larger species such as colonial cormorants or frigatebirds can cause extensive damage to vegetation during nest building, landing and taking off (Mulder *et al.* 2011). Other species such as the marbled murrelet *Brachyramphus marmoratus* are relatively smaller and consequently cause very little physical disturbance (Piatt *et al.* 2006, Mulder *et al.* 2011). Nest building and use, in general, can result in the suppression of plant growth within the area due to the activities of forming the nest, incubation and chick development (Mulder *et al.* 2011).

### 1.1.3 Seed dispersal

There are several documented cases of seabirds initiating vegetative changes on islands due to the dispersal of seeds (Gillham 1956, Wait *et al.* 2005, Ellis 2005, Sekercioglu 2006, Mulder *et al.* 2011). Seabirds have become such a prolific and effective vector of seeds that many species of plant have developed obvious features to facilitate this mechanism (Howe and Smallwood 1982, Burger 2005), *e.g.* cypselae of Asteraceae commonly have viscid extensions which enhance adhesion to animals (Sorensen 1986). These adaptations to birds have resulted in greater dependence on certain taxa for dispersal than others, *e.g.* a study in the Great Lakes showed that 61% of the flora is adapted to dispersal by birds.

This adaptation favouring dispersal by birds often facilitates the spread of alien species (Gillham 1956). In a review by Ellis (2005) it was shown that the majority of studies documented a greater proportion of cosmopolitan species compared to native plant species within seabird colonies (Morton and Hogg 1989, Vidal *et al.* 2003). For example, seabird colonies can often contain cereals and arable weeds (Gillham 1956). The introduction of alien and cosmopolitan species by seabirds onto islands can result in the disappearance of endemic species and consequent ecological perturbations within the original phytocenosis (Vidal *et al.* 1998, Ellis 2005). Furthermore, the diversity of alien plants and plants capable of producing bird-dispersed seeds is closely correlated with island area size (McMaster 2005) and colony density (Heatwole and Walker 1989), respectively. Overall, it is well established that turnover rates on islands with seabird colonies are notably higher than those without, due to propagule dispersal and patch disturbance (Vidal *et al.* 2000).

### 1.1.4 Indirect influence

Seabirds further influence terrestrial systems by indirectly interacting with island communities through predominantly promoting bottom-up dynamics (Sanchez-Piñero and Polis 2000). The provision of nutrients, compared to physical disturbance or seed dispersal, can be viewed as potentially the largest factor driving community dynamics on seabird islands. For example, the presence of seabirds and their guano can alter whole island systems by fuelling communities of lizards and crabs (López-Victoria *et al.* 2009), increasing beetle abundance (Sanchez-Piñero and Polis 2000), altering soil microbial systems (Wright *et al.* 2010), increasing algal production (Bosman and Hockey 1986) and also altering behaviour of herbivorous mammals (Jakubas *et al.* 2008).

In general, there is an increasing number of studies which document cross-scale interactions of organisms between ecosystems, which can alter and impact upon ecosystem processes and community dynamics (Polis *et al.* 1997, Knight *et al.* 2005, Peters *et al.* 2007, Caut *et al.* 2012, Bultman *et al.* 2014). Studies have shown how a range of species influence ecosystems across apparent ecological boundaries, for example: emergent aquatic insects can subsidise terrestrial systems (Bultman *et al.* 2014), migrating pacific salmon can fuel inland terrestrial populations (Cederholm *et al.* 1999, Adams *et al.* 2010) and sewage discharge can increase aquatic insect populations leading to provision of nutrients for swallows (Wayland and Hobson 2001). These studies highlight the importance of nutrient transfer across ecological boundaries and give insight into ecosystem functioning.

In the context of seabirds, understanding the extent to which terrestrial systems are impacted by seabirds is of critical importance to the conservation of insular biodiversity (Caut *et al.* 2012). However, the influence which seabirds have on terrestrial systems does not consider nutrient transfer in detail from seabirds to mammalian herbivores or passerines. Understanding the processes underpinning nutrient transfer throughout islands is of significant conservation value given the high level of species endemism found on islands globally (Ellis 2005, Bellingham *et al.* 2010, Jones 2010)

Overall, seabirds can be seen to increase habitat heterogeneity by altering plant species richness (Vidal *et al.* 1998) and the probability of plant invasion (Mulder *et al.* 2009). However, at high nest and burrow density plants may not be able to survive the severe disturbance (Vidal *et al.* 2000). The transfer of vast quantities of nutrient onto land from seabirds can be seen to drive primary productivity, which can impact upon higher trophic levels (Mulder *et al.* 2011). It is important to note that seabirds breed within a limited period in the year, so their effects on land are temporally variable (Anderson *et al.* 2008). Importantly, however, is that the effects of seabirds on land are mediated by population size. With an increasing population size and density their effects on land increase concomitantly (Mulder *et al.* 2011, Kolb *et al.* 2012) Therefore, to fully understand how seabirds influence islands, reliable data on seabird population sizes, collected via appropriate monitoring schemes is required.

## 1.2 **Monitoring**

There are several reasons and techniques for counting birds (Jones 1992, Montevecchi 1993, Walsh *et al.* 1995, Anker-Nilssen *et al.* 1996, Bertram *et al.* 1999, Bibby 2000). Choosing an appropriate method is key to provide accurate records of population size, which can provide in part an insight into the influences of both natural and anthropogenic change on seabirds (Bellingham *et al.* 2010). Counting colonially breeding seabirds however poses certain issues, which must be determined prior to any study. These issues include, but are not constrained by, the problems of estimating the proportion of breeding to non-breeding birds, locating and counting birds in remote, difficult terrain, evaluating the proportion of the population feeding away from the colony and the influence of weather on colony numbers (Bibby 2000).

The choice of monitoring scheme is dependent upon each species with a variety of methods suggested for both within and across species. For relatively cryptic species, such as burrow or crevice nesters, then determination of nesting location can be subjective, unless direct confirmation of the presence of eggs or chicks is possible (Anker-Nilssen and Røstad 1993, Walsh *et al.* 1995). Other methods for monitoring cryptic species range from knock-down tags to determine burrow occupancy to radio telemetry for locating nests (Gaston *et al.* 1988, Kenward 2001). Counts of more visible species either use numbers of nesting locations or apparently occupied sites, given that determination of actual occupancy can be difficult with distance or densely nesting species (Walsh *et al.* 1995).

Monitoring of seabirds must also consider the temporal variability in abundance at different scales. Many studies have shown how seabird abundance varies over the season and this variation must be understood prior to any monitoring scheme (Nettleship and Birkhead 1985, Klomp and Furness 1990, Finney *et al.* 2003, Regular *et al.* 2010, Harris and Wanless 2011). For example, the erratic attendance of many alcid species can limit the reliability of counts of individuals as an estimate of population size (Walsh *et al.* 1995, Calvert and Robertson 2002a, Harding *et al.* 2005).

Each method of monitoring used often produces variable results and the discrepancy between monitoring methods elucidates the need for a meaningful, comparable and standardised method (Nettleship and Birkhead 1985). Some methods of monitoring are also known to adversely affect seabird populations by the continued presence of observers, which can promote nest abandonment, in particular during the early incubation stage (Gotmark 1992, Rodway *et al.* 1996, Albores-Barajas *et al.* 2009, Shoji and Gaston 2010). Monitoring seabirds without human disturbance is of importance in maintaining and recording natural breeding success.

Monitoring schemes often have logistical constraints, which can limit the scope of recording (Dickinson *et al.* 2008). Counting seabirds manually, often in remote locations under harsh conditions, can become impractical and/or incur significant costs of labour and time (Anker-Nilssen *et al.* 1996, Trathan 2004, Dickinson *et al.* 2008). Consequently, automated approaches to monitor seabirds have been developed to negate some of the limitations from manual monitoring. In particular, the use of photography has become prevalent within wildlife monitoring in general (Martin and Geupel 1993, Cutler and Swann 1999, Gula *et al.* 2010) and also for seabirds (Wanless and Harris 1986, Hatch 2002, Huffeldt and Merkel 2013). The use of photography to monitor seabirds has been undertaken from ground-based (Mudge *et al.* 1987, Harding *et al.* 2005), aerial (Buckland *et al.* 2012) and even satellite platforms (Lynch *et al.* 2012). However, there are greater costs involved with photographic approaches not based on the ground (Lynch *et al.* 2012). Also, for aerial platforms there is the potential for disturbance to seabirds, for example from low flying planes (Trathan 2004, Buckland *et al.* 2012). Limitations for ground-based photography include a need to access and find vantage points to photograph a colony, but for some scenarios, ground-based photography is the only sensible option if photography is to be used. Ground-based photography can be used for monitoring species which nest on cliffs and/or in burrows and whose detectability is reduced when monitored with aerial or satellite platforms.

Time-lapse photography provides one way in which to monitor seabird populations by repeated photographs across a period of time with relatively low cost, providing detailed insight into seabird populations (Lorentzen *et al.* 2012, Huffeldt and Merkel 2013). Although technology has become possible for long-term monitoring using photography, the approach has not been fully explored for its potential (Huffeldt and Merkel 2013). There is a need to explore long-term monitoring of seabirds using time-lapse photography to examine changes in population size. However, whenever monitoring is undertaken there is a need to ensure that the same approaches are undertaken over time for comparability and that any change in methodology considers sampling limitations and error between different methods (Buckland *et al.* 2012)

Overall, knowing the size of seabird populations is of importance, not least for understanding their effect on island systems, but also for their close association with the marine environment. This association has allowed seabirds to be viewed as indicators of the state of the oceans' health (Harris and Bailey 1992, Montevecchi 1993). The ability of seabirds to exert top-down control within trophic networks and also respond to bottom-up influences makes them important ecological bioindicators (Fort *et al.* 2011). Furthermore, birds can be viewed as bioindicators as the concept is readily understood by the public and policy-makers, due to their popularity and often iconic status (Crick 2004). Using seabirds as bioindicators allows a wide-spread understanding of the survival, recruitment and productivity of seabirds, which is imperative for any initiation of conservation and management (Nettleship and Birkhead 1985). Seabirds can also allow for an indication of prey abundance, whereby a particular choice of prey can be a short-term indicator of prey availability and allow inferences to be made on the health of the marine ecosystem (Montevecchi 1993). Equally, the numbers of non-breeding seabirds could provide a sensitive indication to the effects of environmental change, since non-breeders act as a buffer to such stress (Klomp and Furness 1992).

## 1.3 Project rationale and study species

Within the United Kingdom, there are over seven million breeding adults of 25 species of seabird (Lloyd *et al.* 2010, Wanless *et al.* 2010) and within Scotland, and the islands of the Outer Hebrides and Shetland in particular, seabirds are a common part of the fauna. Consequently, seabirds on these islands can have a significant role in ecosystem processes and community structure. However, there are relatively few studies examining the influence of seabirds on islands in Scotland with most studies focussing upon systems in the Pacific (Anderson *et al.* 1998, Anderson and Polis 1999, Maron *et al.* 2006) and the islands around New Zealand (Hawke and Newman. 2004, Roberts *et al*. 2007, Bellingham *et al.* 2010). Consequently, there is a need to explore the influence of seabirds on islands in more temperature latitudes, such as in Scotland.

This study was limited to two study species in Scotland: the great skua *Stercorarius skua* and the Atlantic puffin *Fratercula arctica*. These species were chosen for their different nesting habits, their variable nesting density and different behaviours, which may all affect their influence on island systems. Given the importance of understanding population size a novel method for monitoring Atlantic puffins is trialled using time-lapse photography. Studies were conducted on three islands around Scotland: Mingulay and Hirta (St. Kilda), Outer Hebrides, and Fair Isle, Shetland.

To discuss each species in further detail, the great skua is a large generalist predator, which inhabits islands across the North Atlantic from Iceland east to Svalbard (Lloyd *et al.* 2010). The great skua is a surface nester typically found on moorland close to the sea with an estimated global population of *c.* 16,000 pairs, of which 9,600 pairs are within Scotland (Mitchell *et al.* 2004, Lloyd *et al.* 2010). Their influence on land is however not well documented with only limited observations on their immediate influence to the colony surface (Engelskjon 1986, Furness 1987, Klomp and Furness 1990). The ability to monitor skuas is relatively easy with estimates of the number of pairs derived from visible signs of territory occupancy on the colony surface or also in part by their relatively aggressive nature (Furness 1987, Walsh *et al.* 1995).

Secondly, the Atlantic puffin is a small species of auk with a distribution from the East coast of North America to the Northern coast of Russia with a global population estimated up to 6 million pairs (Lloyd *et al.* 2010). The Atlantic puffin is a colonial burrow-nesting seabird, with colonies scattered around the UK, although the largest colonies and most of the UK population is in Scotland (Lloyd *et al.* 2010). Atlantic puffins create their burrows in suitable substrate or they may nest in crevices and boulder scree. This subterranean habit combined with their erratic colony attendance makes monitoring Atlantic puffins complicated (Nettleship 1976, Walsh *et al.* 1995). The influence which Atlantic puffins have on land has only been documented for their immediate influence on the colony but their wider impact on island systems is poorly understood (Boag and Alexander 1996, Harris and Wanless 2011).

## 1.4 Project aims

The following chapters of this thesis are thus structured to primarily explore the effect of Atlantic puffins and great skuas on islands in Scotland. An understanding of the population size is critical to predicting the effect of Atlantic puffins on land. Therefore, an alternative method to monitor Atlantic puffins using time-lapse photography is trialled.

**Chapter 2** aims to determine how the attendance of the Atlantic puffins varies over different temporal and spatial scales and in response to environmental variables. However, rather than using direct observations of puffin attendance this method employs time-lapse photography. Cameras are installed across a wide geographical range to explore variation in attendance within and between colonies, with consequences for methods in monitoring.

**Chapter 3** aims to show how time-lapse photography can be used to monitor Atlantic puffins directly as a stand-alone approach. This study gives further consideration to sampling intensity and the relationship between the numbers of puffins observed and the actual breeding population. Finally, a novel approach of associating the spatial position of Atlantic puffins in relation to burrows is studied.

**Chapter 4** estimates the mass of nutrients that a population of Atlantic puffins and great skuas brings onto the island of Mingulay, Outer Hebrides, Scotland, during the breeding season. Estimates of nutrient input focus upon nitrogen and phosphorous and are calculated using a bioenergetics approach.

**Chapter 5** explores how Atlantic puffins and great skuas influence island ecology in Scotland. The study looks at plant community diversity and also variation in nitrogen within grasses over different islands in response to seabird presence. The study also aims to describe how nutrients are transferred from seabirds to mammalian herbivores and how this may influence their populations.

**Chapter 6** investigates how nutrients are moved around different components of island systems. This study specifically looks at how nutrients are moved from a large colony of common guillemots *Uria aalge* and razorbills *Alca torda* to a large passerine population of house martins *Delichon urbica* in the Baltic Sea.

**Chapter 7** brings the thesis together in a General Discussion, which ties how seabirds influence island ecology with a potentially wide reaching issue of conservation. The applicability of using time-lapse photography is further discussed.

# Chapter 2

# Variation in Atlantic puffin *Fratercula arctica* colony attendance; monitoring using time-lapse photography

# Abstract

Attendance, the observable numbers of seabirds at a colony, is often used to reflect population size. Obtaining detailed of counts of seabirds to determine attendance requires access to monitor colonies, which are often in places that are logistically difficult to access and have harsh environmental conditions. Consequently, significant costs time and labour can be incurred in determining attendance. The Atlantic puffin *Fratercula arctica* is a species where detailed counts of attendance are required given it has both a notoriously erratic pattern of attendance and also a subterranean presence. An understanding of those factors influencing attendance needs to also be considered if attendance is used for purposes of monitoring. Time-lapse photography is proposed as a novel method with which to obtain high resolution temporal data on puffin attendance across the season, with minimal costs of installation and processing. For this study, time-lapse cameras were installed on islands around Scotland and demonstrated that detailed attendance patterns of the Atlantic puffin can be detected using time-lapse photography. The cameras showed that puffins exhibited a general pattern of increasing attendance throughout the day, with a cyclic pattern of attendance across days with a periodicity of around 5 to 7 days. Puffin attendance was shown to significantly decrease with spring tides and one colony showed decreased attendance with increasing wind speed. There was no observable effect of temperature on puffin attendance and predator presence caused decreased attendance. The use of high temporal resolution data to define periods of attendance lends support to the possibility that counts of puffins could be used for purposes of monitoring.

## 2.1 **Introduction**

Monitoring seabirds is of importance to establish how the size of each species' population changes over time. The inextricable link between seabirds and the marine environment has resulted in seabirds being viewed as indicators of the oceans' health (Montevecchi 1993, Lloyd *et al.* 2010). Estimating the size of a seabird population can be undertaken using the number of individuals observable in a colony, termed attendance (Walsh *et al.* 1995, Calvert and Robertson 2002a). Attendance can however vary markedly over time, both within and between days, which has implications when estimating population size from counts of individuals (Slater 1976, Cairns 1979, Hatch 2002, Harding *et al.* 2005, Huffeldt and Merkel 2013). Understanding the variability in colony attendance is therefore of importance if indices of population size are to be reliably derived.

The Atlantic puffin *Fratercula arctica* (hereafter termed "puffin") is an example of a colonial, burrow-nesting seabird that breeds in both burrows and crevices, and which is known to be notoriously variable in its colony attendance (Brooke 1972, Calvert and Robertson 2002b, Harris and Wanless 2011). Studies have shown how attendance varies on both a daily and seasonal scale. On average daily attendance increases after midday and peaks from the late afternoon to evening, although day length can also influence attendance (Corkhill 1971, Harris and Wanless 2011). Over a seasonal scale puffins can have cycles of attendance with variable periodicity. Periodicity can vary from 7 days as on Great Island, Canada (Nettleship 1972), to 4 to 11 days as on Lovunden, Norway (Myrberget 1979, Harris and Wanless 2011), although cyclicity is often around 5 days (Corkhill 1971, Lloyd 1972, Calvert and Robertson 2002a, Harris and Wanless 2011). Different colonies have also been found to be both synchronous and asynchronous in their attendance within and between islands (Corkhill 1971, Harris and Wanless 2011). In addition, attendance can vary across the season with breeding stage and also the arrival of non-breeding prospecting puffins (Lloyd 1972, Cairns 1979, Harris and Wanless 2011).

Attendance of puffins, and seabirds in general, can also be influenced by environmental factors (Walsh *et al.* 1995, Calvert and Robertson 2002a, Harris and Wanless 2011). Attendance for many species of, for example alcid, has been shown to be differentially influenced by atmospheric conditions. Studies have shown how increased wind speed decreases attendance by reducing flight efficiency (Lloyd 1972, Hatch 2002, Calvert and Robertson 2002a), although some studies find no significant effect (Blet-

Charaudeau *et al.* 2010). Equally, some studies find no influence of temperature on Atlantic puffin attendance (Calvert and Robertson 2002a), whilst others do (Blet-Charaudeau *et al.* 2010). Furthermore, wind direction, precipitation and cloud cover are observed to have little influence on attendance (Hatch 2002, Calvert and Robertson 2002a).

Tidal conditions may also influence colony attendance by its effect on prey availability and consequently foraging behaviour (Piatt *et al.* 1990, Irons 1998). As the magnitude of tidal oscillations increases with both daily tides and longer spring/neap tidal cycles, seabird prey, *e.g.* zooplankton and their prey, may become concentrated at tide rips and offshore fronts (Piatt *et al.* 1990). Studies have shown an effect of tidal state on colony attendance for a range of seabird species (Slater 1976, Piatt *et al.* 1990, Vermeer *et al.* 1993, Irons 1998). However, other studies show no effect of tide on attendance or even contradict prior studies (Piatt and McLagan 1986, Piatt *et al.* 1990), though this may be a result of variation in local tidal range (Cairns 1979). There are limited studies looking at the variation in puffin attendance with regards to tides (Corkhill 1973), although there have been contradicting studies on the interaction of puffins with tidal state (Wanless *et al.* 1990, Robbins 2012).

Although not considered an external factor influencing attendance, the extent of colony attendance may be in part governed by how long individual puffins spend on land. Previous studies have shown that the length of time a puffin spends on land is correlated with colony attendance (Calvert and Robertson 2002a). There may be an advantage to spending more time on land when surrounded by conspecifics to reduce the chance of predation (Calvert and Robertson 2002a).

In general, the range of contradicting results for the influence of environmental variables on puffin attendance requires further study. The variation in attendance and influence of environmental variables may be colony specific (Harris and Wanless 2011). Understanding which factors influence puffin attendance can lead to further improvements in the reliability of counts of individuals, as an index of population size.

For puffins, estimates of colony attendance are often undertaken by manually counting in the field the numbers of individuals present (Corkhill 1971, Lloyd 1972, Calvert and Robertson 2002a). This method can however take significant time to undertake and consequently attendance is often monitored at a lower resolution and/or frequency

(Myrberget 1979). This limited monitoring of puffins can therefore lead to an unrepresentative estimate of the population size given the high variation in attendance. Equally, very few studies look at attendance in detail across colonies and time, which is likely to be due to the significant man-hours and cost involved in manually recording attendance at multiple colonies (Corkhill 1971, Lloyd 1972). An automated approach to monitor puffins could allow high resolution temporal data to be collected across the breeding season and between colonies, providing detailed information on the variability in attendance.

Time-lapse photography provides a way in which to record puffin attendance automatically over time. Time-lapse photography and video are both methods which have been used in avian applications, such as in studies of behaviour and breeding success (Dickinson *et al.* 2008, Lorentzen *et al.* 2010, 2012, Gula *et al.* 2010, Huffeldt and Merkel 2013). Studies have also used time-lapse to count individuals of different seabird species for purposes of monitoring (Harris and Wanless 1983, Mudge *et al.* 1987, Piatt *et al.* 1990, Zador and Piatt 1999, Harding *et al.* 2005). The use of time-lapse photography to monitor puffins is however limited to one study, which demonstrates how productivity of puffins can be inferred from attendance (Anker-Nilssen 2010).

In general, time-lapse photography could be used in remote locations with visits only to install and collect the camera system at the beginning and end of the season, respectively (Huffeldt and Merkel 2013). The increased commercial viability of camera systems means that the use of time-lapse photography could become competitive with visual methods for monitoring (Buckland *et al.* 2012, Huffeldt and Merkel 2013). Automated photography can furthermore be used to collect data on attendance at a high temporal resolution with minimal cost and effort from remote areas.

The aims of this study were to examine the attendance of Atlantic puffins over daily and seasonal scales, using time-lapse photography at a resolution not recorded before. The study also aimed to understand the effect of environmental variables on puffin attendance. Understanding puffin attendance has implications for monitoring populations. The installation of cameras on islands around Scotland aims to also give an indication of the geographical variation in attendance within and between colonies.

## 2.2 Methods

This study was conducted on five Scottish puffin colonies; three colonies on Mingulay (termed “Original”, “Otter” and “Arnamul”), Outer Hebrides, one colony on Fair Isle and one colony on Unst, Shetland (Hermaness) (Figure 2.1). Data were collected over 2011 and 2012 for the two colonies: Original on Mingulay, and Fair Isle. In 2012 two more sites were added on Mingulay: Otter was within the same larger, cliff-top colony on the east side of Mingulay as Original but the two observation areas were separated by *c.* 150 m and the census areas did not overlap. Arnamul was a colony on the west of Mingulay on the side of a stack, *c.* 100 m offshore and *c.* 2.5 km from the Original and Otter colonies. Hermaness is *c.* 600 km North-East from Mingulay and was located on the side of a cliff whereas Fair Isle is *c.* 150 km South of Hermaness and represented a cliff-top colony. Multiple colonies and years were chosen in order to examine variation in inter-colony and inter-year attendance patterns.

Because hatching dates in different puffin colonies around Scotland within the same year can be similar (Harris 1982, Harris and Rothery 1985, Mavor *et al.* 2006) the median hatching date observed on Mingulay (11th June in both years, pers. obs.) was used to split the study period into a pre-hatching (incubation) and post-hatching (chick-rearing) stage. Observations on Fair Isle started on 1st July in 2011 and ended on 1st June in 2012 and thus would be unlikely to cover the pre- and post-hatch stage, respectively. Observations on Hermaness started on the 14th June 2012 and these data were considered to come from the post-hatch stage only, although admittedly this may be within the range of hatch dates. Thus, five of the seven datasets contained data for the pre-hatch stage and of these five datasets four also had data for the post-hatch stage (Table 2.1). The post-hatch stage has a further two datasets from colonies not studied in the pre-hatch stage, thus a total of 6 datasets.

### 2.2.1 Counts of puffins using photography

Colony attendance at each site was established using time-lapse photography. At each site a camera with an attached timer device was positioned and set to take photographs over time. A digital single-lens reflex camera (Canon 500D or 550D) with a zoom lens (Canon EF-S 18-55 mm) was used with a minimum 8 GB SD card for storing photographs. A simple unbranded timer device was fitted to the camera, which allowed the camera to take repeated photographs (time-lapse photography) with a user-defined interval. The interval is defined as the time elapsed between successive photographs. The camera and timer device were then installed in a custom-built weatherproof housing. The cameras were located to maximise the field of view of the puffin colony, whilst considering image resolution. The final positioning was a balance between distance from colony, topography and underlying substrate.

The interval set on the timer device varied between colonies and year, to explore the effectiveness of different sampling intervals and also to fit with logistical constraints of the time available for camera maintenance by volunteers. On average the battery and SD card were changed every two to seven days, depending upon photographic interval. A minimum of 10 minutes was intended as the sampling interval; however due to storage limitations or if maintenance visits could not be carried out with high frequency then the sampling interval may have been longer (Table 2.1).

The periods the cameras operated covered mid-late incubation to late chick-rearing. On Mingulay, cameras were installed and set-up from around mid-May until mid-July, coinciding with logistical availability. The study duration on other colonies was defined by volunteer availability. Cameras were installed and left to run between 17 and 60 days (Table 2.1). Photographs were taken when light levels allowed for correct exposure; thus images at night are often excluded. Due to camera malfunctions there were periods of time when the cameras were not working, which reduced the effective temporal coverage (Table 2.1). Furthermore, a small percentage of individual photographs could not be used (mean = 1.4 % ± 1.9 SD) when, for example, adverse weather obscured the lens (Table 2.1). For analyses, these data are assumed missing at random and those periods separated by more than one missing day are treated as separate time series. Hermaness was the only colony which had its time series split based upon periods of missing data. Two periods of camera malfunction on Hermaness, which lasted 10 and 8 days respectively, resulted consequently in three shorter time series. Two of the shorter time series were less than 9 days each and were discarded, whilst the longer time series retained and used within this study was 17 days long.

At the end of the season, the numbers of puffin present on the ground were visually counted on each usable photograph. A sample of photos from Original in 2012 was independently counted by two different observers and showed a high correlation between observers (Pearson’s correlation = 0.98, $n = 133$, $P < 0.001$). The numbers of observable puffins on the ground represented a measure of colony attendance.

### 2.2.2 Attendance patterns

Counts of attendance over different times of day can be very variable (Brooke 1972, Harris and Wanless 2011). To observe the average change in daily attendance the numbers of puffins over time were aggregated based upon two daily time scales, following Calvert and Robertson (2002a).

Firstly, to illustrate the daily attendance pattern at relatively fine temporal resolution the mean number of puffins within every 30 minute interval across the day was calculated. The mean number of puffins was taken from averaging the number of puffins each day across the season into 30 minute intervals from midnight. However, an analysis exploring variation in attendance between times of day using 30 minute intervals would provide too many levels within a factor for interpretable analysis. Thus, the day was split into five equal periods of ~ 5 hours: Early Morning (00:00 to < 04:48 h), Morning (04:48 to < 09:36 h), Afternoon (09:36 to <14:24 h), Evening (14:24 to < 19:12 h) and Night (19:12 to < 00:00 h). Calvert and Robertson (2002a) only included four periods of diurnal activity (from 07:00 to 21:00); however the presence of nocturnal activity, in particular on Hermaness, required inclusion of a further period.

Many colonies are known to have cycles of attendance which persist across the season, with a varying periodicity from 4 to 11 days, although on average around 5 days (Nettleship 1972, Myrberget 1979, Calvert and Robertson 2002a, Harris and Wanless 2011). Given the potential variability in puffin attendance when plotting numbers of puffins over time (Anker-Nilssen 2010, Harris and Wanless 2011) a smoother was used to reduce the variation associated with attendance into an observable pattern. Spatial synchronicity in colony attendance is also explored by relating attendance over time between different puffin colonies.

### 2.2.3 Factors related to attendance

#### 2.2.3.1 Environmental variables

Environmental variables were related to colony attendance to understand what factors potentially influence the numbers of puffin seen on land. Data on daily weather for Mingulay were obtained from Tiree (63 km away). Although there is a closer weather station (South Uist, 57 km away), Tiree's location is geographically more similar to Mingulay, in that the effect of topography on weather is relatively less, than South Uist with a relatively greater land mass and topographic relief upwind (Mayes and Wheeler 1997, Owen *et al.* 2004). Weather data for Hermaness came from the closest weather station at Sella Ness, Shetland (48 km away). Meteorological data (mean temperature ($^{o}$C) and mean wind speed (km $h^{-1}$)) for these weather stations were collected from Weather Undergroud (2014). A strong, positive correlation between data from Weather Underground and limited data obtained from the Met Office for Tiree (2nd June to 15th July 2011), ensured that the data from Weather Underground and the Met Office were comparable for that station (mean Pearson's correlation (± 95 % confidence interval) = 0.81 (0.70 – 0.89). To calculate the mean Pearson's correlation both weather time series were first-differenced by subtracting the value at $t_i$ from $t_{i+1}$ to remove any long-term trend (Bjornstad *et al.* 1999). However, given serial correlation within each time series data are not independent (Buonaccorsi *et al.* 2001). A bootstrap 95 % confidence interval for the mean synchrony was produced from sampling ($n$ = 1000) with replacement between each time series and recalculation of Pearson's correlation (Bjornstad *et al.* 1999, Buonaccorsi *et al.* 2001). Bootstrapping provides a measure of significance by randomisation, whilst accounting for serial correlation (Bjornstad *et al.* 1999).

The behaviour and attendance of seabirds has been found to be associated with the magnitude of tidal oscillations, which could influence the concentration of seabirds' prey (Slater 1976, Cairns 1979, Vermeer *et al.* 1993, Irons 1998). Consequently, mean daily tidal height was related to mean daily attendance of puffins to observe any influence of seasonal tidal rhythms, *e.g.* spring and neap tides, on attendance. The resolution of tidal data on a daily scale does not allow for examination of the effect of within-day high and low tides. The mean daily tidal height was obtained from Barra Head (~ 3 km from Mingulay) in 2011 and 2012 and Burra Firth (adjacent to Hermaness) in 2012. All tidal data were obtained from the UK Hydrological Office (2013). The association between attendance, and meteorological and tidal data were not analysed for Fair Isle given the short study duration and long intermittent periods of missing data (Table 2.1).

#### 2.2.3.2 Predators

Original 2012 also had the presence and absence of the predators of puffins recorded for each photograph. Predators were defined as the great black-backed gull *Larus marinus*, the herring gull *Larus argentatus*, the lesser black-backed gull *Larus fuscus*, the great skua *Stercorarius skua* and the hooded crow *Corvus cornix* (Harris and Wanless 2011). The presence of predators was recorded to explore their effect on the numbers of puffin present.

### 2.2.4 Statistical analyses

#### 2.2.4.1 Daily attendance patterns

The change in daily attendance patterns between the five daily periods was analysed using a Generalised Linear Mixed Model (GLMM) with a Gaussian error structure. The mean number of puffins was firstly calculated for each of the five daily periods each day. The GLMM was used to analyse the difference in the mean number of puffins between daily periods and colonies. The fixed effects of period of day and colony were used with an interaction between the two terms. The GLMM was used with a random effect of day of year nested within colony to account for repeated measurements over time and within colonies. The model included data from the colonies of Mingulay, Fair Isle and Hermaness over both 2011 and 2012. Model structure: Mean number of puffins ~ daily period * colony, random effect = day of year/colony.

A GLMM with a Gaussian error structure was also used to analyse the difference in the mean number of puffins between daily periods over two different stages of the puffin's breeding cycle: pre-hatch and post-hatch. Fixed effects included period of day, breeding stage and colony with interactions between breeding stage and colony, breeding stage and period of day and a three-way interaction between all three fixed effects. A random effect of day of year nested within colony was included to account for repeated measurements over time and within colonies. Only colonies from Mingulay were analysed given applicable data over both the pre- and post-hatching stages. Model structure: Mean number of puffins ~ breeding stage * daily period breeding stage * colony + breeding stage * colony * daily period, random effect = day of year/colony.

#### 2.2.4.2 Seasonal attendance patterns

The seasonal change in attendance was inferred using Generalised Additive Models (GAMs) with a Poisson error structure in an exploratory fashion (Hastie and Tibshirani 1990, Regular *et al.* 2010). GAMs were chosen to extend the Generalised Linear Model by application of smoothing terms to explanatory variables (Hastie and Tibshirani 1990, Wood 2006). Smoothing is undertaken by fitting splines, using piecewise polynomials. The degree of smoothing is defined by the number of knots supplied (Fewster *et al.* 2000).

Selection of the number of knots is however not based upon an objective criterion. The number of knots can be determined through generalised cross validation (GCV) (Wood 2006, Forcada *et al.* 2006); however the number of knots chosen must also consider the scientific relevance of any observed pattern over time (Fewster *et al.* 2000, Ruppert *et al.* 2003).

By varying the number of knots the change in the pattern of attendance is observed. Final selection of the number of knots was based upon the point at which the pattern of attendance becomes poorly defined, with regards to the objective (Fewster *et al.* 2000). Whilst this approach is subjective displaying the results of a range of knots demonstrates the potential variation in defining change in attendance over time and between colonies.

The robustness of any change in attendance over time is improved by presenting results of two different summaries of the response variable. The form of the response variable included using: 1) raw counts of the number of puffins, and 2) taking the mean of the number of puffins in each of the five ~5-hour periods each day. Aggregating data into five ~5-hour periods also reduced the proportion of zeros from ~60 % to ~20 %, improving model fit. Corroboration between patterns of attendance from GAMs using different numbers of knots and the two response variables indicates the persistence and robustness of any pattern within the data.

The degree of spatial synchrony between colonies is analysed using the same procedure as used for the correlation between weather variables at two different sites. In summary, data are de-trended by first-differencing and then, given serial correlation, the mean Pearson’s correlation is calculated by bootstrapping with replacement (Bjornstad *et al.* 1999, Buonaccorsi *et al.* 2001). Bootstrapping produces 95 % confidence intervals to also test the significance of any correlation when comparing between time series.

Using the mean Pearson’s correlation from bootstrapping, all comparisons showed a positive and significant correlation between raw counts and aggregated counts of puffins ($r > 0.95$, 95 % confidence interval ranging from 0.92 - 1.00), for all colonies and with different numbers of knots. Aggregating raw data into ~5-hour periods and the inclusion of daily period as a covariate further takes into consideration autocorrelation within the model residuals (Legendre and Legendre 2012). Therefore all further analyses are based upon the aggregated data. The seasonal attendance of puffins was not modelled for Fair Isle given extensive periods of missing data and thus the short length of the time series (Table 2.1). GAMs were run using the function *gam* from the ‘mgcv’ package (Wood 2006, R.Core-Team 2014).

For analysis of spatial synchrony between colonies on Mingulay GAM-fitted values using the aggregated data (from the five ~5 hour periods) were correlated using the mean Pearson’s correlation from bootstrapping.

### 2.2.4.3 Factors related to attendance

The effect of environmental variables (mean daily temperature (˚C), mean daily wind speed (km $h^{-1}$) and mean daily tidal height) on mean daily puffin attendance was tested by comparing the mean numbers of puffins before and during an above-average environmental event. An above-average event is defined as daily temperature > 13 ˚C, wind speed > 18.5 km $h^{-1}$ (as defined within Hatch 2002), and the day of a spring or neap tide. These cut-off points for weather represent across colonies the 70th percentile for temperature and the 58th percentile for wind speed and were based upon a consideration for sample size and also prior study for wind speed (Hatch 2002). Data were not analysed using the entire daily mean time series given both the confounding effect of seasonal attendance, which may mask any influence of environmental variable on attendance and the coarse scale of the covariate data.

The effect of temperature and wind speed compares the daily mean number of puffins between the days of an above-average event and the preceding, consecutive day with a value below the threshold. The effect of tide compares the daily mean number of puffins between the days of a spring or a neap tide and the mid-point to the preceding neap or spring tide, respectively. The midpoint prior to the spring/neap peak or trough is ~3 days before.

Comparisons of attendance before and during high temperatures, winds or tidal heights are made using a Wilcoxon matched-pairs signed-rank test, given non-normality of the count data. For weather variables data were analysed both within individual colonies and across colonies by grouping, using colonies on Mingulay and from Hermaness. Tidal data only from Mingulay were analysed by grouping across colonies, given the small sample size within a colony ($n = 3$). Hermaness was not analysed given the presence of only one tidal cycle ($n = 1$).

The effect of a predator’s presence on puffin numbers was modelled using a Wilcoxon matched-pairs signed-rank test, given non-normality of the data. The data comprised every instance of the paired numbers of puffins in two consecutive photographs without predators and then with predators, respectively. Given ties within the analysis data were jittered by adding a miniscule amount of random noise (0.01) to the numbers of puffins (Robert and Casella 2009). The Wilcoxon matched-pairs signed-rank test was then iteratively run 1000 times to model the significance of the relationship with the addition of random noise (Robert and Casella 2009).

Significance is reported as $P < 0.05$ with statistical tests using a two-tailed test. Error values associated with mean values are standard deviation (SD), unless reported as standard error (SE). Model selection to produce the minimum adequate model (MAM) was determined by stepwise backwards removal of parameters from a fully parameterised model using maximum likelihood (ML). The significance of a fixed effect was determined by using likelihood ratio (LRT) chi-square tests between the GLMM and a GLMM excluding the fixed effect of interest (Pinheiro and Bates 2000, Miles 2010). Only significant terms are reported from model selection. MAMs were run using restricted maximum likelihood (REML) for presentation of model coefficients. To test for differences between model groups *post-hoc* Tukey Honest Significant Difference tests are used. The function *lmer* from the 'lme4' package was used to implement GLMMs (R.Core-Team 2014). Tests for autocorrelation were done using the *acf* from the 'stats' package. Model fit was assessed on the basis of normalised model residuals versus fitted values testing for heteroskedascity, low AIC values, a lack of over-dispersion and collinearity. All analyses are carried out in R *v*. 3.03 (R.Core-Team 2014).

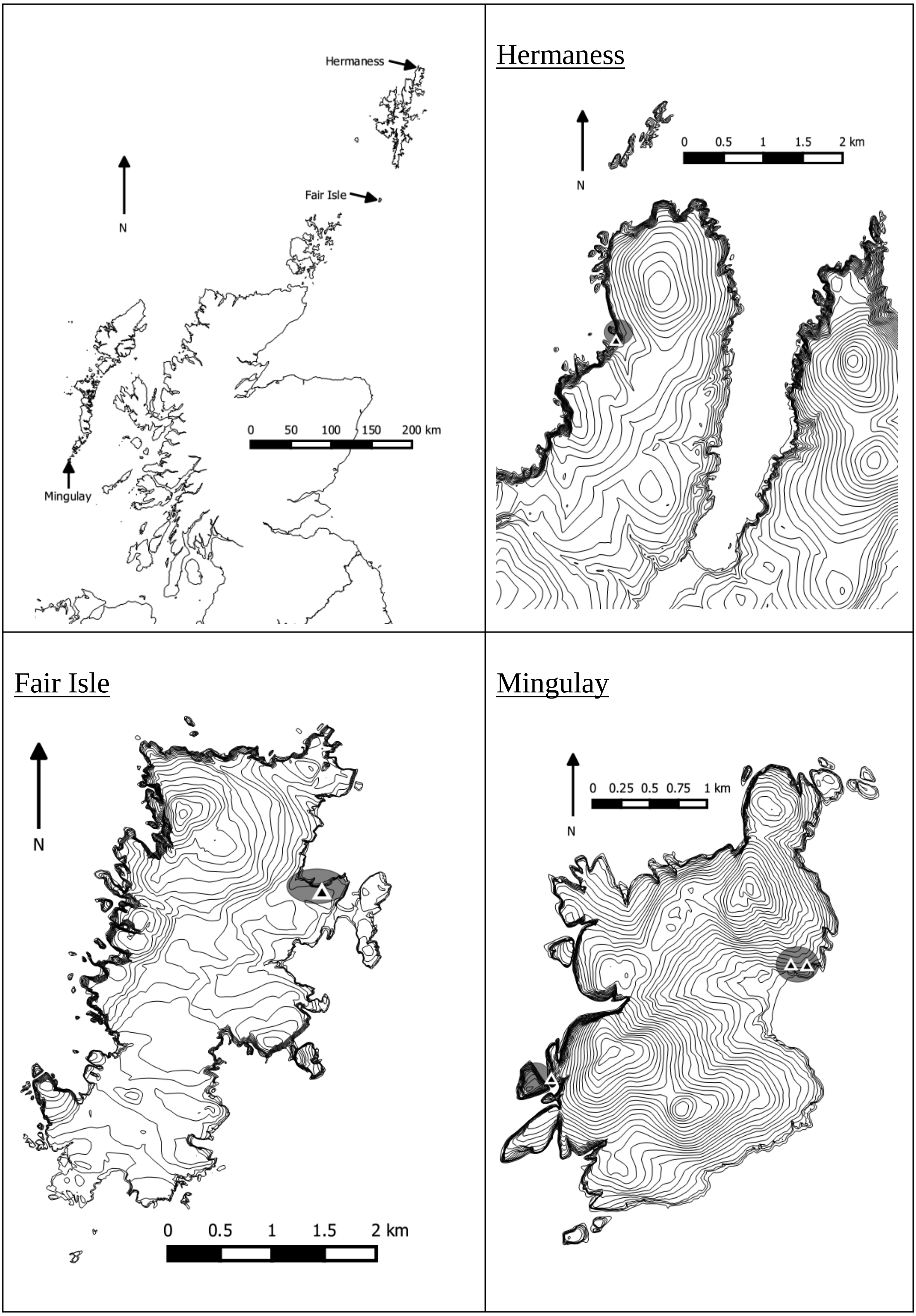

**Figure 2.1.** Location of the three islands where cameras were installed. Top left: UK overview of island locations. Camera positions denoted by triangles and monitored puffin colonies in shaded ellipses.

# 2.3 Results

## 2.3.1 Daily attendance patterns

Figure 2.3 shows the variation between colonies in daily attendance from across the study duration using counts of puffins aggregated into both 30 min intervals and the five daily ~5-hour periods. There is a strong similarity in attendance pattern between the two time scales, and therefore the aggregated data from the five daily ~5-hour periods were analysed to test for differences in mean attendance between colonies and within a day. The results showed a significant difference in daily attendance pattern between colonies (LRT, period of day*colony: $\chi^2_{24} = 221.68$, $P < 0.001$). Within individual colonies *post-hoc* Tukey tests (as denoted by letters in Figure 2.3) showed on all Mingulay colonies (except Otter 2012) that mean attendance was greatest from the period termed Night (19:12 to 00:00 h) to all other periods of the day (Figure 2.3). There was also a significant increase in attendance from Early Morning (00:00 to 04:48 h) and Morning to Evening (14:24 to 19:12 h) for Original 2011 (Figure 2.3). On Hermaness mean attendance significantly decreased from Early Morning to all other periods of the day, except Night. Mean attendance also significantly increased from both Morning and Afternoon (09:36 to 14:24 h) to Night. Fair Isle (both years) and Otter 2012 had no significant change in puffin attendance across the daily periods.

### 2.3.1.1 Pre- and post-hatching attendance

There are broadly similar daily attendance patterns before and after hatching (Figure 2.4). Within each breeding stage there is again similarity in the daily attendance pattern of puffins between the two aggregated time scales (Figure 2.4). The average change in attendance every 30 min across colonies on Mingulay between breeding stages is shown in Figure 2.5. Attendance appears to vary with breeding stage and time of day, with a slight increase in attendance from pre- to post hatching in the morning before 07:00 h, and more noticeably from 20:00 h onwards (Figure 2.5). This difference across hatching stage indicates a possible interaction between time of day and breeding stage.

Using the five ~5 h daily periods showed that the effect of breeding stage on attendance depended on both colony and period of day for the colonies on Mingulay (LRT:

breeding stage*colony*period, $\chi^2_{24} = 79.47$, $P < 0.001$). Model coefficients estimated that there was significantly greater attendance from pre- to post-hatching across colonies (GLMM: $\Delta_{\text{pre- to post-hatching}} = 9.6$ puffins ± 3.1 SE, $P = 0.002$, Table 2.2). *Post-hoc* Tukey tests showed that attendance increased significantly from pre- to post-hatching for the period Night for the colony Original 2012; whilst all other colonies had a non-significant increase for the same time through the breeding season. For all other times of day there were non-significant decreases in attendance with hatching, with the exceptions of Arnamul in the Early Morning and Evening, and Original 2011 in the Evening, which both showed a non-significant increase (Figure 2.4).

To examine the difference in attendance within different breeding stages separate GLMMs were run on each breeding stage (Table 2.3, Table 2.4). During the pre-hatching stage there was no significant interaction between period of day and colony on the mean puffin attendance, although an interaction existed in the post-hatching stage (LRT: colony*period; pre-hatching, $\chi^2_{12} = 18.72$, $P = 0.095$; post-hatch, $\chi^2_{12} = 60.61$, $P < 0.001$). During the pre-hatching stage puffin attendance varied with both period of day and colony (LRT: period of day, $\chi^2_4 = 20.45$, $P < 0.001$; colony, $\chi^2_3 = 30.37$, $P < 0.001$). *Post-hoc* Tukey tests showed that Arnamul had significantly higher numbers of puffins than the other colonies, whilst there were no significant differences in attendance between the colonies of Original 2011 and 2012, and Otter. *Post-hoc* Tukey tests further showed significant increases in mean numbers of puffins from the Early Morning to Evening and a significant increase from Early Morning to Night. During the post-hatching stage *post-hoc* Tukey tests showed a significant increase in mean numbers of puffins throughout the day and attendance peaked at Night, except for Otter, which had no significant difference between periods of day. Original 2011 also had significant increases in attendance from the two periods Early Morning and Morning to Evening (Figure 2.4).

### 2.3.2 Seasonal attendance pattern

Across the season there is considerable variation in attendance for each colony from the raw counts of puffins (Figure 2.6). Although, cyclicity at other colonies has a periodicity on average around five days (Harris and Wanless 2011), the GAMs identified a change in attendance over time with varying periodicity dependent upon the degree of smoothing.

For all models, increasing the number of knots decreased the GCV score suggesting a better model fit; however with increased knots the useful signal to noise ratio decreased (Appendix I A). Below 16 knots the change in attendance over time appears to be overly smooth, missing distinct periods of attendance as seen from raw counts and the mean daily counts (Figure 2.6). With 16 knots, a regular periodicity in attendance is detected; however at 25 knots additional peaks in attendance are observed. At 32 knots, the change in attendance over time becomes less smooth with irregular attendance, which could be construed as noise. Discerning the point, however, at which a signal becomes noise is difficult to define (Fewster *et al.* 2000). Therefore, results are presented for models using 16 and 25 knots to demonstrate seasonal attendance within and between colonies. The number of knots for Hermaness was chosen with a similar rationale as before. Below 7 knots the GAM appeared overly smooth and from 7 knots above the models detected more peaks. There were slight differences between 12 and 15 knots using raw counts compared to aggregated data; however aggregated data at 15 knots produced a pattern of attendance similar to the raw counts and mean daily data (Figure 2.6, Appendix I B and C). Consequently, Hermaness is modelled with 7 and 15 knots.

Using 16 knots and aggregated counts of puffins, results show that puffin attendance shows regular cycles for each colony (Figure 2.6). The period of cyclicity is taken as the interval between two successive peaks. For Mingulay there is a mean period (days) ± SD of: 7.6 ± 1.9 for Original 2011 (*n* = 5), 7.0 ± 0.7 for Original 2012 (*n* = 6), 6.9 ± 0.4 for Otter 2012 (*n* = 6) and 6.6 ± 0.4 for Arnamul 2012 (*n* = 6), where *n* is the number of observed cycles within a season. Hermaness was also modelled with a restricted time range and only 7 knots given the lack of continuous data across the season. Given the restricted time range there is an estimated mean cyclic period on Hermaness of 6.0 days ± 1.0 (*n* = 2).

Using 25 knots, there is a more variable periodicity in puffin attendance; however the pattern of attendance closely matches the mean daily attendance when using 16 knots (Figure 2.6). For Mingulay there is a mean period (days) ± SD of: 5.5 ± 1.7 for Original 2011 (*n* = 7), 5.4 ± 1.1 for Original 2012 (*n* = 8), 5.3 ± 0.9 for Otter 2012 (*n* = 9) and 6.0 ± 1.9 for Arnamul 2012 (*n* = 7), where *n* is the number of cycles within a season. Hermaness, using 15 knots, had an estimated mean cyclic period of 6.2 days ± 0.5 (*n* = 2). In comparison to the GAM using 16 knots the GAM using 25 knots on Mingulay shows there is shorter periodicity by on average 1.9 days ± 0.3 SD. The periodicity on Hermaness increases by 0.2 days from 7 to 15 knots.

### 2.3.2.1 Synchronicity within Mingulay

In comparing cyclic attendance between the three sites on Mingulay in 2012, there is remarkable synchronicity when using both 16 and 25 knots (Figure 2.7). The peaks and troughs are positively correlated over time suggesting that within an island the attendance pattern of puffins is spatially synchronous across colonies (Figure 2.7). The significance of spatial synchrony was determined using bootstrapped estimates of Pearson's correlation, which showed that all colonies were significantly different from zero and all positively correlated (Mean Pearson's *r*, (± 95 % CI); 16 knots; Arnamul – Original, 0.55 (0.34 – 0.73); Arnamul – Otter, 0.66 (0.36 – 0.73); Original – Otter, 0.96 (0.95 – 0.97); 25 knots, Arnamul – Original, 0.51 (0.38 – 0.64); Arnamul – Otter, 0.56 (0.46 – 0.66); Original – Otter, 0.92 (0.89 – 0.95)). In addition there was a significant, negative correlation over 2011 and 2012 for the colony Original using 16 knots, whilst colonies were not significantly correlated with 25 knots (Mean Pearson's *r*, (± 95 % CI); 16 knots,-0.78 (-0.84 – -0.72 ); 25 knots, -0.23 (-0.66 – 0.12)), which suggests that over seasons synchrony can be different.

Using mean daily counts of puffins instead of GAM-fitted values shows that there is still a degree of synchrony across colonies. Again, spatial synchrony is determined using bootstrapped estimates of Pearson's correlation, which showed that Original and Otter, and Otter and Arnamul, were significantly and positively correlated over time, whilst Original and Arnamul were non-significantly but positively correlated over time on average (Mean Pearson's *r*, (± 95 % CI); Original – Otter, 0.75 (0.55 – 0.90); Otter – Arnamul, 0.38 (0.05 – 0.67); Original – Arnamul, 0.12 (-0.20 – 0.44).

## 2.3.3 Factors influencing attendance

### 2.3.3.1 Weather

When comparing the numbers of puffins attending a colony after the occurrence of above-average temperature there was no significant change in attendance for any colony (Table 2.5). Colonies showed variable responses to increasing temperature with both increases and decreases in attendance. Grouping data across colonies (Mingulay and Hermaness) to increase sample size still showed no effect of temperature on median attendance (Table 2.5).

Colonies all showed a decrease in attendance with increasing wind speed, except for Hermaness which showed an increase in attendance. None of the differences in median attendance were however significant, except for the colony Original 2012 (*P* = 0.039; Table 2.5).

### 2.3.3.2 Tides

Data across the Mingulay colonies were aggregated into two groups: before and during a spring and neap tide. Data across colonies were grouped given the small sample size within a colony (*n* = 3). Comparing across colonies there was a non-significant decrease in the median number of puffins with the effect of a neap tide. There was however a significant decrease in attendance with the effect of a spring tide (*P* = 0.021; Table 2.5).

### 2.3.3.3 Predators

The presence of predators on average reduced puffin attendance by ~ 68 % between consecutive photographs without and with predators, respectively on the Original colony in 2012 (mean numbers of puffins: before predator presence = 1.9 ± 6.07; with predator presence = 0.6 ± 1.24; *n* = 66; Wilcoxon matched-pairs signed-rank test with iterations: *V* = 742.6 ± 61.3, *P* = 0.031 ± 0.036).

**Table 2.1.** Summary statistics of the photographs and number of puffins in photographs for each colony.

| | Shetland | | | Mingulay | | | |
|---|---|---|---|---|---|---|---|
| | Fair Isle | | Hermaness | Original | | Otter | Arnamul |
| | 2011 | 2012 | 2012 | 2011 | 2012 | 2012 | 2012 |
| Coordinates | 59°32’ N,<br>01°36’ W | | 60°49’ N,<br>00°53 W | | 56°48’ N,<br>07°37’ W | | 56°48’ N,<br>07°39’ W |
| Start date | 01/07 | 14/05 | 14/06 | 29/05 | 22/05 | 23/05 | 25/05 |
| End date | 30/08 | 01/06 | 02/08 | 16/07 | 12/07 | 12/07 | 12/07 |
| Study duration | 60 | 17 | 50 | 48 | 51 | 51 | 48 |
| Total number of days missing | 28 | 1 | 16 | 3 | 1 | 0 | 0 |
| % Days Missing | 47 | 6 | 0.32 | 6 | 4 | 0 | 0 |
| Total number of useful photos | 895 | 380 | 986 | 3531 | 5007 | 1352 | 1188 |
| Percentage useful | 100 | 95.2 | 100 | 100 | 100 | 97.6 | 97.1 |
| Image Quality (Megapixels) | 15.1 | 15.1 | 18.0 | 15.1 | 18.0 | 15.1 | 18.0 |
| Interval (min) | 30 | 20 | 20 | 20 | 10 | 10 | 10 |
| Interval used (min) | 30 | 40 | 40 | 20 | 10 | 40 | 40 |
| Minimum number of puffins per photo | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1st Quartile of the number of puffins | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| Median number of puffins per photo | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| Mean number of puffins per photo | 1.75 | 0.46 | 7.07 | 7.9 | 4.37 | 2.42 | 16.85 |
| Standard error of number of puffins | 0.29 | 0.12 | 0.59 | 0.27 | 0.18 | 0.21 | 0.55 |
| 3rd Quartile of the number of puffins | 0 | 0 | 3 | 5 | 1 | 1 | 25 |
| Maximum number of puffins per photo | 80 | 26 | 159 | 93 | 109 | 64 | 125 |
| Total puffin count | 1565 | 173 | 6975 | 27787 | 21876 | 3266 | 20020 |
| Total number of photos | 895 | 399 | 986 | 3531 | 5007 | 1385 | 1224 |
| Total number of photos with puffins | 104 | 26 | 471 | 1612 | 1876 | 495 | 1107 |
| Percentage of photos with puffins | 11.6 | 6.8 | 47.8 | 45.7 | 37.5 | 36.6 | 93.2 |

**Table 2.2.** Model coefficients for the analysis of the effect of breeding stage, daily period and colony on attendance of Atlantic puffins.

| Parameter | Estimate | SE | df | *t* | *P* |
|---|---|---|---|---|---|
| Intercept | 8.18 | (2.47) | 607.50 | 3.08 | 0.001 |
| Hatching | 9.61 | (3.12) | 626.90 | 3.88 | 0.002 |
| Period2 | 10.29 | (2.65) | 698.80 | 2.04 | 0.000 |
| Period3 | 5.37 | (2.63) | 702.70 | 3.12 | 0.042 |
| Period4 | 8.20 | (2.63) | 702.70 | 3.57 | 0.002 |
| Period5 | 9.39 | (2.63) | 702.70 | -1.82 | 0.000 |
| Original2011 | -7.02 | (3.85) | 849.90 | -2.02 | 0.068 |
| Original2012 | -6.53 | (3.24) | 583.60 | -2.29 | 0.044 |
| Otter2012 | -7.22 | (3.16) | 554.60 | -3.14 | 0.023 |
| Post-hatch:Period2 | -10.57 | (3.36) | 698.90 | -3.27 | 0.002 |
| Post-hatch:Period3 | -10.93 | (3.34) | 702.30 | -3.20 | 0.001 |
| Post-hatch:Period4 | -10.69 | (3.34) | 707.90 | -0.20 | 0.001 |
| Post-hatch:Period5 | -0.66 | (3.37) | 707.50 | -2.48 | 0.846 |
| Post-hatch: Original2011 | -10.87 | (4.39) | 878.30 | -2.50 | 0.013 |
| Post-hatch: Original2011 | -10.19 | (4.08) | 572.00 | -2.37 | 0.013 |
| Post-hatch: Otter2012 | -9.64 | (4.06) | 564.70 | -2.18 | 0.018 |
| Pre-hatch: Period2: Original2011 | -10.12 | (4.64) | 702.90 | 0.28 | 0.029 |
| Post-hatch: Period2: Original2011 | 0.74 | (2.66) | 696.70 | -0.44 | 0.780 |
| Pre-hatch: Period3: Original2011 | -2.04 | (4.61) | 695.90 | 3.01 | 0.659 |
| Post-hatch: Period3: Original2011 | 7.96 | (2.65) | 700.40 | -0.48 | 0.003 |
| Pre-hatch: Period4: Original2011 | -2.14 | (4.46) | 717.40 | 3.75 | 0.631 |
| Post-hatch: Period4: Original2011 | 9.90 | (2.64) | 709.90 | 0.77 | 0.000 |
| Pre-hatch: Period5: Original2011 | 3.45 | (4.50) | 713.40 | 4.45 | 0.444 |
| Post-hatch: Period5: Original2011 | 11.97 | (2.69) | 709.80 | -2.79 | 0.000 |
| Pre-hatch: Period2: Original2012 | -10.31 | (3.70) | 694.20 | -0.17 | 0.005 |
| Post-hatch: Period2: Original2012 | -0.47 | (2.82) | 696.50 | -0.84 | 0.868 |
| Pre-hatch: Period3: Original2012 | -3.10 | (3.70) | 702.50 | 1.90 | 0.402 |
| Post-hatch: Period3: Original2012 | 5.32 | (2.81) | 699.50 | -1.00 | 0.058 |
| Pre-hatch: Period4: Original2012 | -3.76 | (3.75) | 711.90 | 2.25 | 0.317 |
| Post-hatch: Period4: Original2012 | 6.35 | (2.82) | 708.30 | -1.34 | 0.025 |
| Pre-hatch: Period5: Original2012 | -4.97 | (3.70) | 732.30 | 2.58 | 0.179 |
| Post-hatch: Period5: Original2012 | 7.40 | (2.87) | 709.10 | -2.95 | 0.010 |
| Pre-hatch: Period2: Otter2012 | -10.56 | (3.58) | 695.60 | -0.08 | 0.003 |
| Post-hatch: Period2: Otter2012 | -0.23 | (2.91) | 698.90 | -1.16 | 0.937 |
| Pre-hatch: Period3: Otter2012 | -4.12 | (3.56) | 697.70 | 1.68 | 0.248 |
| Post-hatch: Period3: Otter2012 | 4.84 | (2.88) | 702.80 | -1.45 | 0.093 |
| Pre-hatch: Period4: Otter2012 | -5.15 | (3.56) | 697.70 | 1.24 | 0.149 |
| Post-hatch: Period4: Otter2012 | 3.56 | (2.87) | 712.70 | -2.02 | 0.216 |
| Pre-hatch: Period5: Otter2012 | -7.19 | (3.55) | 702.80 | -0.59 | 0.043 |
| Post-hatch: Period5: Otter2012 | -1.72 | (2.91) | 711.90 | 3.08 | 0.554 |

**Table 2.3.** Model coefficients for the analysis of the effect of daily period and colony on attendance of Atlantic puffins during the pre-hatching stage.

| Parameter | Estimate | SE | df | *t* | *P* |
|---|---|---|---|---|---|
| Intercept | 11.06 | 2.16 | 70.73 | 5.11 | 0.000 |
| Period2 | 2.70 | 1.47 | 221.54 | 1.83 | 0.068 |
| Period3 | 2.77 | 1.47 | 223.07 | 1.88 | 0.062 |
| Period4 | 5.07 | 1.47 | 226.87 | 3.44 | 0.001 |
| Period5 | 6.11 | 1.46 | 231.84 | 4.17 | 0.000 |
| Original2011 | -9.93 | 2.61 | 44.48 | -3.80 | 0.000 |
| Original2012 | -10.94 | 2.20 | 42.21 | -4.98 | 0.000 |
| Otter2012 | -12.73 | 2.15 | 38.19 | -5.92 | 0.000 |

**Table 2.4.** Model coefficients for the analysis of the effect of daily period and colony on attendance of Atlantic puffins during the post-hatching stage.

| Parameter | Estimate | SE | df | *t* | *P* |
|---|---|---|---|---|---|
| Intercept | 17.95 | 1.83 | 463.30 | 9.82 | 0.001 |
| Period2 | -0.31 | 2.02 | 485.00 | -0.15 | 0.878 |
| Period3 | -5.62 | 2.01 | 486.70 | -2.80 | 0.005 |
| Period4 | -2.57 | 2.01 | 496.40 | -1.28 | 0.201 |
| Period5 | 8.63 | 2.06 | 495.70 | 4.19 | 0.000 |
| Original2011 | -17.78 | 2.26 | 442.20 | -7.87 | 0.000 |
| Original2012 | -16.77 | 2.38 | 407.70 | -7.04 | 0.000 |
| Otter2012 | -16.90 | 2.46 | 424.70 | -6.88 | 0.000 |
| Period2: Original2011 | 0.77 | 2.60 | 483.30 | 0.30 | 0.767 |
| Period3: Original2011 | 7.97 | 2.59 | 486.20 | 3.08 | 0.002 |
| Period4: Original2011 | 9.90 | 2.58 | 492.80 | 3.84 | 0.000 |
| Period5: Original2011 | 11.98 | 2.63 | 492.90 | 4.56 | 0.000 |
| Period2: Original2012 | -0.44 | 2.76 | 483.10 | -0.16 | 0.873 |
| Period3: Original2012 | 5.36 | 2.74 | 485.10 | 1.96 | 0.051 |
| Period4: Original2012 | 6.41 | 2.75 | 490.90 | 2.33 | 0.020 |
| Period5: Original2012 | 7.48 | 2.80 | 491.60 | 2.67 | 0.008 |
| Period2: Otter2012 | -0.20 | 2.84 | 484.70 | -0.07 | 0.943 |
| Period3: Otter2012 | 4.88 | 2.81 | 487.40 | 1.74 | 0.083 |
| Period4: Otter2012 | 3.62 | 2.80 | 493.70 | 1.29 | 0.197 |
| Period5: Otter2012 | -1.65 | 2.84 | 493.40 | -0.58 | 0.562 |

**Table 2.5.** The change in attendance in response to environmental variables, before and during an above-average event.

| | Median attendance (range) | | Median difference | Wilcoxon matched-pairs signed-rank test | | |
|---|---|---|---|---|---|---|
| | Before | During | | *n* | *V* | *P* |
| **Temperature** | | | | | | |
| Original 2011 | 8.76<br>(7.4 – 16.08) | 11.31<br>(7.35 – 18.61) | 2.55 | 5 | 6 | 0.813 |
| Original 2012 | 5.10<br>(0.07 – 16.60) | 3.80<br>(0.27 – 9.32) | -1.30 | 8 | 22 | 0.641 |
| Otter 2012 | 4.31<br>(0.10 – 9.67) | 1.58<br>(0.38 – 5.28) | -2.73 | 7 | 19 | 0.469 |
| Arnamul 2012 | 17.79<br>(6.52 – 39.83) | 22.69<br>(1.75 – 39.79) | 4.90 | 6 | 12 | 0.844 |
| Hermaness 2012 | 7.62<br>(3.6 – 16.69) | 8.08<br>(0.00 – 10.26) | 0.46 | 3 | 5 | 0.500 |
| Across colonies | 7.52<br>(0.08 – 39.83) | 5.27<br>(0.00 – 9.79) | -2.25 | 29 | 262 | 0.347 |
| **Wind speed** | | | | | | |
| Original 2011 | 9.49<br>(1.62 – 20.20) | 5.31<br>(0.51 – 9.69) | -4.18 | 6 | 6 | 0.438 |
| Original 2012 | 9.49<br>(0.70 – 16.6) | 5.77<br>(0.14 – 9.32) | -3.72 | 8 | 33 | 0.039 |
| Otter 2012 | 2.78<br>(0.50 – 9.67) | 1.10<br>(0.04 – 7.52) | -1.68 | 10 | 41 | 0.193 |
| Arnamul 2012 | 16.05<br>(4.76 – 37.79) | 11.94<br>(1.64 – 34.93) | -4.11 | 10 | 39 | 0.275 |
| Hermaness 2012 | 7.81 (3.60 – 25.40) | 16.69<br>(0.00 – 23.47) | 8.88 | 7 | 10 | 0.578 |
| Across colonies | 7.62<br>(0.50 – 39.79) | 5.12<br>(0.00 – 34.93) | -2.50 | 41 | 488 | 0.464 |
| **Tides** | | | | | | |
| Spring | 10.42<br>(0.38 – 31.83) | 2.23<br>(0.07 – 15.64) | 8.19 | 12 | 68 | 0.021 |
| Neap | 3.45<br>(1.41 – 25.55) | 2.05<br>(0.05 – 39.83) | 1.45 | 14 | 70 | 0.296 |

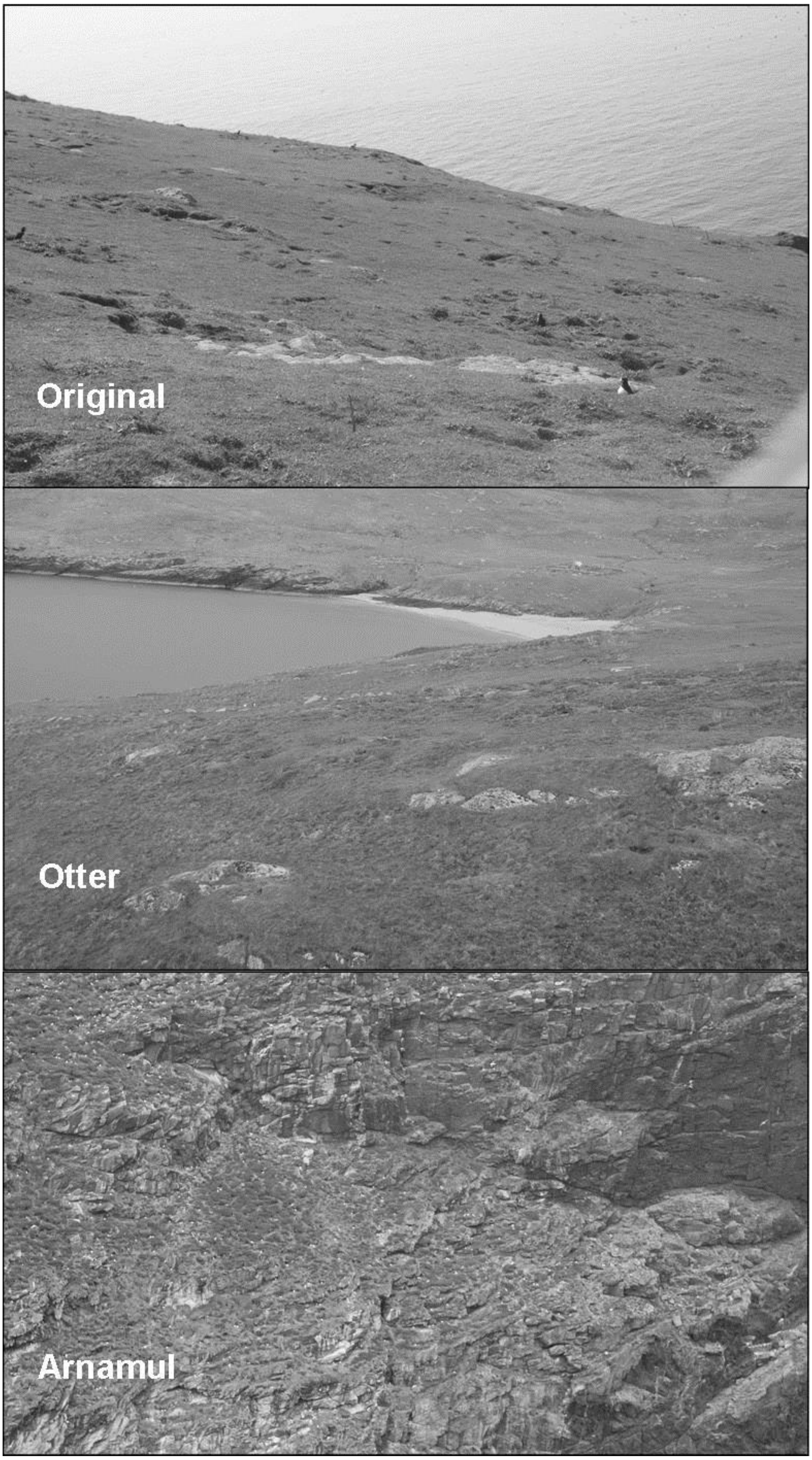

**Figure 2.2.** Photographs of each colony.

**Figure 2.2 continued.** Photographs of each colony

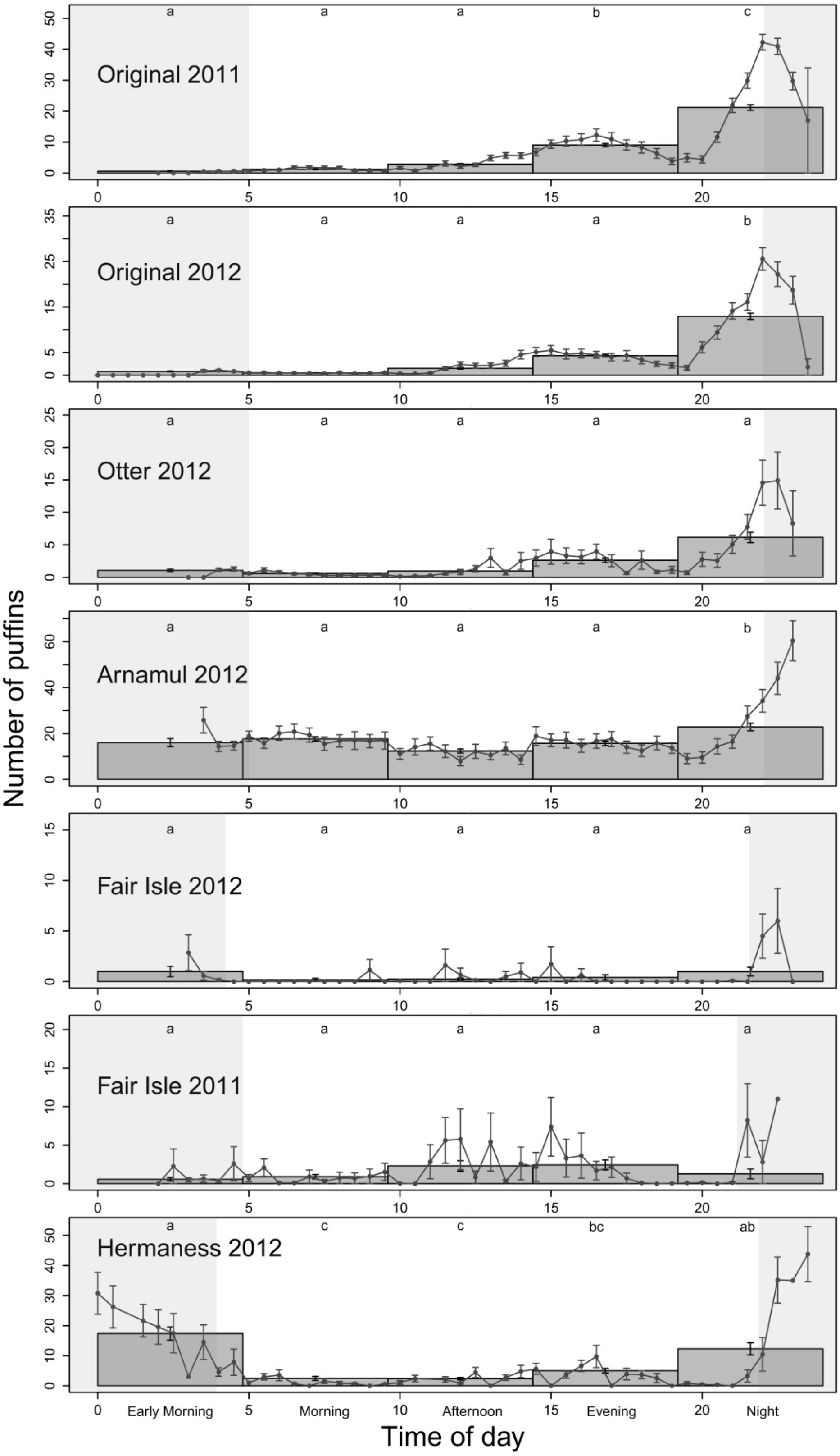

**Figure 2.3.** The change in attendance of Atlantic Puffins throughout the day with data across the study duration averaged into half-hourly intervals (line) and into five daily ~5-hour periods (bars). Values represent the mean (± SE). Shaded areas represent the average extent of night over the study period for each site. Letters at the top of each panel denote differences from the Tukey *post-hoc* comparison; groups with different letters were significantly different from each other.

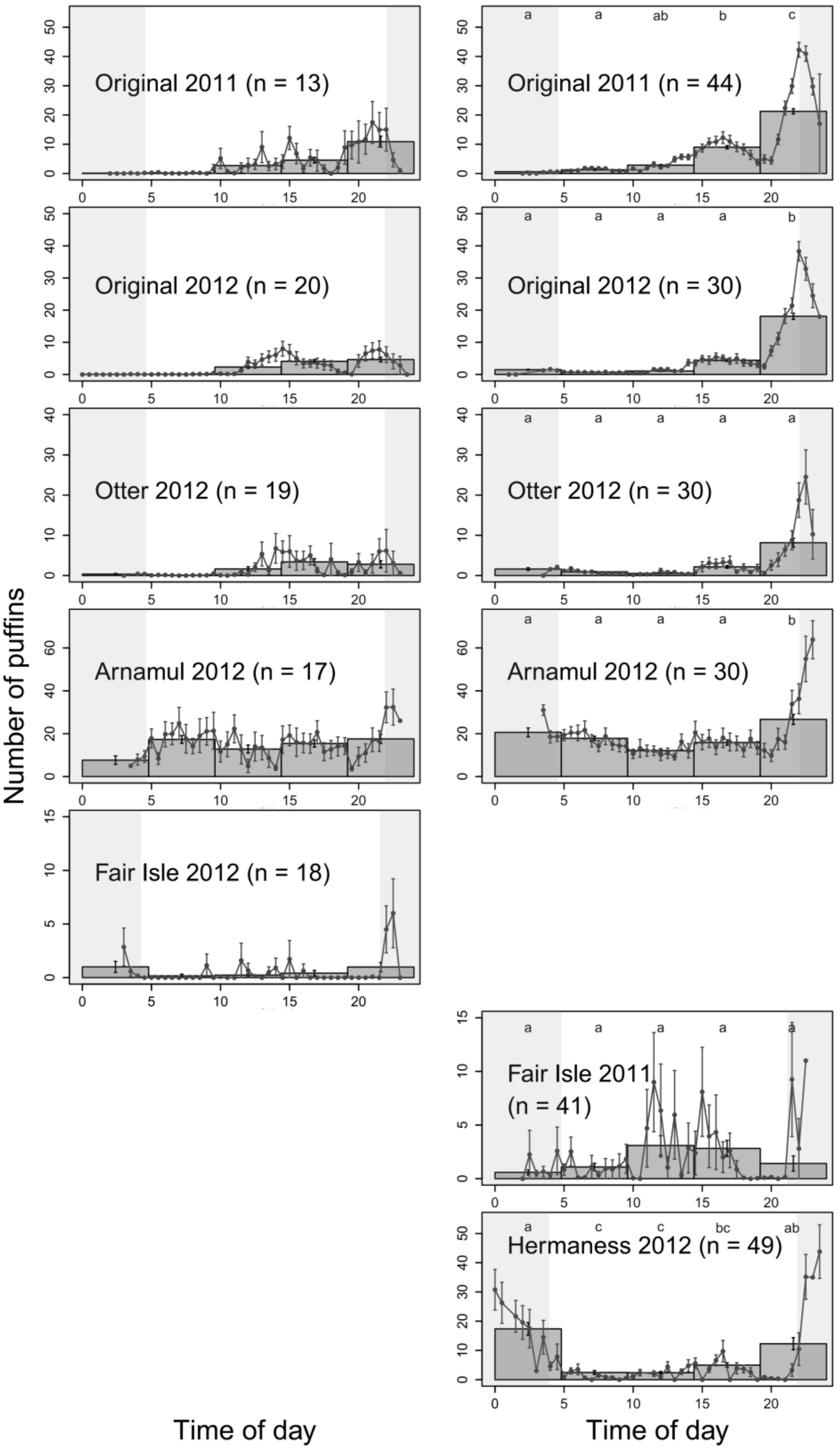

**Figure 2.4.** The half-hourly (line) and ~5-hourly periods of daily attendance (bars) of Atlantic Puffins across the pre-hatch (left) and post-hatch (right) periods. Values represent the mean (± SE). Shaded areas represent the average extent of night over the study period for each site, defined by the average time of sunrise and sunset across the study period. *n* = number of days within period. Letters denote Tukey groups. Tukey groups with different letters are significantly different from each other.

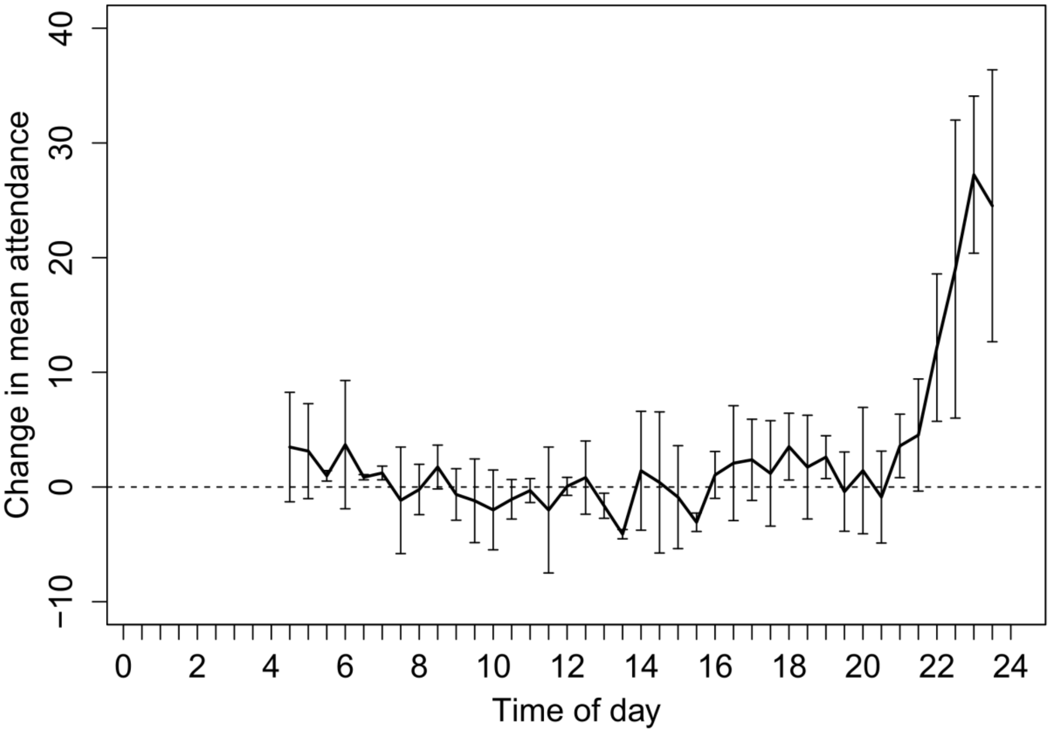

**Figure 2.5.** The mean change (± SD) in the half-hourly mean numbers of Atlantic puffins from the pre- and post-hatching stages over colonies on Mingulay in 2011 and 2012. The dotted horizontal line represents the point where there is no average change in attendance across hatching stage. Positive values on the vertical axis refer to higher attendance post-hatching as compared to pre-hatching stage.

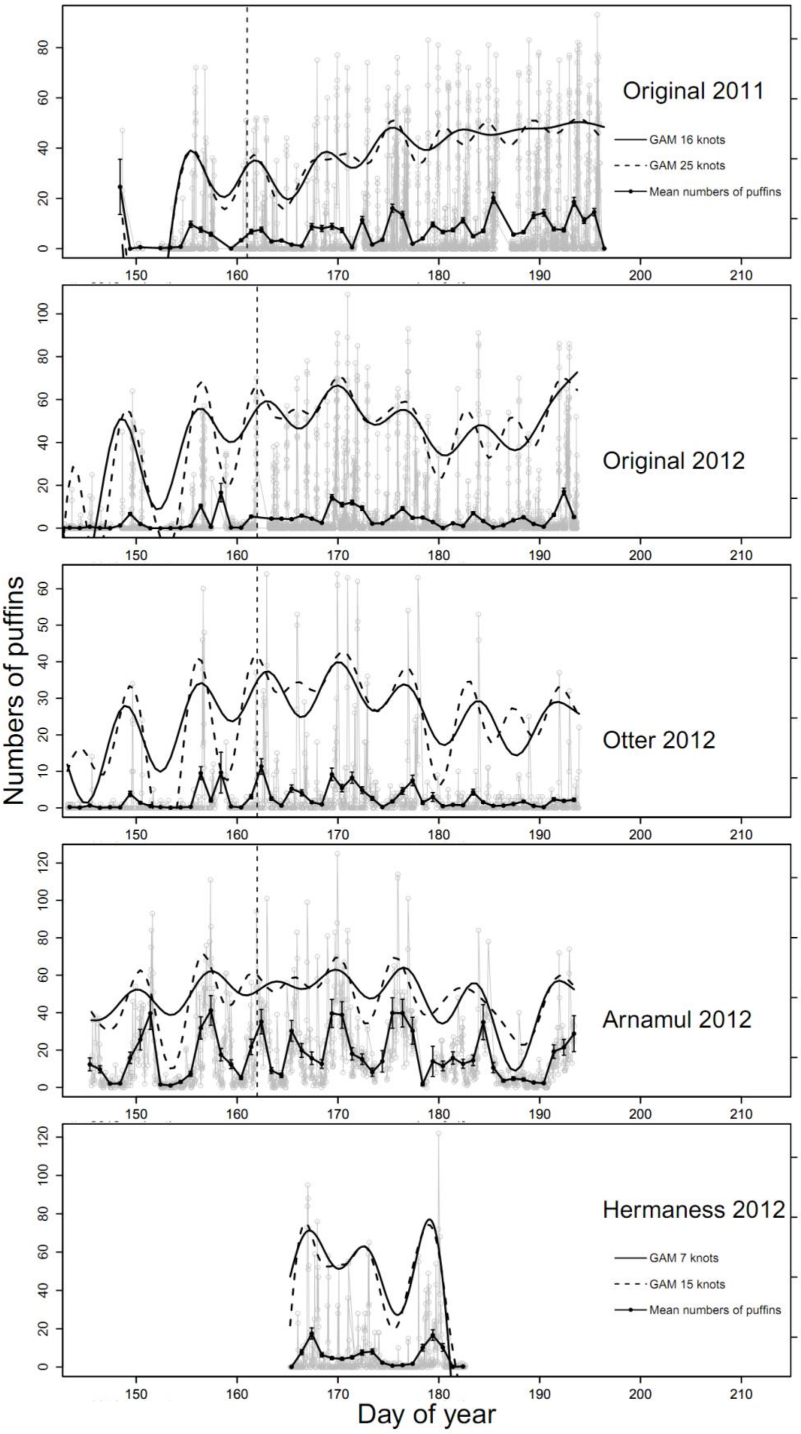

**Figure 2.6.** The seasonal change in attendance of Atlantic puffins across colonies. The raw counts of puffins are in light grey and the mean daily number of puffin (± SE) is the thick, lower, black line. The GAM-fitted values (second y-axis) of seasonal attendance using different knots from aggregated counts of puffins are overlaid with the thinner, upper black line and the dashed line. The time series of Hermaness is cropped until day 183 given 10 days of missing data after this period. Day 150 = 31st May in 2011 and 30th May in 2012. Some values of GAM-fitted lines are cropped out of the plot for clarity in viewing. The vertical, dashed line at day 161 in 2011 and day 162 in 2012 represents the approximate day of hatching (11th June).

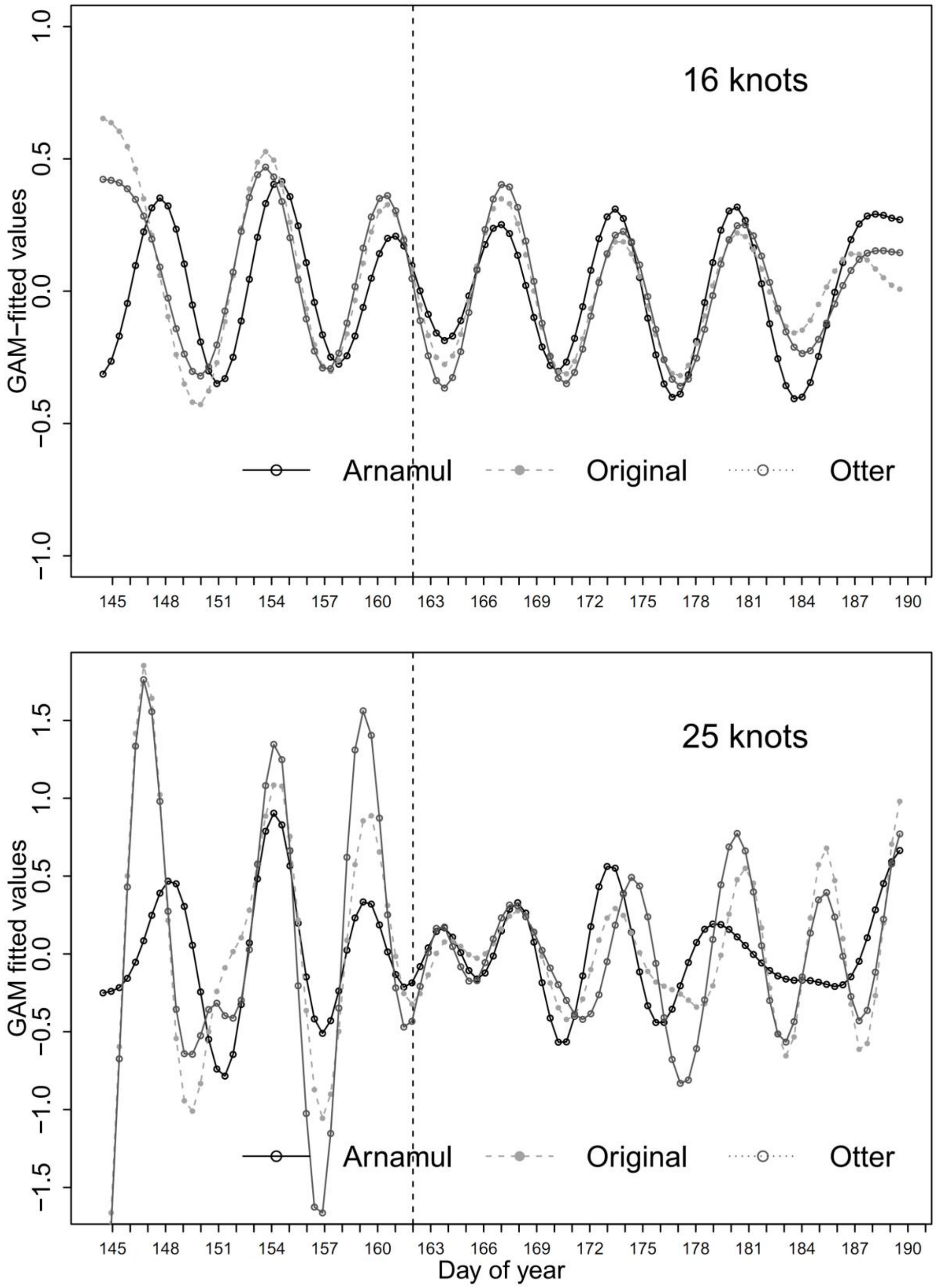

**Figure 2.7.** The scaled, de-trended attendance pattern of Atlantic puffins over three colonies on Mingulay in 2012. Values are derived from GAM-fitted values using (top panel) 16 knots and (bottom panel) 25 knots. The x-axis scale, vertical, dashed line, and number of knots are as Figure 5.

## 2.4 **Discussion**

This study shows a clear pattern of daily attendance, which for all colonies is often lowest in the morning with a small rise in attendance around mid-afternoon, before a pronounced peak in attendance at sunset. This pattern of attendance is documented for other puffin colonies; although, none use time-lapse photography to record this daily change (Cairns 1979, Myrberget 1979, Calvert and Robertson 2002a, Blet-Charaudeau *et al.* 2010, Harris and Wanless 2011). The general increase in attendance throughout the day is likely to represent a balance between the effort spent foraging (Gaston and Nettleship 1982, Harding *et al.* 2007, Huffeldt and Merkel 2013), day-length (Myrberget 1979, Harris and Wanless 2011) and incubation shifts (Wernham 1993). Puffins will typically raft at sea if not incubating or guarding a chick and will forage at first light (Blet-Charaudeau *et al.* 2010), returning to the colony to switch incubation shifts (predominantly at first light or in the late evening) or provision young (Wernham 1993, Harris and Wanless 2011). As the day progresses attendance will increase until nightfall when puffins again depart to sea or enter burrows (Harris and Wanless 2011). The increased attendance of puffins at night for Hermaness is likely to be associated with the relatively high light levels during the night, compared to lower latitude colonies. Increased attendance at later times of day for higher latitude colonies is a relationship detected in other studies (Myrberget 1979, Harris and Wanless 2011). There may also be the suggestion that increased attendance at times of lower light levels around dusk (which are later with increasing latitude) is also a response to limit predation, as observed in Jones *et al.* (1990) for ancient murrelets *Synthliboramphus antiquus.* Given that fish often rise to the surface in the evening the increased attendance later in the day may also be a response to impaired foraging with decreasing light levels (Blet-Charaudeau *et al.* 2010).

The stage of breeding is shown in this study to also influence attendance. Broadly, the same pattern of daily attendance exists across both stages; however the magnitude of attendance varies. During the post-hatch stage there are significantly more puffins attending the colony. This increase in attendance may be explained by the considerable influx of prospecting sub-adult and non-breeding puffins, which predominantly return to the colony from early June onwards (Harris and Wanless 2011). Furthermore, after incubation finishes the need for parents to remain underground is reduced and the visible proportion of birds at the colony may increase.

For the period termed ‘Night’ daily attendance increased in the post-hatching stage but the difference was significant only for the Original colony in 2012. This increase may be explained by a combination of: an increasing population size with the arrival of non-breeders during the post-hatching stage, variation in attendance of breeding birds across hatching stage, and also changes in day length across the season, which as discussed above, may influence attendance. The significance reported for the colony Original 2012 may be due to the presence of a loafing spot in the middle of the field of view, which often had a disproportionate number of puffins on it in relation to the local number of breeding pairs (pers. obs.). Patterns of observable attendance may therefore be influenced by locations of increased and disproportionate attendance within the camera’s field of view. Equally, variation in the number of days cameras were operational across the pre-hatch and post-hatch stage may influence the significance of results by a variable sample size. Furthermore, Original 2012 had a photographic interval of 10 min, which was shorter than the other colonies which were on 20 or 40 min. Variation in interval may alter the observed numbers of birds in attendance, although as this study dealt with the mean numbers of puffins per daily period the change due to interval is likely to be minimal.

During the pre-hatching stage on Mingulay the extent of attendance varied with each colony. The pattern of increasing attendance throughout the day was constant across colonies suggesting similar factors driving attendance, although differences in magnitude may be explained by colony size, with larger colonies having greater attendance. The population of Arnamul was not quantified exactly; however repeated manual observations of burrow use over *c.* 7 hours suggested this colony had *c.* 100 pairs. From the studied colonies on Mingulay this would make Arnamul the largest, which may explain the lower attendance observed at all other colonies.

During the post-hatching stage daily attendance varied differently between colonies on Mingulay. All colonies showed a significant increase towards the end of the day, except for Otter. The colonies of Otter and also Fair Isle both had increasing attendance towards the end of the day, and with Fair Isle also having peaks in attendance in the morning and mid-afternoon. Statistically however there was no change in attendance across the day. This is perhaps explained by both these colonies being relatively small and also that the five daily periods may be too coarse to capture the relatively smaller change in daily attendance.

This study also showed that in addition to the daily cycle there was evidence of a cyclic pattern in attendance over the season. Other studies have shown how cyclicity and its periodicity can vary between colonies (Nettleship 1972, Myrberget 1979, Calvert and Robertson 2002a). For Mingulay periodicity varied from on average 5 to 7 days, with variation arising from the choice of the GAM used. It is therefore important to consider the degree of smoothing within models defining periodicity. Harris and Wanless (2011) suggest that the periodicity observed is possibly an innate cycle altered by local conditions. Consequently, the pattern of attendance observed from GAMs may represent some balance between underlying periodicity and local modification, *e.g.* from weather. Therefore, both GAMs on Mingulay may well be appropriate; however, they may be defining different periodicity as a consequence of their degree of incorporation of the influence of local conditions.

Equally, for Hermaness, there is an estimated periodicity of 6 days, which differed by 0.2 days with the choice of GAM. The little variation between GAMs on Hermaness may be due to the much shorter time series compared to Mingulay, or perhaps attendance varies less over the season in response to local conditions at larger colonies.

The daily mean counts of puffins, which are not subject to smoothing, also exhibited irregular cyclicity over the season. This apparent cyclicity from mean daily counts lends support to the observation that the cyclicity observed from GAMs is not entirely an artefact of smoothing.

Remarkably, the three colonies on Mingulay in 2012 were all significantly correlated with each other over time. This spatial synchrony is detected using a variety of GAMs and also the mean daily counts, although the correlation between Original and Arnamul became non-significant with mean counts. The spatial synchrony across the island suggests that there is a common factor driving cyclicity over Mingulay. Other puffin colonies have also had similar cyclicity detected (Corkhill 1971, Lloyd 1972, Nettleship 1972, Calvert and Robertson 2002a) and other species of auk can also exhibit inter-species cyclicity (Lloyd 1972). Various factors have been suggested for driving cyclicity of puffins from weather patterns (Myrberget 1959), foraging cycles (Lockley 1953) and the social benefit of synchronous attendance in predator avoidance (Corkhill 1971). There is also the possibility that, as discussed  before, cyclicity is governed by an internal physiological cycle, which causes regular periodicity (Corkhill 1971, Harris and Wanless 2011).

The most pronounced period of cyclicity is often observed early in the season before egg laying (Lloyd 1972, Harris and Wanless 2011), where synchronicity is most marked, perhaps related to a reluctance to come ashore (Corkhill 1971). However, this study is limited by the fact that observations start from around mid-late incubation to late chick-rearing on Mingulay. Commenting on the seasonal trend in attendance using GAMs is therefore limited to this period and just Mingulay, as the time series for Hermaness is not long enough to discuss seasonal change. In 2011, attendance showed a gradual increase across the season, whilst in 2012 attendance for all three colonies on Mingulay appeared to decrease from hatching onwards. The expected trend is for increasing attendance over time as the numbers of non-breeding individuals build-up. This increase progresses until around fledging when attendance decreases towards the end of the breeding season (Harris and Wanless 2011). Equally, productivity has also been shown to influence attendance of Atlantic puffins with breeding failure resulting in decreased attendance (Anker-Nilssen 2010). It is therefore possible that the difference observed across 2011 and 2012 for the Original colony is a result of poorer productivity in 2012, compared to 2011. Equally, attendance may be related to varying proportions of non-breeders, which can make up to 50 % of the observed attendance (Harris and Wanless 2011). A combination of the two preceding factors may however be most plausible. The related trend in attendance across the colonies in 2012 suggests also that there was both similar attendance of non-breeding individuals and that productivity may have been similar.

Across the season there is varying amplitude in cyclic attendance. Typically, there appears to be decreasing amplitude after hatching. However, the considerable variation between GAMs using different numbers of knots (Appendix I A and B) results in quantitative interpretation being more difficult. It is likely that the variation in amplitude observed in attendance is a result of local conditions, *e.g.* weather or predator presence, or varying synchrony with the arrival of non-breeding individuals.

The choice of hatching date for this study, for colonies other than Original in 2011 and 2012, is an assumption. However, even with the variation in hatching dates the choice of the 11th June to be applied to other colonies is not unreasonable. A study by Harris and Rothery (1985) showed that the mean hatch date from 1973 to 1979 varied from the 31st May to the 13th June on the Isle of May. However, hatch date may increase with latitude. The mean hatch date for Røst, Norway (67.5 ˚N) was the 20th June (Anker-Nilssen 2010), whilst Skomer, Wales (51.2 ˚N) was the 25th May (Mavor *et al.* 2006). Therefore, given the lower latitude of Fair Isle and Hermaness (~60 ˚N), relative to Norway, the hatch date may well be earlier than the 20th June. Equally, the time series for Hermaness does not start until the 14th June, which limits the data potentially within the incubation period. The data from Fair Isle equally started on the 1st July in 2011 and ended on the 1st June 2012, which limits their time series to the appropriate breeding stage.

The general cyclicity of puffins across the season is, as suggested above, to be possibly controlled, in part, by local conditions. Many studies have shown how atmospheric conditions influence attendance, however the results can be conflicting (Calvert and Robertson 2002a, Blet-Charaudeau *et al.* 2010). The results of this study show that there was no effect of temperature on mean daily attendance. Whilst other studies have also shown no effect of temperature (Calvert and Robertson 2002a) other studies have shown an effect (Blet-Charaudeau *et al.* 2010). It is possible that the range of temperature across the colonies (mean range within a colony 9 ± 1.4 ˚C) did not provide enough variation for an effect to be visible. Similarly, a combination of factors may be required in concert with temperature, *e.g.* cloud cover, to affect attendance. Blet-Charaudea *et al.* (2010) suggest that an increased temperature reduces attendance by increasing the need for puffins to stay at sea to regulate body temperature.

The Original 2012 colony showed a significant decrease in attendance with wind speeds above 18.5 km $h^{-1}$. For this colony the results agreed with prior studies that increasing wind speed reduced attendance by perhaps making flight more difficult at low wind speeds (Calvert and Robertson 2002a, Blet-Charaudeau *et al.* 2010). Whilst this one colony suggested a decrease in attendance with increasing wind speed, the other colonies showed no significant effect. This contrasting result may be explained by local variation in topography, with Arnamul being relatively sheltered from the west, on the landward side of a sea stack. Given that Otter is part of the same colony as Original, it is unlikely that local variation in wind can explain this observation. Implicit in this study is the assumption that the observable presence of puffins from photography is in response to environmental conditions. There may be variation in colony attendance, which occurs outside the field of view of the camera. Therefore, spatial variation in where puffins stand may obscure any observable effect on attendance from weather. Given that Otter is on the edge of the colony, compared to the Original colony, puffins may well loaf on the colony differently under different conditions.

For tidal data, there was a significant decrease in attendance during a spring tide, although there was also a (non-significant) decrease in attendance with a neap tide. The significant decrease in attendance with a spring tide is unexpected, given that concentrated seabird prey during a spring tide is likely to reduce time spent foraging and lead to increased attendance (Gaston and Nettleship 1982, Irons 1998). There is the possibility, although it is unknown, that local hydrodynamics within the waters surrounding Mingulay do not improve foraging conditions at spring tides, although this goes against other recent studies (Piatt *et al.* 1990, Irons 1998). The decreased attendance at neap tides is expected given dispersal of fish at lower current velocities (Irons 1998). Given that puffins have attendance with a periodicity ~ 7 days it is therefore expected that there will be to some extent a relationship with tide, which occurs on a ~ 14 day cycle for spring and neap tides. This therefore limits the reliability of these results and increases the chance they have arisen not as an effect of tide but as a consequence of periodicity. Disentangling whether periodicity in attendance is because of tidal cycles or modified by tides is unknown.

Overall, for all environmental variables studied (weather and tides) the resolution of the data on a daily scale may mask any of the influences observed at finer resolution. Furthermore, it is possible that the range of temperature and wind speed (mean range within a colony 26 ± 3.9 km $h^{-1}$) across the colonies does not provide enough variation for an effect to be visible overall. Similarly, a combination of factors may be required in concert with temperature or wind speed to affect attendance. For environmental variables, it is also possible their influence may have a delayed effect on attendance (Jones *et al.* 1990, Calvert and Robertson 2002a). For all atmospheric variables the distance with which data were recorded from the colonies on Mingulay (63 km) limits the accuracy and precision of these results. Overall, this study showed no clear effect of environmental variables on puffin attendance and interpretation is with caution.

There was also a significant reduction in attendance following the presence of a predator. Mass departure and flight of puffins when a predator is observed is a common observation (Nettleship 1972, Harris 1980). Flight of puffins and subsequent aerial wheeling may help reduce the risk of predation or kleptoparasitism (Harris 1980, Blackburn *et al.* 2009). A limitation to this study is that predator presence was determined from photographs and therefore excludes any effect of predators outside the field of view, which may influence attendance. However, if predators do cause puffins to fly off the colony, then the unobservable presence of a predator may either cause attendance to be reduced or be zero, prior to the predator becoming visible within the camera's field of view. In this scenario, the results of this study are thus likely to be conservative. There may also be different responses between predator species and also over time (Corkhill 1971), which this study does not consider.

In general, these results show that attendance of Atlantic puffins varies over different temporal scales, as recorded in prior studies. This study addresses the issue of monitoring attendance through the use of time-lapse photography, which allows for considerably high temporal resolution to be obtained. Given that a common method of monitoring Atlantic puffins requires counts of individuals, understanding those factors governing attendance is of considerable importance. Puffins were shown to not be significantly influenced by temperature or wind speed overall. However, one colony showed a significant decrease in attendance with increasing wind speed. There was a significant decline in attendance with spring tides and a non-significant decline in attendance with neap tides. Caution should be exercised from the methodology used in examining the effects of environmental variables and tides on attendance. The presence of predators resulted in a significant decrease in attendance. Knowing how Atlantic puffin attendance varies over time can be used to refine periods of when monitoring should occur. Calvert and Robertson (2002a) conclude in their study that numbers of Atlantic puffins, as an index of population size, would require many counts to be undertaken to make this approach justifiable. Time-lapse photography overcomes this issue by providing the possibility of repeat counts to derive a more reliable index of population size, although there are many factors to consider such as sampling intensity, study duration and the consideration that photography may only focus upon a limited extent of a puffin population.

In conclusion, this study shows that attendance of puffins varies markedly over both daily and seasonal scales, in agreement with prior studies (Cairns 1979, Harris and Wanless 2011). Patterns of attendance can equally be detected from using time-lapse photography, which also shows variation in attendance between colonies over time. This study failed to show any clear link between attendance and environmental variables. The use of time-lapse photography has the potential to reflect ecological connections between the marine environment and the colony (Gaston and Nettleship 1982, Anker-Nilssen 2010, Huffeldt and Merkel 2013). Furthermore, attendance has also the potential to suggest colony productivity (Anker-Nilssen 2010), although more work is needed to define relatively small changes in productivity. However, the main benefit of time-lapse photography is the ability to collect high resolution data with a reduction in time compared to manual approaches, which can provide detailed insight into variation in attendance within and between colonies.

# Chapter 3

# Monitoring Atlantic puffins *Fratercula arctica* using time-lapse photography

# Abstract

Monitoring of Atlantic puffins *Fratercula arctica* is currently undertaken using a variety of methods. The best method, where access is possible, is to count the numbers of apparently occupied burrows. When areas cannot be accessed then counts of individuals is an alternative approach. However, counts of puffins are notoriously erratic over time and this can potentially limit the reliability of inferences made on the size of the population. This study proposes the use of time-lapse photography to take high temporal resolution data to capture reliable estimates of population size. The results of this study, although of limited sample size, show that there is a significant and positive relationship between the maximum numbers of puffins observed and the numbers of apparently occupied burrows. The study stresses that in using time-lapse photography there must be a standardised sampling intensity to ensure comparability between estimates of population size between colonies and over time. The study also proposes a novel avenue of estimating puffin population size by relating the spatial position of puffins to burrows, although more work is needed. Overall and in contrast to prior studies, the use of colony attendance as an estimate of population size has limited potential, although further study is required to refine the error associated with population estimates.

## 3.1 **Introduction**

Monitoring burrow-nesting seabirds is currently undertaken using a variety of methods (Harris and Murray 1981, Gaston *et al.* 1988, Anker-Nilssen and Røstad 1993, Walsh *et al.* 1995, Schumann *et al.* 2013). Often, where access is possible, the best method for population monitoring is counting the number of burrows deemed occupied (Nettleship 1976, Harris and Murray 1981, Walsh *et al.* 1995). However, when access is restricted then counts of burrows becomes unsuitable and other methods must be adopted, such as counts of individuals (Walsh *et al.* 1995, Bertram *et al.* 1999, Calvert and Robertson 2002b).

For diurnal species, counting the numbers of individuals observable at a colony is an approach which can give an indication of population size (Nettleship 1976, Piatt *et al.* 1990, Walsh *et al.* 1995, Hatch 2002). The ease in determining the extent of colony attendance can be species dependent. Those species breeding on exposed cliffs are often relatively easy to count whilst those breeding underground in burrows are more difficult to count (Harding *et al.* 2005). Furthermore, counts of individuals can vary markedly within and between days and this can lead to their use as an index of population size to be inconsistent over time if not standardised (Lloyd 1972, Harris and Wanless 1983, Hatch 2002, Calvert and Robertson 2002a).

The Atlantic puffin *Fratercula arctica* (hereafter referred to as “puffin”) is an example of a burrow-nesting diurnal seabird, which is notoriously erratic in its attendance at a colony (Lloyd 1972, Nettleship 1976, Walsh *et al.* 1995, Calvert and Robertson 2002a). Counting the number of apparently occupied burrows (AOBs) is the most appropriate method for monitoring puffin colonies when access is possible, *i.e.* not on a cliff, sea stack or other dangerous terrain (Harris and Rothery 1988, Anker-Nilssen and Røstad 1993, Walsh *et al.* 1995). However, given inaccessibility of some colonies the maximum numbers of puffins on the colony surface, and also in flight and at sea (< 200 m offshore) are also counted in the UK recommended census method (Walsh *et al.* 1995).

Counts of individual puffins to estimate population size are recommended to be undertaken over successive periods across a season, and most often confined to the early part of the season, ideally during the pre-laying period (Brooke 1972, Nettleship 1976, Jones 1992, Walsh *et al.* 1995, Hatch 2002). However, the ratio between the maximum number of puffins and the actual number of breeding pairs is usually unknown (Nettleship

1976, Walsh *et al.* 1995). Consequently, counting puffins currently provides an indication of population size, but with an estimated accuracy to only within an order of magnitude (Walsh *et al.* 1995).

Within the UK there are approximately 580,000 pairs of Atlantic puffin, as estimated from the Seabird 2000 survey. These data, totalling 599 records, were collected from both counts of individuals and counts of pairs. 514 records (85.8%) were of counts of individuals on sea/flight/land and 71 records (11.9%) were of counts of occupied nests/burrows/sites. Although most records are comprised of counts of individuals the percentage of the UK population monitored with this approach equates to only 11.7 % of the UK population. 88.3 % (513,000 “pairs”) of the UK population is monitored using the preferred approach of counting occupied nests/burrows/sites. There is therefore a small, but not insignificant, proportion of the population which could benefit from the use of photography when counting individuals in monitoring schemes.

At present, monitoring of puffins can be limited as many colonies are relatively remote, or in areas which can incur significant costs of time and labour from repeated visits (Lloyd *et al.* 2010). An automated approach of recording puffin attendance would therefore negate some of the costs involved of repeat visits, whilst also providing a way to minimise variation in attendance of puffins and standardise estimates of population size.

Time-lapse photography can be used as a method to record the numbers of puffins over time. Time-lapse photography has been used in prior studies to monitor seabird behaviour and populations (Harris and Wanless 1983, Piatt *et al.* 1990, Hatch 2002, Harding *et al.* 2004, Dawin-Initiative 2012), although it is limited to only one study for Atlantic puffins, where productivity is inferred from coarse-scale attendance (Anker-Nilssen 2010). Time-lapse photography can potentially improve estimates of population size by taking successive counts of puffins over the whole season from all times of day on terrain which is normally considered inaccessible. This approach could thus provide a potentially more reflective estimate of the true maximum number of individual puffins present on land, compared to a single visit. Many studies adopt the maximum count of puffins as an index of population size given the relative ease and practicality in determining the maximum count; however this value is likely to vary with sampling intensity. Time-lapse photography provides a method in which to test the effect of varying sampling intensity by varying the interval between photographs and changing the study duration. Relating the known number of AOBs to the maximum count of puffins derived from photography provides an indication of the strength of the relationship.

Nettleship (1976) also suggests a method to estimate the size of a colony's breeding population by calculating a correction factor between the number of breeding pairs and the maximum count of puffins observed within a control area. This correction factor, termed '*k*', can be used to correct the maximum count of puffins from the colony containing the control area to estimate the number of pairs for the whole colony (Nettleship 1976). Following on from Nettleship's (1976) manual method, time-lapse photography could provide the same approach, assuming the control area can be counted, but also reducing the effort, cost and potential disturbance (Rodway *et al.* 1996) of repeat visits by automatically counting puffins systematically at all times.

Time-lapse photography also provides scope for further study on novel approaches to monitor seabirds. A study by Lorentzen *et al.* (2012) showed how automatic cameras can be used to estimate egg survival, hatching success and chick survival rates in Brünnich's guillemots *Uria lomvia*, based in part upon occupancy of nesting positions. Puffins tend to sit close to their burrows (Gillham 1956, Harris and Wanless 2011) so plotting the positions of puffins over time may result in distinct clusters of puffins, which could be associated with an occupied burrow. Therefore, numbers of occupied burrows from photography may be determined based upon the density of puffin positions.

The purpose of this study will therefore aim to evaluate how the maximum count of Atlantic puffins observed on land relates to the number of AOBS, and also how this varies with study duration and sampling frequency, using time-lapse photography. Furthermore, the relationship between the maximum count of puffins and the number of AOBs gives an indication of variability between colonies using time-lapse photography. In addition, the spatial distribution of puffins in relation to the location of AOBs is evaluated as a novel census method using time-lapse photography. Data from this study are used to suggest some general recommendations for the use of time-lapse photography to monitor Atlantic puffins.

## 3.2 Methods

### 3.2.1 Study site and photography

Digital cameras were placed at five puffin colonies and set to take time-lapse photography over the breeding seasons of 2011 and/or 2012. The method involves, in summary, installing cameras, which are set to take photographs of the puffin colony with a pre-determined interval. The photographs are then visually counted for the numbers of observable puffins on the ground (termed "attendance") in each photograph.

The rationale behind deriving counts of puffins from photography is, as for direct observations following recommended methods, to find the maximum count of puffins (hereafter termed "$P_{max}$") within a census period. Ideally, the census period for puffins would be from pre-laying to approximately mid-incubation (Walsh *et al.* 1995, Harris and Wanless 2011). Given cameras were only operational after the recommended census period $P_{max}$ is calculated across the season when the cameras were operational (mid-late incubation to late-chick rearing).

To record puffin attendance and derive estimates of $P_{max,}$ as an index of population size, three cameras were placed on colonies termed 'Arnamul', 'Original' and 'Otter' on Mingulay, Outer Hebrides, one at Fair Isle and one at Hermaness, Unst, Shetland. Repeated measurements over time also allows for another photographic metric to be derived: the mean count of puffins, $P_{mean}$. The mean count may provide a better estimate of population size than $P_{max}$. $P_{mean}$ is calculated for each camera by taking the mean of the number of puffins from each photograph over the period the camera was operational.

### 3.2.2 The effect of sampling intensity

Cameras at each colony were set to variable intervals accommodating logistical constraints and time taken to process photographs (Table 3.1). The variation in intervals and study duration at different colonies could however bias inter-colony comparisons of the maximum count of puffins, $P_{max,}$ as it would be predicted that a higher count would be achieved with a larger number of photographs being processed.

$P_{max}$ is therefore plotted against an increasing interval to investigate the change in the maximum count of puffins with a variable interval (and hence number of counts in a defined period). The interval is changed by resampling every $i^{th}$ photograph, where $i$ relates to the interval set initially. For example, Original 2012 took a photograph every 10 minutes, thus taking every second photograph ($i = 2$) increases the interval to 20 minutes. A range of intervals are chosen from 10 to 80 min, based upon each camera's initial interval used. An interval of 80 min was chosen as the largest interval as it is both a multiple of the lowest interval common to all colonies (40 min) and also because it is longer than the suggested photographic interval (60 min) used in two other time-lapse studies monitoring seabirds (Anker-Nilssen 2010, Huffeldt and Merkel 2013).

Furthermore, the length of time in which a camera is left monitoring a colony could influence $P_{max}$. By refining the survey window, *e.g.* the number of days sampled, the relationship between sampling effort and $P_{max}$ is derived. As shown in Chapter 2 attendance of puffins appears to exhibit cyclicity on Mingulay between ~ 5 and ~ 7 days. A short sampling window could therefore possibly underestimate $P_{max}$, if sampling coincided with a trough in attendance. The results of this approach could also be analogous to the effect of the number of days over which manual counts of individual puffins are done. Fair Isle is removed from analyses over time as cameras experienced technical issues, which limited the numbers of days of photography.

Using an interval of 40 min between photographs for each colony the daily $P_{max}$ is calculated. The maximum count of daily $P_{max}$ is then taken from within a survey window of variable length. The length of the window increases systematically by one day extra starting from day 1 to the end of the study duration for each time series. Equally, the reliability of an estimate of $P_{max}$ varies with when the sampling started. Therefore the start date is increased systematically by one day as well. The mean $P_{max}$ for each survey window is then calculated and plotted against the length of the survey window.

### 3.2.3 The number of apparently occupied burrows

In order to compare the relationship between any population metric derived from photography, *e.g.* $P_{max}$, the number of AOBs within each camera's field of view on

Mingulay was calculated. The area delimiting the view of each camera's field of view was firstly marked and then the total number of AOBs were counted, following the recommendations of Walsh *et al.* (1995) in defining an AOB. The Original colony was counted on the 5th June 2011 and the 29th May 2012. The Otter colony was counted on the 30th May 2012. On Hermaness the number of AOBs was counted within an area delimited by topography and counted by Alex Robbins on the 25th May 2012. The number of AOBs on Fair Isle was not counted and all analyses involving population estimates are done without Fair Isle.

An additional puffin colony was also used from Hernyken, Røst, Norway (67˚ 25' N, 11˚ 52' E) in 2006 with data provided by Tycho Anker-Nilssen. Calculation of the number of AOBs for Hernyken was made by counting the number of AOBs on the 10th May 2013 and back-calculating the number of AOBs to 2006 when the time-lapse camera was deployed using the change in population size over the entire colony (derived from plot counts undertaken by Tycho Anker-Nilssen). Extrapolation of the data will introduce some error however the Norwegian colony is an order of magnitude larger than the Scottish colonies so the proportional error is likely to be small. The time-lapse camera on Hernyken ran from early May to early August with one photograph per hour facing a boulder scree with the slope approximately perpendicular to the camera's line-of-sight. $P_{max}$ was obtained on the 12th July for Hernyken as assumed to come from the post-hatch stage, given the mean hatching date for the colony is the 20th June (Anker-Nilssen 2010).

Linear regression can provide an estimate of the relationship between photographic metrics and the number of AOBs. To use this linear model in a predictive manner, prediction intervals can be calculated to provide an estimate of the error associated with future observations (Fowler *et al.* 2006). Firstly, the number of AOBs can be regressed against $P_{max}$ using both a 40 min and 80 min interval between photographs to explore the effect of sampling interval on the slope and prediction interval of the regression. An interval of 40 min is used as it is the lowest common interval to all colonies used for linear regression and, as described before, an 80 min interval is longer than the suggested interval for other seabird colonies using time-lapse photography. For both regressions using 40 min and 80 min intervals the colony Hernyken (with a 60 min interval) is both removed and retained to observe the effect of the colony on model performance. Secondly, the number of AOBs can also be regressed against the mean number of puffins, $P_{mean}$. The colony

Hernyken is removed from analysis with $P_{mean}$ as data only exist as $P_{max}$. Data are not split with regards to breeding stage for use in regression given the limited data set.

### 3.2.4 Correction factors

Although Nettleship's (1976) proposed method of relating the correction factor of $P_{max}$:breeding pairs from a control area to a larger colony was not undertaken within this study the correction factors are calculated for each colony. Correction factors (Number of AOBs/$P_{max}$) are reported to explore differences between colonies and in relation to hatch stage. Hatch date is taken as the 11th June for both 2011 and 2012. The rationale behind this date is explained in Chapter 2.

### 3.2.5 The positions of puffins in relation to AOBs

Puffins can often be found standing outside or near their burrow entrance (Gillham 1956, Harris 1983). This proximity to their burrows can arise from a need to protect the burrow and egg or chick from predators and intruders  and also to provide cover for themselves (Hatch 2002, Harris and Wanless 2011). Over time, it is therefore assumed that spatially distinct, clusters of puffin locations within the colony could be associated with a burrow and could therefore be used to infer an occupied burrow. To explore this possibility the position of 192 puffin sightings over a sample of 46 photographs were plotted for the colony termed Original on Mingulay 2011. Photographs were chosen randomly from a period during incubation between 2nd and the 5th June 2011. Only 46 photographs were used as most photographs contained no puffins in this period. Photographs were chosen from the incubation period to reduce the chance of encountering large proportions of non-breeding individuals, which arrive later in the season (Harris and Wanless 2011) and may confound the position of breeding puffins in relation to burrows.

The position of puffins within the colony was determined based upon a 5 m x 5 m grid that was physically overlaid onto the puffin colony in 2011 (Figure 3.1). Digitising this grid from photographs allows the coordinates of each puffin (taken from their feet) standing in the colony to be manually determined to an accuracy of ~10 cm. The position of puffins was only digitised up to ~ 35 m from the camera (on the y-axis) as inaccuracy increased with perspective. Beyond 35 m the colony topography increased the effects of perspective. The position of burrows (from the centre of the entrance) were also determined from measurements in the field to an accuracy of 1 cm. Areas of high use by puffins, or "hotspots", were identified from the bivariate normal kernel utilisation distribution using a smoothing parameter (*h*) of 0.385 m and a grid size of 0.1 m, and implemented in the package 'adehabitatHR' (Calenge 2011).The smoothing factor (*h*) was manually defined because automated approaches using least-squares cross validation or the *ad ho*c method produced over-smoothed and under-smoothed results, respectively (Calenge 2011). The overlap between puffins and burrows was then estimated by counting the number of burrows that fell within the 95% kernel contour.

The position of puffins in relation to burrows was then tested to observe whether puffins were randomly distributed. The distance from every puffin position to its nearest burrow was calculated and also the distance from randomised positions in the colony to the nearest burrow was calculated. Random positions were calculated by randomising coordinates within the gridded area (Figure 3.1). Distances were calculated using the *get.knnx* function within the package 'FNN' (R.Core-Team 2014).

Confidence intervals were created to test the null hypothesis that the difference between mean distances from randomised puffin positions and actual puffin positions to the nearest burrow was zero. The mean distance of 10 bootstrapped samples from each distribution was calculated and repeated 1000 times to generate normal distributions of the mean.

### 3.2.6 Statistical analyses

A Generalised Linear Model (GLM) with a Poisson error structure was used to examine the effect of varying the interval on the maximum number of puffins observed. Fixed effects of interval length and colony with an interaction between the two were used. Model structure: Max ~ interval length * colony.

A GLM with a Gaussian error structure was used to examine the effect of a varying photographic interval on the relationship between $P_{max}$ and the number of AOBs. Fixed effects included $P_{max}$ and the photographic interval with an interaction between them. Model structure: AOB ~ Max * interval length.

Significance is reported as $P < 0.05$ with statistical tests using a two-tailed test. Error values associated with mean values are standard deviation (SD), unless reported as standard error (SE). Model selection to produce the minimum adequate model (MAM) was determined by stepwise backwards removal of parameters from a fully parameterised model using maximum likelihood (ML). The significance of a fixed effect was determined by using likelihood ratio (LRT) chi-square tests between the GLM and a GLM excluding the fixed effect of interest (Pinheiro and Bates 2000, Miles 2010). Only significant terms are reported from model selection. The function *glm* from the ‘stats package was used to implement GLMs (R.Core-Team 2014). Tests for autocorrelation were done using the *acf* from the ‘stats’ package. Model fit was assessed on the basis of normalised model residuals versus fitted values testing for heteroskedascity, low AIC values, a lack of over-dispersion and collinearity. All analyses are carried out in R *v*. 3.03 (R.Core-Team 2014).

## 3.3 **Results**

In total 13,427 photographs were taken over the two seasons and from the photographs a total of 81,662 puffins were manually counted. The numbers of AOBs for each field of view are reported in Table 3.1. Cameras had variable photographic intervals from 10 min to 40 min, reflecting logistical constraints.

### 3.3.1 The effects of sampling intensity

Figure 3.2 shows that the count of maximum puffin numbers, $P_{max}$, decreases with an increasing sampling interval between photographs in all colonies and absolute levels differed between colonies (LRT, interval, $\chi^2_1 = 1395.80$, $P < 0.001$; colony, $\chi^2_6 = 19442.00$, $P < 0.001$; interval*colony, $\chi^2_6 = 1.65$, $P = 0.949$). As the interval increased $P_{max}$ typically decreases (Interval (min): GLM estimate = -0.004 ± 0.001 SE), suggesting that with decreased sampling intensity there is less chance of observing a peak count. Using the GLM coefficients decreasing the sampling interval from 40 min to 80 min reduces the $P_{max}$ by ~ 12 individuals. The percentage change is dependent upon the initial population size, however averaging across colonies there was a decrease in attendance of ~ 13 % when increasing sampling interval from 40 min to 80 min. Given variation in the interval between colonies the lowest common interval of 40 min is subsequently used.

Furthermore, the number of days a camera is left in the field taking photographs is another factor which could influence $P_{max}$. Figure 3.3 shows that as the sampling duration increased the value of $P_{max}$ increased. The increase is, however, non-linear and colonies reach their $P_{max}$ on average after 29 days ± 8.5 SD, with a range of 24 to 44 days. This suggests that with a sampling interval of 40 min these data across all colonies could have derived $P_{max}$ after 44 days. Data were not separated by breeding stage as $P_{max}$ could be found spuriously in a short length of time limited by the short incubation study duration.

### 3.3.2 Predicting population size

Only the field of view of the cameras on the eastern side of Mingulay (Original and Otter) were able to have both the area and number of AOBs counted. The field of view of the Original colony had a similar density of AOBs in the two years and its density of AOBs was approximately twice as high as in Otter. Hernyken has the highest burrow density at 0.65 AOBs $m^{-2}$. The area of Hermaness was not calculated and density could not be estimated.

Regression of the number of AOBs against $P_{max}$ with an interval of 40 min produces a positive relationship with a ratio of 0.75 AOBs to 1 puffin (Table 3.2, Figure 3.4). Taking the mid-point of $P_{max}$ (147.5) across colonies the model predicts 111 ± 59 AOBs, with the error derived using prediction intervals (Table 3.2). Regressing the number of AOBs against $P_{max}$ with an interval of 80 min also produced a positive relationship with a similar ratio (0.80 AOBs to 1 puffin, Table 3.2) as the 40 min interval. Taking the mid-point of $P_{max}$ (147.5) across the five colonies the model predicts 118 ± 87 AOBs, with the error derived using prediction intervals (Table 3.2). Using an interval of 80 min, compared to 40 min, produces an estimate of the number of AOBs from $P_{max}$ with a larger error (Table 3.2); however there is no significant difference in the slope of the two regressions (LRT, interval*$P_{max}$, $\chi^2_1 = 1.99$, $P = 0.946$). Equally, removing the data point from Hernyken, given its interval of 60 min, shows no significant difference between the slopes of the two regressions with different intervals of 40 and 80 min (Table 3.2, LRT, interval*$P_{max}$, $\chi^2_1 = 276.31$, $P = 0.428$). In general, removing the data point from Hernyken removes the significant relationship between AOBs and $P_{max}$ and further reduces model fit and increases the error associated with prediction intervals (Table 3.2). Given the intercept for all models is negative there is the suggestion that some puffins occupy a plot without breeding; likely due to the presence of non-breeders. Therefore, these limited data suggest that estimates of the breeding population from $P_{max}$ may incorporate a percentage of non-breeders.

Using $P_{mean}$ produces models with much larger error compared to using $P_{max}$ (Table 3.2, Figure 3.4). A positive relationship between AOBs and $P_{mean}$ produces a ratio of 12.05 AOBs to 1 puffin. Taking the mid-point of $P_{mean}$ (5.2) across colonies the model predicts 63 ± 223 AOBs (Table 3.2).

### 3.3.3 Correction factors

Table 3.1 shows that the correction factor of AOBs to $P_{max}$ varies between breeding stage and colony. During the pre-hatching stage the ratio is higher than during the post-hatching stage, attributable to a lower $P_{max}$. Otter 2012 however remains the same with an equal $P_{max}$ across both the pre- and post-hatching stages. The larger colonies of Hermaness and Hernyken had the two highest ratios with proportionally fewer individual puffins seen in relation to the number of AOBs.

### 3.3.4 The position of puffins

Figure 3.5 shows that the locations of puffins in the territory appear to occur in several distinct clusters. Some clusters are likely to arise through the presence of surface features. For example, a large rock makes a suitable loafing spot (Figure 3.1, Figure 3.5), whilst other clusters could perhaps be associated with burrows. Twenty four (69 %) of the 35 AOBs within the camera's field of view were found within the 95 % kernel. Furthermore, the distances puffins were found from the nearest burrow were significantly closer than expected from a random distribution. The null hypothesis that puffins are found at random distances from their nearest burrow is rejected as the confidence intervals do not bound zero (95 % confidence intervals (CI): 0.627 to 0.697). Puffins are found closer to a burrow by 0.66 m (with CI given before) than if distributed randomly (Figure 3.6).

**Table 3.1.** The area, density of apparently occupied burrows (AOBs) and the ratio of AOBs to the maximum number of puffins seen (Pmax) pre-hatch and post-hatch. Hatch date was taken as the 11th June for both years in Scottish colonies. Hatch date for Hernyken is unknown and all observations on Hermaness were after the hatch date. *k* is the ratio of the number of apparently occupied burrows to the maximum number of observed individuals ($P_{max}$).

| | Original 2011 | Original 2012 | Otter 2012 | Hermaness 2012 | Hernyken 2006 |
|---|---|---|---|---|---|
| Start date | 29/05 | 22/05 | 23/05 | 14/06 | Early May |
| End date | 16/07 | 12/07 | 12/07 | 02/08 | Early Aug |
| Useable days* | 45 | 50 | 50 | 34 | - |
| Photographic interval (min) | 20 | 10 | 40 | 40 | 60 |
| Area ($m^2$) | 750.0 | 812.5 | 1462.5 | - | 248 |
| Number of AOBs | 39 | 45 | 42 | 138 | 192 |
| Burrow density (AOB $m^{-2}$) | 0.05 | 0.06 | 0.03 | - | 0.65 |
| Pre-hatch | | | | | |
| $P_{max}$ | 72 | 66 | 64 | - | - |
| $k$ | 0.54 | 0.68 | 0.66 | - | - |
| Post-hatch | | | | | |
| $P_{max}$ | 91 | 91 | 64 | 159 | 231 |
| $k$ | 0.43 | 0.49 | 0.66 | 0.87 | 0.83 |

* Useable photos represents the total study duration minus those days of camera malfunction.

**Table 3.2.** Results of linear regression and its predictive ability for the relationship between puffin attendance and the number of Apparently Occupied Burrows (AOBs).

| Scenario | Linear model output | | | | | | Predictions | | |
|---|---|---|---|---|---|---|---|---|---|
| | No. colonies | Adj. $r^2$ | *F* | *P* | m (± SE) | c (± SE) | Mid-point of Metric | Predicted AOBs (± PI) | Ratio of AOBs: Puffins |
| **40 min interval with Hernyken** | | | | | | | | | |
| Max | 5 | 0.94 | 66.32 | 0.004 | 1.01 (0.12) | -38.21 (17.58) | 147.5 | 111 (59) | 0.76 |
| **80 min interval with Hernyken** | | | | | | | | | |
| Max | 5 | 0.88 | 29.38 | 0.012 | 1.00 (0.18) | -29.12 (24.78) | 147.5 | 118 (87) | 0.80 |
| **40 min interval without Hernyken** | | | | | | | | | |
| Max | 4 | 0.83 | 15.94 | 0.057 | 1.12 (0.28) | -48.12 (30.22) | 111.5 | 77 (95) | 0.69 |
| Mean | 4 | 0.07 | 1.25 | 0.380 | 11.75 (10.53) | 1.59 (62.16) | 5.2 | 75 (108) | 14.34 |
| **80 min interval without Hernyken** | | | | | | | | | |
| Max | 4 | 0.79 | 12.00 | 0.074 | 1.53 (0.44) | -75.71 (42.38) | 98.5 | 75 (106) | 0.76 |

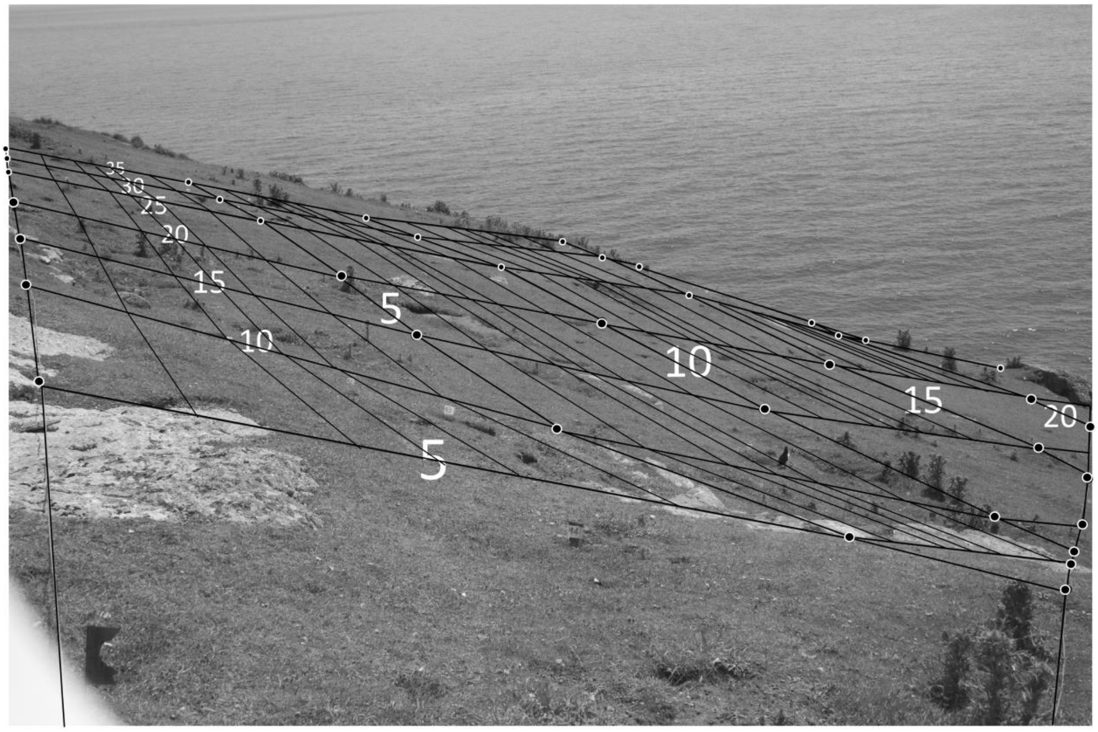

**Figure 3.1**. A photograph of the Original colony in 2011 showing the overlaid grid to mark the position of Atlantic puffins.

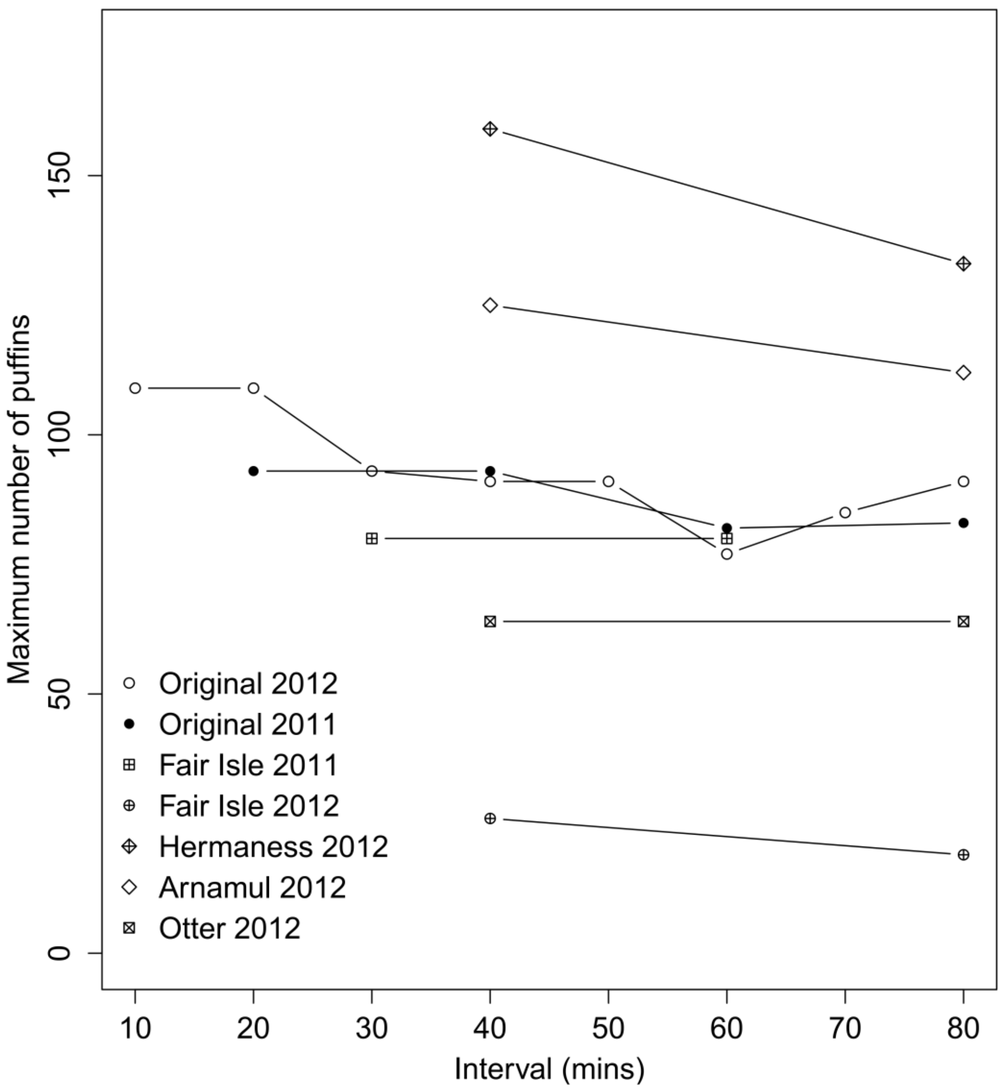

**Figure 3.2.** The change in the maximum number of Atlantic puffins recorded over the whole season with varying photographic interval.

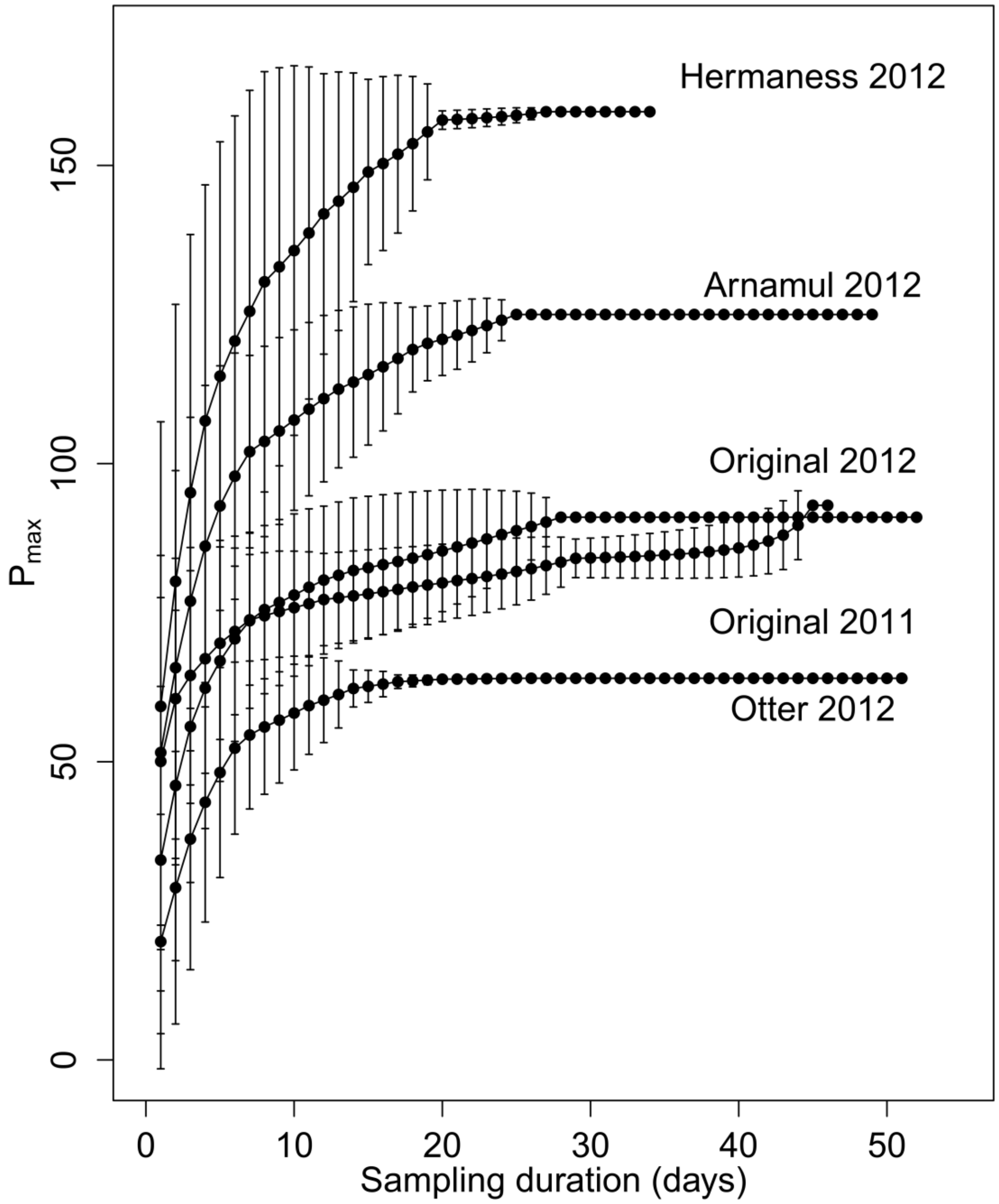

**Figure 3.3.** The change in daily maximum number of Atlantic puffins with sampling duration using a photographic interval of 40 min. Error bars represent standard deviation.

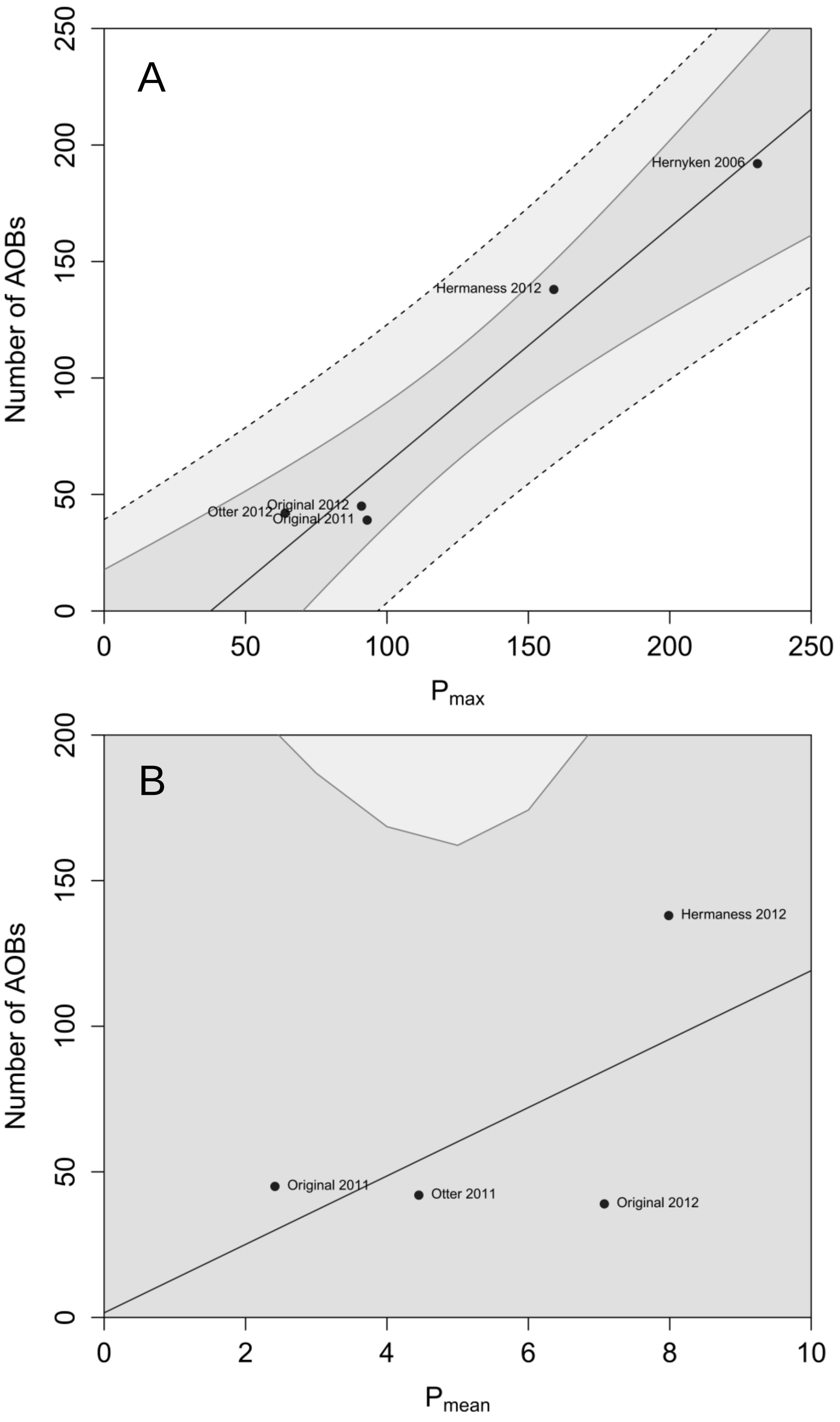

**Figure 3.4.** The results of linear regression between: A) $P_{max}$ and B) $P_{mean}$ (using a 40 min interval) against the number of apparently occupied burrows. The dark shaded, inner band represents the 95 % confidence interval, whilst the lighter, outer band represents the 95 % prediction intervals.

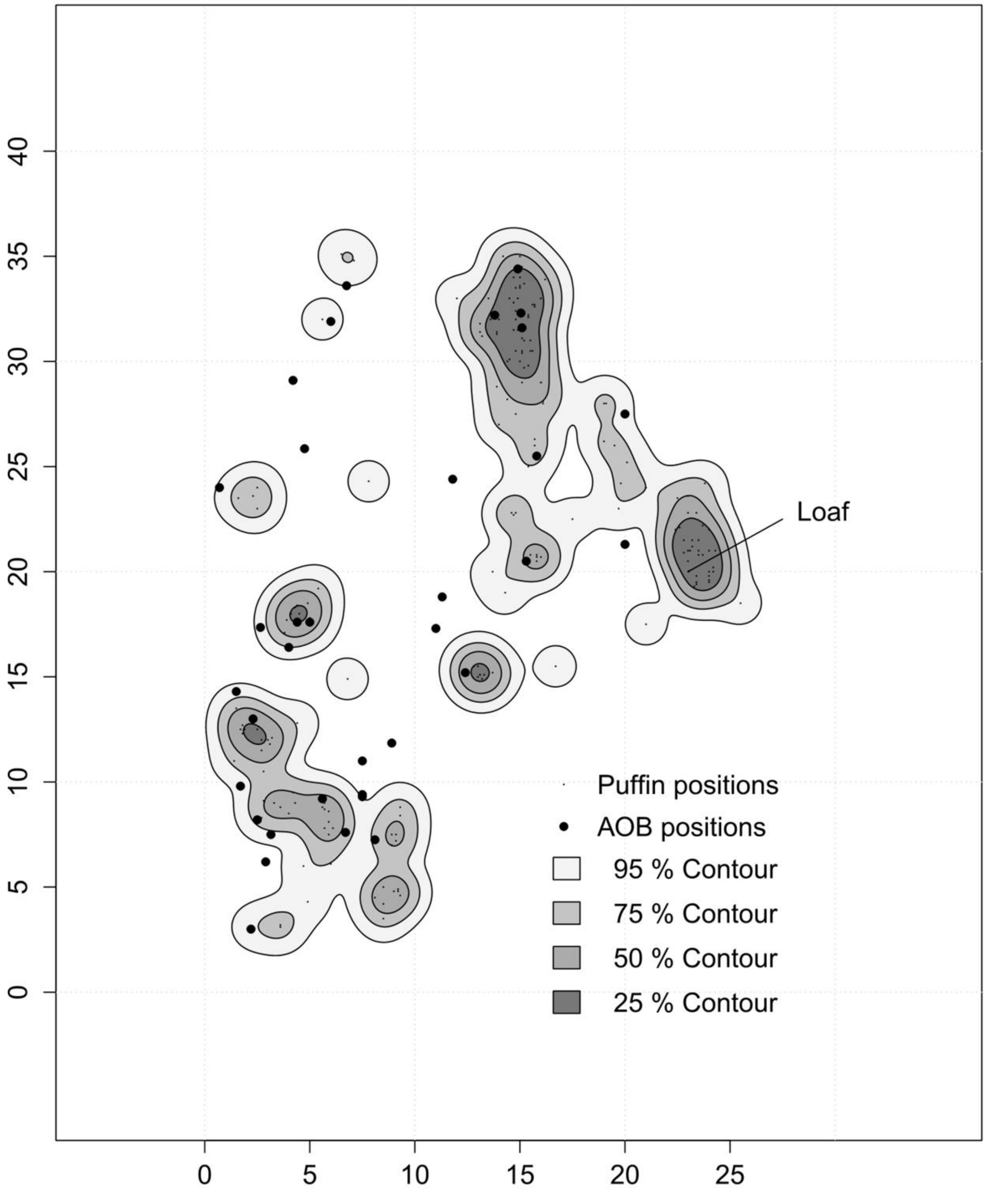

**Figure 3.5.** Kernel density distribution of Atlantic puffins during the incubation period on land in relation to apparently occupied burrows (AOB) on the colony termed Original on Mingulay 2011. Both axes are in metres.

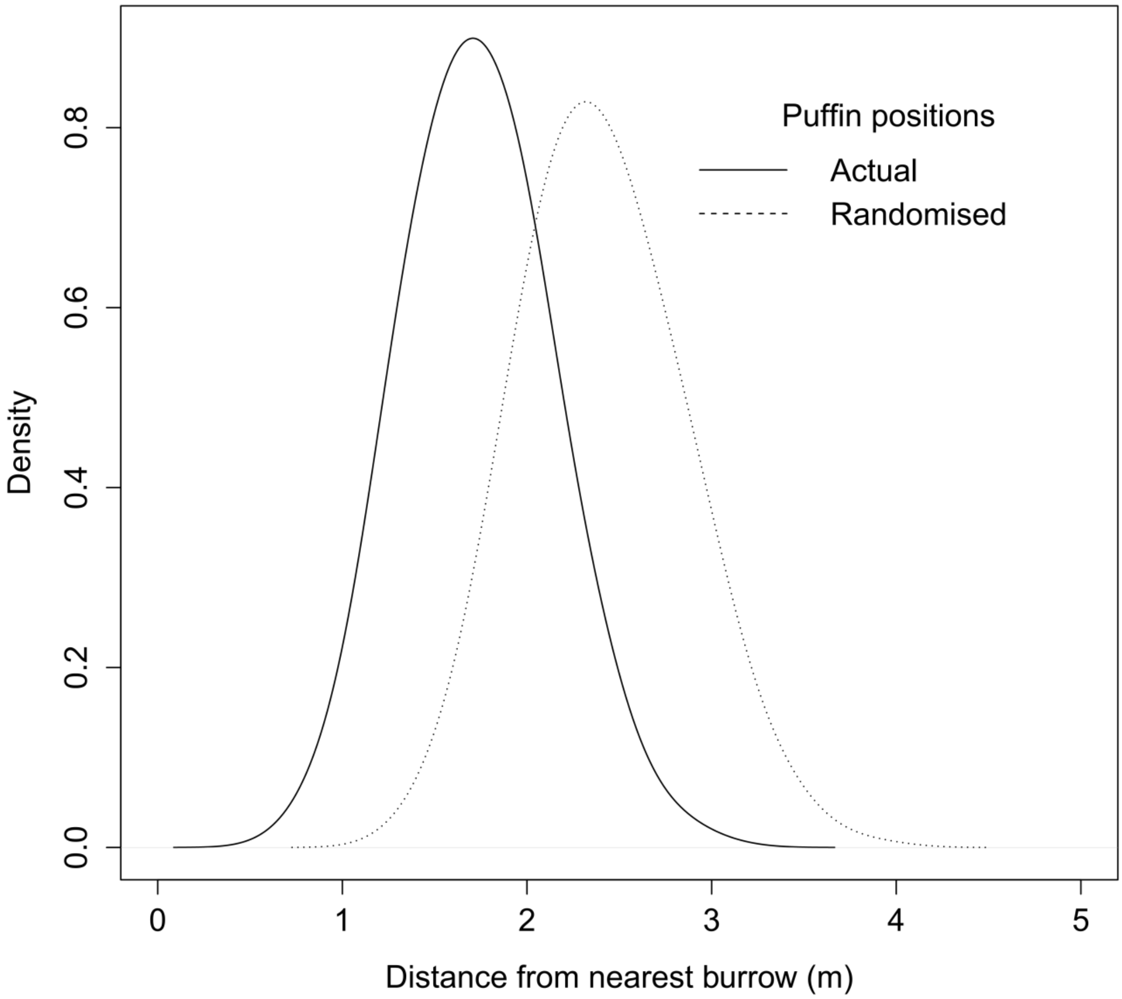

**Figure 3.6.** The probability density function of the distance of Atlantic puffins to their nearest burrow for two scenarios: 1) using actual puffin positions; and 2) randomised puffin positions. Distance is in metres.

## 3.4 **Discussion**

The purpose of this study was to evaluate the potential time-lapse photography has to obtain estimates of population size using counts of individuals. Many studies estimating the size of a puffin population strive to obtain the highest count of puffins, with the assumption that a higher count leads to a better index of the breeding population size (Nettleship 1972, Cairns 1979, Walsh *et al.* 1995). However, the maximum count of puffins, $P_{max}$, can be unknown and is likely to be dependent upon survey intensity, time of year, weather and the variability of puffin attendance over time (Nettleship 1972, Calvert and Robertson 2002a, Blet-Charaudeau *et al.* 2010, Huffeldt and Merkel 2013).

This study shows that from repeated sampling across the season using photography a value of $P_{max}$ can be derived. $P_{max}$ is however dependent upon the photographic interval used. The chance of observing a higher $P_{max}$ decreases with an increasing interval between photographs. Linear models show a significant decline with interval length over time, with an estimated decline of 12 puffins from 40 to 80 min. Caution should be exercised from the use of linear models however given slight heteroscedasticity in the fixed effect of interval length. Equally, there may well be a non-linear component to the rate of decline with interval length. Overall, without using linear models the $P_{max}$ is observed to decline by on average 8 puffins ± 9.5 SD from 40 to 80 min across colonies. Therefore, using a shorter interval is more likely to capture a higher $P_{max}$; however, there is a trade-off between a shorter interval and the time taken to process photographs.

A further consideration to the use of time-lapse photography is the number of days a camera is left at the colony. This study showed that across the colonies monitored $P_{max}$ was not found until after 29 days on average, with a maximum duration of 44 days, using a 40 min interval. This suggests that cameras need to be operational for a minimum of 44 day period in order to obtain a higher estimate of $P_{max}$; however, interpretation should be cautious. Given the data come from predominantly the chick-rearing period the numbers of puffins are expected to increase over time with the arrival of non-breeding birds and then decrease before and around fledging (Harris and Wanless 2011). The point at which a camera observes $P_{max}$ for this study may therefore reflect the increasing population rather than sampling intensity. Furthermore, variations in study duration and the time within the season each camera started will influence the generality of this result.

A further assumption to this study is the implicit relationship between counts of individuals and the number of breeding pairs. The limited data from this study show a positive and significant relationship between $P_{max}$ and AOBs; however the error is within an order of magnitude of the population size. The strength of this relationship furthermore decreases with an increasing interval. One considerable limitation to this study is that data for each colony are taken from variable periods across the season. Data for Hermaness arise from the chick-rearing period, whilst Mingulay cover both incubation and chick-rearing. However, all counts of $P_{max}$ occur within the chick-rearing period. The camera from Hernyken, Norway was also on an interval of 60 min, which as previously stated will limit the generality between colonies in obtaining $P_{max}$. However with and without the Norwegian colony there is still a positive and marginally significant relationship (without Norway, $P = 0.057$) with no statistical difference in the slope of the two regressions between $P_{max}$ and the number of AOBs. Data from the Original colony over the two years (2011 and 2012) can also be considered to be not independent. Removing each year's data from this colony separately still results in a significant and positive relationship (without 2011, $y = 0.97$ x - 27.92, $F_{1,2} = 67.96$, Adj. $r^2 = 0.96$, $P = 0.014$; without 2012, $y = 0.99$ x – 32.50, $F_{1,2} = 44.09$, Adj. $r^2 = 0.94$, $P = 0.022$).

Although there is likely to be a relationship between $P_{max}$ and the number of AOBs, at present there is too much error associated with prediction intervals in which to reliably predict the number of AOBs from novel values of $P_{max}$. Further work to decrease the error associated with this regression and to increase the chance of deriving some form of calibration from $P_{max}$ to the number of AOBs could be achieved by the addition of more colonies with standardised intervals, study length and time within the season. The use of $P_{mean,}$ although again across variable breeding stages, shows little promise in relating mean counts of puffins to the number of AOBs. Although a positive relationship exists between $P_{mean}$ and the number of AOBs the error is considerable. Observing a mean count of 5.2 puffins yields an estimate of 75 AOBs with an error of plus or minus 108 AOBs, with the error increasing considerably away from the mid-point of the regression. It is important to acknowledge that the sample size for these relationships, both using max and means, is very small and the results only suggest initial, limited indications.

There is also the assumption that the number of apparently occupied burrows is equivalent to the breeding population. However, it is also important to remember that there is a difference between an occupied burrow and an apparently occupied burrow. When conditions are good, *e.g.* suitable weather and plentiful food sources, occupancy can remain as high as 95 %, whilst with poor conditions this value can decrease to 60 % (Harris and Wanless 2011). Furthermore, there is also error introduced in estimates of the number of apparently occupied burrows by inter-observer error and a variable proportion of breeding birds that do not lay (Anker-Nilssen and Røstad 1993). Therefore, it is important to note that the observed number of apparently breeding pairs is not an indication of the actual population size.

An alternative approach to estimating the size of a breeding population is through the use of the *k* correction factor, produced from the number of pairs divided by $P_{max}$ (Nettleship 1976). Calculating *k* within a control area and relating this correction factor to $P_{max}$ of a larger area within the camera's field of view, whilst still containing the control area could be possible. This method is untested within this study and has the caveat that in most scenarios if a control area can be physically accessed then manual methods of monitoring may be more appropriate for the colony. Therefore, this approach of applying Nettleship's *k* is most relevant for areas where estimating the number of AOBs is difficult given high population density, inaccessibility or problematic in defining an AOB, as in boulder scree (Cairns 1979, Piatt *et al.* 1990). The results from this study show that *k* varies with breeding stage and between colonies. Although, there is a limited sample size *k* decreases with breeding stage as a result of increasing attendance in the post-hatch stage, which is likely to be a result of the arrival of non-breeders. In general, values of *k* are all below one for the range of populations studied (max. 248 AOBs). The use of linear regression estimates also show values of *k* to be less than one. Values of *k* less than one are to be expected as this indicates more puffins than burrows.

Hermaness and Hernyken (which are the largest colonies studied) have relatively high values of *k* in the post-hatch stage, compared to the colonies of Original and Otter. This suggests that larger colonies have a disproportionately smaller value of $P_{max}$, in relation to the number of AOBs. This may be due to edge effects, where an increasing colony area could equate to a larger proportion of the colony in the field of view and consequently resulting in proportionally less puffins moving into the field of view; leading to a smaller $P_{max}$. However, these prior comments are based on a very small sample size and need further study.

A last approach to monitor puffins using time-lapse photography involves determining whether the positions of puffins over time can reflect the position of occupied burrows. The results of this limited study show that puffins do not sit at random and that they tend to be clustered closer to burrows than on average. However it is important to note that this camera captures again only a proportion of a much larger puffin colony and consequently there are important edge effects which need to be considered. The distribution of puffins is thus influenced by the proportion of the colony outside the field of view. Equally, the accuracy of plotting puffin positions decreases with distance. Therefore, there should be some caution in interpretation given this study is limited to one site; further work photographing a proportionally larger colony extent would reduce this issue.

From mapping the utilisation distribution 69 % of the AOBs are found within the 95 % kernel, further suggesting that puffins sit close to burrows. The smoothing factor determining kernel size and shape was subjectively chosen based upon observation that automated approaches appeared over- and under-smoothed. This subjective choice does not however influence the observation that puffins sit on average closer to their burrow than at random. There is the possibility that puffins are however not sat closer to burrows but actually to features associated with burrows. From personal observation puffins did not often sit at their burrow entrance but would sit above or near the burrow on raised features, which perhaps provided greater observation for potential predators and/or ease in take-off. The presence of a prominent rock made for a suitable loafing spot; however the lack of burrows immediately nearby suggests also that puffin density may not be related to burrow positions.

To use this approach to enumerate the number of burrows requires further work increasing the sample size of puffin positions, different colony densities and areas, and consideration for colony-specific topographic features, *e.g.* boulder scree habitat, or more vertical or more horizontal colonies (cliffs *versus* cliff tops). Successful determination of an occupied burrow from the position of puffins would also allow novel insight into the breeding success of individual burrows, assuming that upon failure or success, puffins would spend less time around the burrow entrance. In general, this example provides the novel suggestion that the position of puffins over time could enumerate burrows, although more work is needed based upon these limited data.

The following sections detail some of the disadvantages and advantages of time-lapse photography with suggestions for the use of photography to monitor puffins. Firstly, time-lapse photography as demonstrated from this study can derive indices of population size, which are positively related to colony size. However, this study was conducted across an unfavourable period for population monitoring with a limited study duration and number of colonies. Although there are limitations to this current study, this does not limit the applicability of this methodology in principle.

Installation of cameras during the pre-laying period onwards to approximately mid-incubation can provide a value of $P_{max}$, which could more closely represent the size of the breeding population that year. With regards to the length of time a camera is operational the duration should cover multiple cycles of puffin attendance to provide a more reliable estimate of $P_{max}$ (assuming an average cycle of 5 days; Corkhill 1971, Lloyd 1972, Myrberget 1979, Harris and Wanless 2011) and also to minimise the occurence of severe weather events reducing puffin attendance (Hatch 2002, Calvert and Robertson 2002a, Blet-Charaudeau *et al.* 2010; Chapter 2). Any use of time-lapse photography could relate attendance to weather, from appropriate weather records.

If possible, leaving a camera operational for the entire breeding season is preferable. Data across multiple entire seasons could provide valuable information on puffin attendance, potentially reflective of the availability of food and/or variation in colony productivity (Harding *et al.* 2007, Anker-Nilssen 2010, Huffeldt and Merkel 2013). Equally, data over multiple seasons would provide a greater understanding of the variability in puffin attendance, which could be used to refine appropriate times to undertake manual counts of puffin attendance in the future. Depending upon distance from the camera to the puffin and the camera resolution photography may also be able to detect colour-ring combinations of ringed puffins, useful for studies on survival (Harris 1983) or show interactions with other species, for example, quantifying predator presence or human disturbance.

The installation of cameras is assumed to have little influence on breeding success of puffins, although this is unquantified. If the camera did not need to have the battery and memory card changed then the puffins would only be disturbed during installation and collection of the camera. For this study, the need to change the battery and memory card was a large limitation. Whilst this was done on a frequent basis (two to seven days) to limit data loss this issue could easily be overcome by using a larger memory card or power source, perhaps through solar panels.

Perhaps the most unappealing aspect of time-lapse photography is the large number of photographs to process. The author aimed for approximately 200-300 photographs to be manually counted a day, although this timeframe will obviously vary with the observable number of puffins. Increasing the photographic interval will reduce the numbers of photographs to be processed. However this will also reduce the temporal resolution of observable puffin attendance and potentially the robustness of the data if the interval is considerable.

In using time-lapse photography, careful consideration of the photographic interval is required. If counts of puffins are to be comparable between colonies there is a need to standardise photographic intervals between cameras. From this study, a shorter interval provides a higher estimate of $P_{max}$, although counts at 40 min and 80 min still showed a positive and significant relationship with the number of AOBs. In general, an interval of 60 min or shorter (to allow further analyses if required) but still divisible into 60 min is advised, *e.g.* 10 or 20 min. An interval of 60 min allows for comparison with other colonies (Anker-Nilssen 2010), whilst considering a balance between the time taken to process photographs from potentially multiple colonies.

With 300 photographs processed a day, a season of monitoring at 60 min intervals from mid-April to the end of July could produce at least a week’s work from one camera (107 days and 18 hours light per day). Decreasing the interval to every 20 min would increase the work to ~ 3 weeks per camera, which on a large scale is likely unviable. Therefore there is an incentive to reduce the numbers of photos taken without compromising the robustness of data by increasing the interval.

From Chapter 2 it is evident that most puffins attend the colony during the evening, with a small peak in the late afternoon. During the morning there are often very few numbers of puffins present on land. In addition, the arrival of non-breeders from late-incubation onwards reduces the robustness of estimating the breeding population. Monitoring puffins therefore from the advised pre-laying period (~mid-April, Walsh *et al.* 1995) to mid-incubation (~mid-May) reduces the numbers of photos considerably without influencing the estimate of the breeding population.

Restricting the camera to only capture photographs every 60 mins from 14:00 hrs to 00:00 hrs (10 hours daily duration to capture the afternoon and evening peak) and across the early incubation period (as above) reduces the number of photographs to ~300. This would equate to 1 or 2 days' work in post-processing. Furthermore, counting only puffins in the evening peak (19:00 hrs to 00:00 hrs, 5 hours daily duration) across the same breeding period as before the number of photos for post-processing reduces to ~150. This would equate to ~1 days' work per camera. However, *a priori* knowledge is required of the daily period in which puffins have on average highest attendance if photographic periods are selectively chosen.

It is also important to consider the applicability of this method; installing synchronous cameras around an island to monitor multiple plots is possible and may glean valuable information on attendance and population size. However, cameras will still only monitor the extent of the field of view and multiple cameras used in a sampling approach may become impractical and costly. As an approximate calculation, the costs of monitoring the 362 unique sites surveyed using counts of individuals across the UK (according to the Seabird 2000 survey) could be substantial. Assuming each site would require a conservative estimate of 1 to 10 cameras and each camera cost £500 the total cost could vary from £181,000 to £1,810,000, excluding costs of installation and autonomous power sources. The numbers of cameras per site would depend entirely upon surface topography and the availability of ground-based photography to view the colony surface. However, whilst some colonies will not be viewable with photographic approaches 78 % of the 362 UK sites are relatively small with < 100 individuals observed and could require only a few cameras for censusing. The cost estimate here is considered vague given that the areas of the colonies are unknown, but it demonstrates an approximate cost on a national scale.

The use of cameras is therefore perhaps suited to detailed studies on particular colonies or plots instead of full island censuses, which are best done from current methods. Equally, multiple cameras will, at present, incur significant costs in processing time. An automated approach to recognising and counting puffins within photographs will have a large consequence on the viability of this method (Huffeldt and Merkel 2013). For this study automated software was commissioned to be developed. The software designers had difficulty in detecting an individual puffin given high rates of occlusion, perspective and variable contrasts in colour reflecting puffin presence. The use of crowd-sourcing is another potential option to count puffins within photos.

An important consideration for time-lapse photography is the often limited extent with which a population is monitored. More often than not only a proportion of a puffin colony can be monitored using photography. Manual counts of puffins can encompass a whole island or different colonies in one visit; however photography is limited to the camera's field of view chosen initially. As shown from this study puffins do not sit at random. Puffins perhaps sit in relation to burrows and/or prominent surface features. Therefore any colony studied with photography must consider the representativeness of the monitored colony to the surrounding terrain and burrow density. Knowledge *a priori* on the density of burrows or areas of high use would be advantageous to choose representative areas to monitor. Encompassing as much of the colony as possible and avoiding areas with disproportionate attendance to an estimated burrow density would be advised to reduce the chance of spuriously inflating $P_{max}$. Although not undertaken in this study, photographs of rafting puffins close inshore could also provide a further estimate of colony size. The limitations and potential error for photography at sea is however not considered here.

Furthermore, colonies where the camera's line of sight is relatively acute to the colony surface results in problems of perspective and also occlusion of puffins, either from conspecifics or surface features. For example, the surface of the Arnamul colony was almost perpendicular to the camera's line of sight which made identifying individuals much easier than compared to Original colony where the line of sight was acute to the colony surface. Issues of detecting a puffin also arise with the distance from the camera to the colony. Puffin colonies can often also be in areas with high vegetation growth, which can obscure burrow entrances and limit the visibility of puffins (Anker-Nilssen and Røstad 1993) to the extent where vegetation can be trampled down to improve visibility (Hatch 2002). Therefore, the viability of photography to monitor attendance will depend upon the camera's line of sight and any growth of vegetation (or grazing regime) upon the colony.

Overall, where possible monitoring of puffins should be undertaken using counts of AOBs given the reliability, comparability of surveys over time and between colonies, and the prolific literature on its use (Nettleship 1976, Harris and Murray 1981, Anker-Nilssen and Røstad 1993, Walsh *et al.* 1995, Harris and Wanless 2011). Manual counts of individuals may also still be preferable for whole island censuses or censuses limited by time. The use of time-lapse photography is suggested as an additional tool with which to monitor puffins for those colonies where access is impaired or where further detail on the maximum number of observable puffins is required.

In conclusion, the results of this study show that time-lapse photography can be used to monitor Atlantic puffins. Although, this study is limited to the mid-breeding season of the puffin, the results show a positive relationship between the maximum count of puffins and the size of the breeding population. At present the error in predicting population size from maximum counts of puffins is still large. However, when counts of apparently occupied burrows are not possible then time-lapse photography can be used to supplement current methods in deriving estimates of population size from counting individuals. Cameras left over the entire season could be used to potentially infer productivity, local conditions and a novel method of spatially defining puffins shows potential to estimate burrow occupancy. Further work is required in general to reduce the error and test this approach in more situations.

# Chapter 4

# A bioenergetic model estimating the nutrient input from Atlantic puffins *Fratercula arctica* and great skuas *Stercorarius skua* onto Mingulay

# Abstract

Seabirds are known to have profound effects on the environments where they breed. Their guano, rich in nutrients including nitrogen and phosphorous, can drive primary productivity and alter island food webs. Within the UK there are an estimated four million pairs of seabirds, which produce vast quantities of ammonia per year. Scotland, which holds a large proportion of the UK population of seabirds, has limited estimates of the nitrogen and phosphorous inputs, with most estimates derived from ammonia emissions. Detailed study of a single island allows for an appreciation of the input of nutrients from seabird populations with consideration for population-specific parameters and an understanding of the importance of nutrient input relative to localised, non-ornithogenic inputs. This study uses a bioenergetics model to estimate the seasonal nitrogen and phosphorous input, as a measure of nutrient input, onto Mingulay, Outer Hebrides, from the Atlantic puffin *Fratercula arctica* and great skua *Stercorarius skua*. These seabirds are used as model species given their different behaviour and breeding habit. Across the breeding season these two seabird species were estimated to input onto Mingulay ~ 0.9 tonnes of nitrogen (after excluding 0.06 tonnes $NH_3$ per year) and ~0.2 tonnes of phosphorous. Further estimates suggest that all seabirds on Mingulay produce 42.7 tonnes N and 9.3 tonnes P per year. This ornithogenic nutrient input is likely to be the greatest source of nitrogen and phosphorous onto Mingulay annually. The concentration of this input is likely to have significant effects upon the local vegetation and consequently also indirectly on other parts of the island’s food web. This input thus represents a significant spatial and temporal resource with potentially wide-ranging impact upon insular communities. Similar effects are likely to be observed on many other Scottish islands with moderate to large colonies of seabirds.

## 4.1 Introduction

Seabirds are known to have profound ecological effects on the terrestrial environments where they breed (Mulder *et al.* 2011). Seabirds can influence their breeding sites by physical disturbance (Furness 1991, Butler 1995, Bancroft *et al.* 2005a), changing seed dispersal (Wait *et al.* 2005, Ellis 2005, Sekercioglu 2006) and predominantly by depositing large quantities of nutrient-rich guano (Mulder *et al.* 2011). Guano is known to have significant effects upon recipient communities; altering diversity, productivity and nutritional quality of vegetation, as well as directly influencing invertebrate communities (Ellis 2005, Ellis *et al.* 2006). These changes can also further affect biotic and abiotic processes and indirectly mediate changes to the local community (Polis and Hurd 1996).

Seabirds have a high metabolic rate (Bryant and Furness 1995) and their principal prey, fish, has a high protein content and therefore nitrogen (N) content (Wilson *et al.* 2004a). As a result their guano is concentrated in N (Bird *et al.* 2008). Consequently, a large quantity of N is collected from the marine environment and transferred onto land through guano (Kolb *et al.* 2012). Guano-derived N deposited onto land can be further distributed within and between islands by volatilisation of N within $NH_3$ (N-$NH_3$) and leaching of nitrogenous compounds from the site of accumulation. Phosphorous (P) is another element also present at high concentrations within seabird guano (Bancroft *et al.* 2005b). Often plants are limited in nutrients containing N and P (Verhoeven *et al.* 1996) so the import of nutrient-rich guano from the marine environment onto land can lead to substantial influences on both the localised area and the surrounding terrestrial habitats (Staunton Smith and Johnson 1995, Schmidt *et al.* 2010, Wright *et al.* 2010, Riddick *et al.* 2012).

Within Britain there are approximately four million pairs of seabirds encompassing 24 regularly breeding species (Lloyd *et al.* 2010), which come every year to breed on land. This significant population produces an estimated 2.7 kt of ammonia per year and a large proportion of it in remote, ecologically sensitive areas of the UK with little agricultural input (Wilson *et al.* 2004a, Blackall *et al.* 2007). As a result, seabird guano can represent the main source of nutrient input into these remote areas (Wilson *et al.* 2004a, Riddick *et al.* 2012). The exact mass of nutrients deposited is however strongly dependent upon the species of seabird present and its interaction with the environment (Wilson *et al.* 2004a). For example, common guillemots *Uria aalge* nest colonially on rocky substrates and their deposits create prime conditions for N volatilisation (Blackall *et al.* 2007; Wright *et al.* 2010), although a large proportion may be washed away. Conversely, the input of guano from Manx shearwaters *Puffinus puffinus*, which nest in burrows retain a larger proportion of guano given the surrounding substrate and vegetation, which limits volatilisation (Blackall *et al.* 2007, Callaham *et al.* 2012). Understanding the difference in nutrient input between species can therefore be useful in interpreting the influence of nutrients on terrestrial systems in the different habitats seabird species occupy.

The inputs of N and P are modelled as a proxy for nutrient input as both elements are relatively high in concentration in guano (Holford 1997, Schachtman *et al.* 1998, Wilson *et al.* 2004a, Bird *et al.* 2008) and are considered important components of macro-nutrients for terrestrial primary productivity and have a low natural availability (Verhoeven *et al.* 1996). Estimates of ornithogenic N and P inputs are produced for the island of Mingulay, Outer Hebrides, Scotland, using a bioenergetics modelling approach, based upon the methods of Sutton *et al.* (1995) and Wilson *et al.* (2004a). Mingulay is chosen as a model island because it has received relatively little scientific attention, parameters specific to Mingulay can be obtained and it also allows for a detailed insight into localised inputs. Furthermore, given Mingulay does not receive fertilizer application, it is relatively isolated and there is limited upwind (from the prevailing direction; Owen *et al.* 2004) anthropogenic activity then most nutrient input is produced naturally *in situ*. In addition, understanding the quantity of nutrient input onto Mingulay allows an assessment of its influence of island systems to be understood, as discussed in the subsequent chapter.

Overall, this study aims to estimate the nitrogen and phosphorous input on Mingulay in one season. This study provides a detailed and novel insight into the mass of nutrients deposited, instead of focussing entirely upon estimating the gaseous nitrogenous emission which other studies often centre on (Wilson *et al.* 2004a, Blackall *et al.* 2007, Riddick *et al.* 2012). For this study, the inputs of N and P are estimated for two of the most important seabird species that could potentially impact the terrestrial vegetation on Mingulay. These two species are the great skua *Stercorarius skua* and the Atlantic puffin *Fratercula arctica* (hereafter referred to as “skua” and “puffin” respectively). Skuas are surface-nesters found typically at relatively low density in comparison to the smaller, burrow-nesting puffin, which can nest at much higher densities (Furness 1987, Harris and Wanless 2011). The two species also nest in different habitat on Mingulay, with skuas nesting in territories spread across the upland habitat whereas puffins nest at high densities in burrows primarily in cliff-top grassland, so their likely differential impacts on vegetation are studied. A detailed discussion of the input of nutrients from other sources and colonies provides a novel insight into the variation in magnitude between sources of nutrients on Mingulay. Overall, estimation of the mass of N and P deposited by puffins and skuas allows the exploration of how nutrients are cycled from seabirds to terrestrial systems.

# 4.2 Methods

## 4.2.1 Study site

This work is based upon the island of Mingulay (56$^{o}$, 48’ N, 07$^{o}$, 38’ W) in the Outer Hebrides. Data are taken from 2013, which is a typical estimate of population size for the last decade (Dunn 2013). The island is approximately 640 ha and is part of the Mingulay and Berneray Special Protection Area under the EC Birds Directive 2009/147/EC designated for both its razorbill *Alca torda* population (5017 individuals in 2013) and assemblage of seabirds. Apart from cliff-nesting species, Mingulay also hosts ground-breeding seabird species of which the largest populations are of puffins with a conservative estimate of *c.* 10,000 pairs (pers. obs. and pers. comm., Rob Dunn 2014) and skuas, which have increased considerably over the last 30 years from a single pair in 1979 to 75 apparently occupied territories (AOTs) in 2013 (pers. obs.). Other ground-nesting seabirds include, with data from 2013, 24 apparently occupied territories of common terns *Sterna hirundo* and Arctic terns *S. paradisaea*, 155 apparently occupied nests (AONs) of European shags *Phalacrocorax aristotelis*, 24 AONs of great black-backed gulls *Larus marinus*, 4 AONs of herring gulls *L. argentatus* and 6785 apparently occupied sites of Northern fulmar *Fulmarus glacialis*. There are also cliff-nesting species contributing 8968 individuals of common guillemots *Uria aalge* and 1123 AONs of black-legged kittiwake *Rissa tridactyla*.

Habitat-specific input of N and P is estimated initially for two localities: (i) a cliff-top grassland occupied by puffins and (ii) all upland habitat occupied by skuas. The input of nutrients for the puffin population is scaled up to an island population from studying a sub-population, which comprises 706 apparently occupied burrows (AOBs) on a grazed, cliff-top community on the east coast (3.6 – 4.4 ha; 56˚48’ N, 07˚37’ W). This sub-population of puffins is modelled given its accessibility and relative ease in which to collect data on species-specific parameters, *e.g.* diet and productivity. Furthermore, this sub-population is the site of subsequent study on how nutrient input influences recipient vegetation. For skuas, the whole population is modelled, which comprises a colony of *c.* 75 AOTs situated on the west of the island on upland mire and heathland habitat (11.4 – 18.8 ha; 56˚49’ N, 07˚39’ W). Parameter values for both study systems are, where possible, specific to Mingulay. Both the puffin and skua populations were counted in late May to early June, following the methods described by Walsh *et al.* (1995).

## 4.2.2 Bioenergetics model

Calculation of nutrient inputs onto terrestrial systems was determined based upon Sutton *et al.* (1995) and Wilson *et al.* (2004a). The premise behind the use of bioenergetics modelling was to determine how much N and P puffins and skuas deposit onto their respective nesting habitats. Species-specific inputs were determined for both the puffin and the skua with estimates for each component of the species' population: chicks (ch), fledglings (fl; only for skuas), non-breeders (nb) and breeders (br), following Furness and Hislop (1981). The birds were modelled as an equilibrium system, where the nutrient mass ingested equalled the nutrient mass excreted, as the amount of N and P incorporated for bird growth and maintenance is relatively small (Furness 1991, Wilson *et al.* 2004b). The daily food intake was estimated from energetic requirements, prey energy content and assimilation efficiencies (Wilson *et al.* 2004a). The mass of nutrient input onto land was taken as the proportion of each element within their prey as a function of the total mass excreted. Total N and P inputs per locality per year were scaled up from the total input per bird per year. A fraction of the N deposited typically becomes volatilised into gaseous ammonia ($NH_3$) and this emission is removed from the terrestrial N input (Riddick *et al.* 2012), although an unknown proportion is likely to be re-deposited across the island (Blackall *et al.* 2007). Values of all parameters and definitions, where not cited explicitly, are stated in Table 4.1 and Table 4.2.

### 4.2.2.1 Estimation of metabolic rates

Values for the field metabolic rate (FMR; kJ bird$^{-1}$ day$^{-1}$) of puffins are reported in the literature from use of doubly-labelled water as 848 kJ bird$^{-1}$ day$^{-1}$ (Shaffer 2011). For skuas FMR was estimated from scaling basal metabolic rate (BMR; kJ bird$^{-1}$ day$^{-1}$) to body mass, following Bryant and Furness (1995) (Equation 4.1). The FMR was considered to be the same for non-breeders and breeders, given that whilst non-breeders require less energy compared to breeders, they are less efficient at obtaining food (Furness 2004). For chicks, FMR is estimated from the total energy metabolised between hatching and fledging (Equation 4.2; $E_{\text{rearing}}$; kJ chick$^{-1}$ year$^{-1}$; Weathers 1992). Following the difference in FMR between breeding skuas and fledged skuas (Phillips *et al.* 1999) the FMR of fledged skuas ($FMR_{(fl)}$, kJ bird$^{-1}$ day$^{-1}$) remaining within the colony is calculated as $FMR_{(br)}$ divided by 2.42.

$$\mathrm{FMR} = 2.83\ (2.3M^{0.774})$$ Equation 4.1

$$E_{rearing} = 28.43\ M_{fledging}^{1.06}$$ Equation 4.2

where M is the mass of bird (g). The conversion factor from BMR to FMR (value = 2.83) is taken from Votier *et al.* (2004).

#### 4.2.2.2 Nutrients excreted

*Breeding birds*

From the method developed by Wilson *et al.* (2004a) the total mass of nutrients (either N or P) excreted by all breeding birds of a population ($Nu_{exc}$ (br); kg nutrient population$^{-1}$ year$^{-1}$) onto land across the entire season is calculated by Equation 4.3.

$$Nu_{exc}(\mathrm{br}) = \frac{\left(\left(\left(\frac{F_{Nu}}{A_{effic}}\right).\left(\frac{1}{F_{Ec}}\right).FMR\right).Population\ .\ t_{breeding}.F_{tc}\right)}{1000}$$ Equation 4.3

where $F_{\mathrm{Nu}}$ is the nutrient content of the food and is taken as 0.036 g N g$^{-1}$ wet mass ($F_{\mathrm{NC}}$) or 0.006 g P g$^{-1}$ wet mass ($F_{\mathrm{PC}}$), following Furness (1991), $A_{effic}$ is the assimilation efficiency of the bird in kJ [energy obtained] kJ$^{-1}$ [energy in food]. $F_{\mathrm{Ec}}$ is the energy content of the food. Population is the population size of breeding seabirds recorded as either AOBs or AOTs for puffins and skuas, respectively, and multiplied by two to account for both parents. $t_{breeding}$ is the number of days spent on land across the breeding season. Date of arrival and departure for puffins is taken from Harris and Wanless (2011), where the date of the first and last puffin has been recorded between 1966-2010 for the Isle of May and

Fair Isle and Grampian (1974-82). Data from west coast colonies in Scotland are assumed the same as east coast colonies, although puffins may return and leave later than the east coast (Harris 1982). $F_{\text{tc}}$ is the time an individual typically spends at the colony compared to over the sea. Surface-nesters, *i.e.* skuas, need to be on the colony for a greater period of time, compared to burrow-nesters, as there is a greater risk of predation on their young if left unattended (Caldow and Furness 2000). Thus puffins can leave their chicks unattended in the safety of their burrow to feed away from the colony, reducing the time spent at the colony. Wilson *et al.* (2004a) use the opinion of M. Harris for estimates of non-breeder $F_{\text{tc}}$. Chicks of both species have an $F_{\text{tc}}$ of 1.

### *Non-breeding individuals*

The total mass of nutrients excreted by non-breeding birds ($Nu_{exc}$ (nb); kg nutrients population$^{-1}$ year$^{-1}$) onto land across the entire season is calculated by Equation 4.4.

$$Nu_{exc}(\text{nb}) = 0.167\ Nu_{exc}\,(\text{br}) \qquad \text{Equation 4.4}$$

The non-breeding population is considered approximately a third of the breeding population with non-breeders spending 50% less time at the colony compared to breeders, which results in their contribution to be 16.7% compared to breeding birds (M. Harris within Wilson *et al.* 2004a).

### *Chicks*

The total mass of nutrients excreted by chicks ($Nu_{exc}$ (ch); kg nutrients population$^{-1}$ year$^{-1}$) across the entire season is calculated by Equation 4.5 (Wilson *et al.* 2004a).

$$Nu_{exc}(\mathrm{ch}) = \frac{\left(\left(\left(\left(\frac{F_{Nu}}{A_{effic}}\right).\left(\frac{1}{F_{Ec}}\right).E_{rearing}\right).(Population\,.\,P_{chicks}).\,F_{tc}\right)}{1000} \qquad \text{Equation 4.5}$$

where $P_{\mathrm{chicks}}$ is the number of chicks fledged per breeding pair. Other parameter values are assumed the same as adults.

*Fledglings*

The nutrient input of fledglings ($Nu_{exc}$ (fl); kg nutrient population$^{-1}$ year$^{-1}$) is estimated by Equation 4.6.

$$Nu_{exc}(\mathrm{fl}) = \frac{\left(\left(\left(\left(\frac{F_{Nu}}{A_{effic}}\right).\left(\frac{1}{F_{Ec}}\right).FMR_{fl}\right).(Population\,.\,Fl_{success}).\,t_{fledgling}.\,F_{tc}\right)}{1000} \qquad \text{Equation 4.6}$$

where $Fl_{success}$ is the number of fledglings per nest that depart from the colony and $t_{fledgling}$ is the time spent on land upon fledging (For skuas ~ 18 days (Phillips *et al.* 1999); upon fledging puffins head to the sea and do not persist at the colony (Harris and Wanless 2011) and therefore $t_{fledgling}$ for puffins is considered zero).

### 4.2.3 Calculating $NH_3$ emissions

A proportion of excreted N becomes hydrolysed, volatilised and subsequently lost through $NH_3$ emissions into the atmosphere (Schmidt *et al.* 2010). All volatilised $NH_3$ is considered to be lost from the island and not deposited on Mingulay through either wet or dry deposition. The following calculation (Equation 4.7), based upon Wilson *et al.* (2004a), estimates the volatilised component of N from guano ($Q_{NH_3}(\mathrm{br, nb, ch, fl})$; kg $NH_3$ population$^{-1}$ year$^{-1}$).

$$Q_{NH_3}(\mathrm{br},\mathrm{nb},\mathrm{ch},\mathrm{fl}) = \frac{\left((Nu_{exc}(\mathrm{br,nb,ch,fl}).1000)\ .F_{NV}.F_{hab}.\left(\frac{17}{14}\right)\right)}{1000} \quad \text{Equation 4.7}$$

where $F_{NV}$ is the fraction of N volatilised taken as 0.325 ± 0.248 (Blackall *et al.* 2004), $F_{\mathrm{hab}}$ is the habitat correction factor used to differentiate between birds which excrete onto different substrates dependent upon nesting habit and habitat, and 17/14 is the mass ratio of $NH_3$ to N. $NH_3$ emission from non-breeders was again assumed to be 16.7 % of that of breeders (see above). Puffin chicks are given a value of 0 because no $NH_3$ emissions could be detected from their burrows (Wilson *et al.* 2004a). All other components of the puffin population and all components of the skua population have an $F_{\mathrm{hab}}$ of 0.2. This value is considered appropriate given that soil and extensive vegetation surrounding the colonies will limit volatilisation (Sutton *et al.* 1995). The volatilisation of P from seabird guano does not readily occur under experimental conditions (Staunton Smith and Johnson 1995) and is not considered in this model as a gaseous emission. The leaching of N, which occurs readily given its solubility (DEFRA 2010) is not considered within this study and the fate of N post-deposition is not modelled. The loss of soluble P through leaching is considered minimal given the strong affinity for P to be adsorbed onto soil particles (Holford 1997, Schachtman *et al.* 1998).

### 4.2.4 Total nutrient input and estimates of density

The total nutrient input for both N and P is calculated through summation of each component's nutrient input minus the fraction of volatilised N. To determine the total nutrient input per hectare (kg Nu ha$^{-1}$), the total nutrient input was divided by the area of the two localities, assuming a uniform distribution of guano across the area. For puffins, the area was assumed to be the extent of the studied colony, as measured *in situ* deriving a range of measurements, based upon difficulties in delimiting boundaries (Walsh *et al.* 1995). For the skuas the area was considered to be the sum of the size of each territory (Table 4.1), as defined in Furness (1987).

### 4.2.5 Model parameterisation and error

To estimate the likely range of nutrient deposition a Monte Carlo simulation was computed. Each model parameter is assumed to follow a distribution associated with literature values and data collected within this study. Model- and species-specific parameters are reported in Table 4.1. Each parameter is modelled with a normal distribution, $N(\mu, \sigma^2)$. The fraction of N volatilised ($F_{NV}$) is modelled with a beta distribution, Beta($\alpha$, $\beta$), to confine values between zero and one. Other parameters which are bounded by zero and one are modelled with a normal distribution, only if values are not generated below zero and above one. Where model parameters do not have variation reported within the literature, two per cent of the mean value is used as the standard deviation; equating to a coefficient of variation of two percent (Table 4.1). This variation is used as it approximates the partial derivatives in analytical sensitivity analysis (Gardner *et al.* 1981, Bartell *et al.* 1986, Beyers *et al.* 1999). The model is then run using a Monte Carlo simulation with 10,000 iterations per parameter allowing for the random generation of model input values from within the specified distributions. The output is the result of varying model input parameter values, which can represent the error associated with the model predictions. Changes associated to individual parameters allow for the exploration of the sensitivity of each parameter to the model output. The sensitivity of models was explored by increasing initial parameter values by 1 % and also increasing parameters to a logical extreme, *e.g.* 10 %, following Phillips *et al.* (1999) and Votier *et al.* (2004). All statistics, models and simulations were carried out in R *v.* 3.03 (R.Core-Team 2014)

**Table 4.1.** Bioenergetics model parameters for the Atlantic puffin and great skua. Values in parentheses are standard deviation.

| Parameter | Puffin | Skua |
|---|---|---|
| Population size (AOB/AOT) | 706 (± 14.12)[1] | 75 (± 1.5)[1] |
| Colony area (ha) | 3.6 – 4.4[1] | 11.4 – 18.8[1] |
| $A_{\mathrm{effic}}$ (kJ [energy obtained] kJ$^{-1}$ [energy in food]) | 0.7796 (± 0.0139)[3] | 0.7600 (± 0.0152)[2] |
| $F_{\mathrm{EC}}$ (kJ g$^{-1}$ wet mass) | 4.63 (± 0.0926)[3] | 6.65 (± 3.48)[2,3] |
| Arrival date | 24/03 (± 15.65)[4] | 24/03 (± 15.65)[4*] |
| Departure date | 24/08 (± 6.05)[4] | 24/08 (± 6.05)[4*] |
| $F_{\mathrm{tc\ (breeder)}}$ | 0.3 (± 0.006)[5] | 0.6 (± 0.012)[5] |
| $F_{\mathrm{tc\ (non\text{-}breeder)}}$ | 0.15 (± 0.003) | 0.3 (± 0.006) |
| $F_{tc\ \mathrm{(chick)}}$ | 1[5] | 1[5] |
| $F_{hab}$ | 0.2 (± 0.004)[5] | 0.2 (± 0.004)[5] |
| $F_{hab\ \mathrm{(chick)}}$ | 0 | 0.2 (± 0.004)[5] |
| Adult body mass (g) | - | 1431 (± 28.62)[6,7,8] |
| Chick body mass(g) | 291 (± 5.82)[6,7,8] | 1150 (± 23)[6,7,8] |
| BMR exponent | - | 0.774 (± 0.01548)[9] |
| Chick exponent | 1.06 (± 0.0212)[13] | 1.06 (± 0.0212)[13] |
| Adult BMR multiplicand | - | 2.3 (± 0.046)[9] |
| Chick FMR multiplicand | 28.43 (± 0.5686)[13] | 28.43 (± 0.5686)[13] |
| Adult BMR:FMR ratio | - | 2.83 (± 0.0566)[10] |
| Adult FMR | 848 (± 16.96) | 1494 (± 29.87)[1] |
| Adult FMR:Fledgling FMR ratio | - | 2.420 (± 0.484) |
| Time on colony post-fledging (days) | 0 | 18 (± 0.36) |
| Mean brood size at 20 days | - | 1.06 (± 0.0212)[11] |
| Mean brood size at fledging ($Fl_{\mathrm{success}}$) | - | 0.84 (± 0.0168)[12] |
| Productivity ($P_{\mathrm{chicks}}$) | 0.73 (± 0.0146)[1] | - |
| Population of non-breeder:breeder ratio | 0.33 (± 0.0066)[5] | 0.33 (± 0.0066)[5] |

[1] This study; [2] Phillips *et al.* 1999; [3] Hilton *et al.* 2000b; [4] Harris and Wanless 2011; [5] Wilson *et al.* 2004a; [6] Cramp and Simmons 1977 ; [7] Cramp and Simmons 1983; [8] Cramp and Simmons 1985; [9] Bryant and Furness 1995; [10] Votier *et al.* 2004; [11] Phillips *et al.* 1999; [12] Phillips *et al.* 1997; [13] Weathers, 1992.

* Dates for skuas are modelled as the same for puffins as the total time on land approximates that reported by Wilson *et al.* (2004a) for skuas (*c*. 5 months).

**Table 4.2.** Parameter definitions for bioenergetics model.

| Parameter | Definitions |
|---|---|
| $A_{\mathrm{effic}}$ | Assimilation efficiency, the efficiency with which organisms convert the food ingested into energy for use. |
| $F_{\mathrm{EC}}$ | The energy content of food |
| $F_{\mathrm{tc}}$ | The proportion of time spent at the colony during the breeding period |
| $F_{hab}$ | Habitat correction factor, which accounts for the variable emissions from different seabird species and their nesting habitat, *e.g.* cliff and surface nesters. |
| $F_{NV}$ | The volatilised fraction of exrected nitrogen |
| BMR | Basal metabolic rate, the metabolic rate of an animal at rest in a postabsorptive state within the thermoneutral zone. |
| FMR | Field metabolic rate, the daily energy requirements for the maintenance and activity of individuals. |
| $E_{rearing}$ | The total energy metabolized between hatching and fledging. |

## 4.3 **Results**

The bioenergetics model and Monte Carlo simulation allow for an estimation of the mean and standard deviation of the nutrient input by each species onto Mingulay. The bioenergetics model shows that in 2013 the puffin and the skua localities received an estimated mean ± SD 644.7 ± 74.5 and 207.8 ± 32.9 kg of N, respectively (Table 4.3). Of this input, 46.0 kg of N is volatilised from the puffin colony (representing 7.1 % of the total input) and 16.6 kg of N is volatilised from the skua colony (representing 7.8 % of the total input). Equally, puffins and skuas input an estimated 118.2 ± 13.2 and 41.1 ± 6.1 kg of P, respectively. Puffins deposited approximately 2.95 times more N and P onto their nesting habitat, when compared to the skua population. When considering nutrient input at the scale of an individual, however, skuas deposited about three times more nutrients than puffins (Table 4.3).

Division of the nutrient input for the puffin locality by the 706 pairs of puffins produces an estimated input per pair of 0.913 kg N and 0.167 kg P. Multiplication of this value by the estimated 10,000 pairs of puffin on Mingulay produces an estimated 9.13 tonnes N $yr^{-1}$ and 1.67 tonnes P $yr^{-1}$ for all puffin habitats. Using the same calculation, removal of the volatilised N component of ~7 % from the island-wide input results in 8.49 tonnes N $yr^{-1}$ being retained from guano. Therefore, the whole puffin population produced ~ 37 times more N and ~40 times more P compared to skuas.

### 4.3.1 Nutrient density

From knowing the nutrient input and also the area of both the puffin colony and the skua territories it is possible to estimate the density of nutrient input. The eastern puffin colony is assumed to range from 3.6 to 4.4 ha (this study) and the average skua territory ranges from 0.15 to 0.25 ha (Furness 1987) equating to 11.4 and 18.8 ha for the total skua colony (75 AOTs). The N input density (after removing the volatilised fraction) is thus estimated to be 136.1 to 166.3 kg N $ha^{-1}$ for puffins and 10.5 to 17.2 kg N $ha^{-1}$ for skuas. The P input concentration is estimated at 26.9 to 32.8 kg P $ha^{-1}$ for puffins and 2.2 to 3.6 kg P $ha^{-1}$ and skuas. The area occupied by puffins surrounding the rest of Mingulay is unknown and therefore an island-wide estimate of the nutrient input density for all puffins is not calculated.

### 4.3.2 Sensitivity analyses

The sensitivity analysis showed that puffins and skuas shared the same most influential parameters. Causes of greatest change to the overall model output were the exponent, $F_{NC}$, $F_{PC}$, population size, assimilation efficiency and $F_{EC.}$ The skua model was additionally influenced by the multiplicand (Table 4.4, Table 4.5).

**Table 4.3.** The nitrogen and phosphorous input per individual and population per year on the colony for the Atlantic puffin and great skua. Mean ± S.D.

| | Nitrogen input (kg) | | Phosphorous input (kg) | |
|---|---|---|---|---|
| | Individual$^{-1}$ year$^{-1}$ | Population$^{-1}$ year$^{-1}$ | Individual$^{-1}$ year$^{-1}$ | Population$^{-1}$ year$^{-1}$ |
| Puffin | | | | |
| Chick | 0.12 ± 0.01 | 60.25 ± 7.86 | 0.02 ± 0.00 | 11.05 ± 1.46 |
| Non-breeder | 0.18 ± 0.03 | 41.03 ± 5.68 | 0.04 ± 0.00 | 8.16 ± 1.00 |
| Breeder* | 0.35 ± 0.05 | 248.64 ± 34.02 | 0.07 ± 0.01 | 49.48 ± 6.00 |
| Great skua | | | | |
| Chick | 0.34 ± 0.06 | 27.41 ± 4.44 | 0.07 ± 0.01 | 5.24 ± 0.84 |
| Fledgling | 0.10 ± 0.01 | 5.59 ± 0.80 | 0.02 ± 0.00 | 1.11 ± 0.14 |
| Non-breeder | 0.54 ± 0.1 | 13.32 ± 2.42 | 0.11 ± 0.02 | 2.65 ± 0.45 |
| Breeder* | 1.08 ± 0.19 | 80.73 ± 14.55 | 0.21 ± 0.04 | 16.27 ± 2.71 |

*In summation of the total nutrient input, the breeder input is to be multiplied by two to account for both parents.

**Table 4.4.** Sensitivity analysis for the bioenergetics model for the Atlantic puffin. Parameters are ranked on the overall change caused by a 1 % increase. The overall change represents the mean change of each component's sensitivity. * denotes a parameter not applicable to that component. Values included are analysed with outputs for N, except for $F_{PC}$ which is modelled with P outputs.

| Parameter | % change in output from 1 % increase | | | | Range of parameter extremes | % change following parameter extremes | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Breeder | Non-breeder | Chick | Overall change | | Breeder | Non-breeder | Chick | Overall change |
| Exponent | * | * | 6.183 | 1.065 | ± 10 | * | * | 82.439 | 14.196 |
| $F_{NC}$ | 0.996 | 0.996 | 0.997 | 0.996 | ± 10 | 10.024 | 10.011 | 9.992 | 10.017 |
| Population | 0.989 | 0.993 | 0.987 | 0.989 | ± 10 | 10.021 | 10.012 | 9.996 | 10.016 |
| $F_{PC}$ | 0.979 | 0.980 | 0.990 | 0.981 | ± 10 | 10.003 | 10.009 | 9.992 | 10.002 |
| Adult FMR | 0.992 | 0.996 | * | 0.821 | ± 10 | 10.057 | 10.046 | * | 8.324 |
| Departure date | 0.985 | 0.983 | * | 0.815 | ± 10 | 9.984 | 9.976 | * | 8.264 |
| $F_{tc}$ | 0.981 | 0.983 | * | 0.812 | ± 10 | 10.024 | 10.019 | * | 8.297 |
| Body mass | * | * | 1.049 | 0.181 | ± 10 | * | * | 10.631 | 1.831 |
| Multiplicand | * | * | 1.007 | 0.173 | ± 10 | * | * | 9.990 | 1.720 |
| Productivity | * | * | 0.997 | 0.172 | ± 10 | * | * | 10.000 | 1.722 |
| Population Non-breeder: Breeder Ratio | * | 1.005 | * | 0.118 | ± 50 | * | 46.889 | * | 5.498 |
| $F_{hab}$ | -0.101 | -0.100 | * | -0.083 | ± 10 | -0.877 | -0.887 | * | -0.727 |
| $F_{NV}$ | -0.112 | -0.108 | 0.001 | -0.092 | ± 40 | -3.431 | -3.441 | 0.002 | -2.841 |
| Arrival date | -1.004 | -1.005 | * | -0.831 | ± 10 | -9.967 | -9.974 | * | -8.252 |
| $F_{EC}$ | -0.992 | -0.989 | -1.006 | -0.994 | ± 10 | -9.070 | -9.074 | -9.091 | -9.074 |
| $A_{effic}$ | -0.993 | -0.997 | -1.020 | -0.998 | ± 8 | -7.381 | -7.388 | -7.439 | -7.391 |

**Table 4.5.** Sensitivity analysis for the bioenergetics model for the great skua. Parameters are ranked on the overall change caused by a 1 % increase. The overall change represents the mean change of each component's sensitivity. * denotes a parameter not applicable to that component. Values included are analysed with outputs for N, except for $F_{PC}$ which is modelled with P outputs. BR = Breeder, NB = Non-breeder, FL = Fledgling.

| Parameter | % change in output from 1 % increase | | | | | Range of parameter extremes | % change following parameter extremes | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Breeder | Non-breeder | Chick | Fledgling | Overall change | | Breeder | Non-breeder | Chick | Fledgling | Overall change |
| Exponent | 5.767 | 5.761 | 7.737 | * | 5.938 | ± 10 | 75.504 | 75.511 | 111.075 | * | 79.859 |
| $F_{PC}$ | 1.010 | 1.003 | 0.993 | 1.024 | 1.007 | ± 10 | 11.071 | 11.076 | 11.117 | 11.097 | 11.083 |
| Population | 1.003 | 0.997 | 1.004 | 0.989 | 1.002 | ± 10 | 10.014 | 10.008 | 10.005 | 10.019 | 10.012 |
| $F_{NC}$ | 0.993 | 0.988 | 1.002 | 0.989 | 0.994 | ± 10 | 11.071 | 11.076 | 11.117 | 11.097 | 11.083 |
| Multiplicand | 0.994 | 0.995 | 0.982 | * | 0.948 | ± 10 | 10.020 | 10.018 | 10.007 | * | 9.576 |
| Departure date | 0.989 | 0.984 | * | * | 0.732 | ± 10 | 9.979 | 9.970 | * | * | 7.386 |
| Adult BMR:FMR ratio | 0.968 | 0.966 | * | * | 0.716 | ± 10 | 10.026 | 10.021 | * | * | 7.422 |
| $F_{tc}$ | 0.949 | 0.944 | * | * | 0.702 | ± 10 | 9.991 | 9.985 | * | * | 7.396 |
| Body mass | 0.742 | 0.734 | -0.002 | * | 0.548 | ± 10 | 7.682 | 7.682 | 10.674 | * | 7.990 |
| Mean brood size 20 days | * | * | 0.917 | * | 0.198 | ± 10 | * | * | 9.538 | * | 2.058 |
| Population NB:BR Ratio | * | 0.962 | * | * | 0.101 | ± 50 | * | 50.008 | * | * | 5.243 |
| Time on colony post-fledging | * | * | * | 1.977 | 0.087 | ± 10 | * | * | * | 10.017 | 0.440 |
| Mean FL brood size | * | * | * | 1.968 | 0.087 | ± 10 | * | * | * | 10.010 | 0.440 |
| BMR FMR:FL FMR ratio | * | * | * | -0.035 | -0.002 | ± 10 | * | * | * | -9.082 | -0.399 |
| $F_{hab}$ | -0.090 | -0.095 | -0.054 | -0.091 | -0.083 | ± 10 | -0.865 | -0.868 | -0.434 | -0.859 | -0.772 |
| $F_{NV}$ | -0.099 | -0.097 | -0.044 | -0.095 | -0.087 | ± 40 | -3.462 | -3.465 | -1.744 | -3.456 | -3.092 |
| Arrival date | -0.992 | -0.998 | * | * | -0.735 | ± 10 | -9.980 | -9.984 | * | * | -7.389 |
| $A_{effic}$ | -1.014 | -1.015 | -0.995 | -1.029 | -1.010 | ± 8 | -7.385 | -7.387 | -7.410 | -7.394 | -7.391 |
| $F_{EC}$ | -1.026 | -1.029 | -0.994 | -1.020 | -1.019 | ± 10 | -9.094 | -9.099 | -9.098 | -9.105 | -9.096 |

## 4.4 **Discussion**

This study estimates the mass of N and P, which puffins and skuas deposit seasonally through their guano into their colony on the island of Mingulay. The model showed uncertainty with each estimate reflecting variability in input parameter values. Greatest uncertainty in model outputs arose from variation in estimates of FMR, food nutrient and energy content, assimilation efficiency and population estimates.

### 4.4.1 Model performance

Prior to the discussion of any inferences derived from this study it is important to consider the accuracy of the bioenergetics model. The sensitivity analysis indicated those parameters which caused the greatest change on the model output, following a 1 % increase in initial parameter values.

Estimation of BMR (through primarily the exponent and also the multiplicand for skuas) yielded the greatest inaccuracy. Estimation of metabolic rates is frequently associated with uncertainty as reported in other studies (Phillips *et al.* 1999, Votier *et al.* 2004, Miles 2010). Estimation of BMR in this study was taken from equations specific to skuas in Scotland (Bryant and Furness 1995) and can be considered appropriate for skuas in this study. However, an error of two percent in estimating the exponent of BMR for skuas will increase or decrease the model output by up to 12 %. This consequently highlights the importance of this value in the error surrounding estimates of nutrient input. The FMR value used for the puffin is taken from the literature, where the value was derived from studies using doubly-labelled water (Ellis and Gabrielson 2002). Variation in the estimate of puffin FMR was not reported within Ellis and Gabrielson (2002); subsequently caution should be exercised given the potential specificity in parameters with latitude (Bryant and Furness 1995).

Other parameters causing uncertainty in the amount of nutrients deposited include estimates of breeding population size and food nutrient content ($F_{NC}$ and $F_{PC}$). Estimates of breeding population size for both species were undertaken following standardized methods (Walsh *et al.* 1995) and often at a greater resolution than necessary for accurate estimates of population size. Although all estimates of a population are subject to uncertainty, the error is considered small for skuas given the intensity of surveys and the ability to determine territory occupancy. For puffins, however determination of an occupied burrow is difficult and varies over time and between observers (Anker-Nilssen and Røstad 1993, Harris and Wanless 2011). For puffins, error with estimation of colony size was minimized by inter-observer standardisation and repeat counts. When considering the island population estimate the error could feasibly vary by up to ~ 30 % (pers. obs. and pers. comm., Rob Dunn 2014). This variation in population size would result in an input of 6.4 to 11.9 tonnes N and 1.2 to 2.2 tonnes P, for the whole island.

The value of food N content for this study is used widely within other studies (Furness 1991, Wilson *et al.* 2004a) and comparable to the N content of a wide range of fish species (Cherel and Ridoux 1992, Brekke and Gabrielsen 1994, Hilton *et al.* 2000b), which puffins and skuas are recorded to eat. Puffins on Mingulay were noted to ingest only fish, predominantly sandeels (assumed to be the lesser sandeel *Ammodytes marinus*) with a small proportion of gadid species (*c.* 1 % gadid; pers. obs.). Skuas were noted, on average, to ingest predominantly fish (~ 80 %), seabirds (~ 13 %) and lesser proportions of goose barnacle *Lepas* spp. (~ 1 %) and rabbit *Oryctolagus cuniculus* (~ 6 %, pers. obs.). Therefore, whilst estimates of N content of puffin prey are appropriate, the inclusion of ~ 20 % non-fish prey in the skua's diet introduces error. Determination of the skua diet was not considered for this study accurate enough to differentiate between prey taxa, and consequently skuas are assumed to only ingest fish, which will influence estimates of N and P input. Estimates of P content are less widely cited, compared to N, and whilst the estimate for fish at 0.006 g P $g^{-1}$ wet mass is cited, the variation is uncertain (Furness 1991). The P content will vary by fish and seabird prey species (Williams *et al.* 1978). Miss-estimations of assimilation efficiency and food energy content were both parameters which resulted in a considerable change in N and P input for both species' nesting habitat. This sensitivity of nutrient input to variation in assimilation efficiency and food energy content arises because it affects the mass of food needed. Assimilation efficiency for both species was measured using controlled captive feeding trials and was therefore considered accurate (Phillips *et al.* 1999, Hilton *et al.* 2000a). $F_{EC}$ for skuas was considered as an average of the $F_{EC}$ of the prey types encountered by skuas (sandeel, whiting and other seabirds), whilst the $F_{EC}$ of the puffin's prey was based upon a diet of only lesser sandeel (Phillips *et al.* 1999, Hilton *et al.* 2000b). $F_{EC}$ values for rabbit are within the range of values considered for fish and seabirds and are therefore treated the same (Votier *et al.*

2004). It is important to note also that the values reported for $F_{EC}$ could also be subject to temporal variation and the size of prey item returned (Hislop *et al.* 1991).

Other parameters within the model having a lesser effect on the overall model output are discussed below. Body mass values are taken from the literature and considered representative of the size of the species (Wilson *et al.* 2004a). The time an individual spends at the colony ($F_{tc}$) is based upon values from Wilson *et al.* (2004b, 2004a), although their study provides little reasoning for the times chosen. $F_{tc}$ is thus perhaps considered an important component of how much nutrient is deposited. Increasing the estimated proportion of time, for example breeding puffins spend on land from 0.3 to 0.4 could potentially increase the mass of nutrient deposition by ~ 28 %. The uncertainty around this value is particularly pertinent given the variation in attendance attributed to puffins (Harris and Wanless 2011). A value of 0.6 $F_{tc}$ for adult skuas can be considered more appropriate, given less variability in attendance, relative to puffins, although attendance is for both species, dependent upon criterion such as time spent foraging, synonymous with prey availability (Caldow and Furness 2000, Barrett 2002). Furthermore, the arrival and departure dates for skuas are considered similar to that of puffins (Wilson *et al.* 2004a), although the variation between the two species is unquantified in this study. Equally, there is an unaccounted proportion of failed breeders, which will influence their total time spent on the colony. Given the relative insensitivity to these parameter input values and the same breeding period as considered in prior models (Wilson *et al.* 2004a) the effect on model output is likely to be minimal. Adult skua BMR:FMR ratios chosen for this study were from published values, calculated specifically for this species (Votier *et al.* 2004).

Changing parameter values from their initial value by 1 % or their extreme resulted in the same parameters being still considered the most influential on the overall model output. Assimilation efficiency was modelled with ± 8 % as this reflects the typical range observed from other bird species (Phillips *et al.* 1999). However, assimilation efficiency is proportionately still influential on the model output. The ratio of adult breeders to non-breeders was set high (± 50 %) to accommodate uncertainty in the size of the non-breeder population for both species. Although this produced a noticeably higher input from non-breeding individuals, the overall change in nutrient input when combining all components of the model was comparatively minor. Furthermore, $F_{NV}$ was set at ± 40 % to accommodate the uncertainty within the original source (Blackall *et al.* 2004). However, the overall change to the model output was relatively minor inferring that this parameter does not strongly influence the remaining N input. $F_{hab}$ is an additional parameter with values taken from the literature (Wilson *et al.* 2004a) with little influence on the model output for both species.

Calculation of the overall change in the sensitivity analysis is an average across each component. Therefore, individual components may have large changes within the sensitivity analysis but the overall input may be relatively insignificant (Table 4.4, Table 4.5). Therefore, those parameters which affect multiple components are likely to have a greater effect compared to parameters influencing a lesser number of components. Consequently, the puffin productivity, the puffin and skua ratio of adult to non-breeders, the time skuas spent on the colony post-fledging and the skua mean brood size at 20 days and fledging appear influential when considering each component individually. However, their relative effect upon the overall model is relatively minor given the overall effect of all components together.

It is also important to note that the sensitivity analyses use the value of nitrogen concentration ($F_{NC}$) to estimate model uncertainty, except for $F_{PC}$ where the concentration of P is used. Therefore, there is an assumption that the model output for N is similar to P. Although, there is a non-linear component to the models its influence is considered minor overall and therefore the uncertainty associated with P is likely to be within the error induced from the stochastic nature of the models in general.

Overall, the greatest sources of inaccuracy are the same as those encountered in prior bioenergetics models (Phillips *et al.* 1999, Votier *et al.* 2004, Miles 2010). The P content within a range of prey is one source of error which could be improved along with estimates of $F_{tc}$. Improving parameters with most error and considering the specificity of some parameters, *e.g.* metabolic rates with latitude (Bryant and Furness 1995) could allow this model to be applied to other seabird sites in Scotland.

### 4.4.2 Comparative seabird inputs

Other factors not considered within this model which could influence nutrient deposition on Mingulay include the contribution from other seabird species and the non-guano input of nutrients from re-deposition of volatilised ammonia and inputs such as prey remains and carcasses.

To put into context the relative input of nutrients from puffins and skuas, the nutrients input from other seabird species are discussed. Using the methods and parameter values, given in Wilson *et al.* (2004a) along with the population estimates of all seabird species on Mingulay, the combined input across all species amounts to ~ 56.0 tonnes N (without removal of the fraction volatilised) and ~ 9.3 tonnes P. Therefore, puffins input ~ 16.5 % and skuas input ~ 0.4 % of the total island input, when considering whole island populations. When considering the sub-colony of puffins this population produces ~ 1.2 % of the nutrient input for the total island seabird input. Therefore, the input of nutrients from this sub-colony is relatively minor, given an island scale. However, considering the puffins' island population, their input is quite substantial, representing approximately a sixth of the island's seabird nutrient input from across nine seabird species.

As the area of the whole population of puffins cannot be accurately estimated on Mingulay, the sub-colony of puffins is used and is estimated to input 0.14 to 0.17 tonnes N ha$^{-1}$ yr$^{-1}$, whilst the skua population inputs 0.11 to 0.17 tonnes N ha$^{-1}$ yr$^{-1}$. Blackall *et al.* (2007) estimate that the puffin population on the Isle of May (42,000 pairs), Firth of Forth, inputs 1.4 tonnes N ha$^{-1}$ yr$^{-1}$, although this also considers the input from common guillemot and black-legged kittiwake populations. The Bass Rock, Firth of Forth, with 44,110 pair of Northern gannet *Morus bassanus* inputs 52.2 tonnes N ha$^{-1}$ yr$^{-1}$ (Blackall *et al.* 2007). Estimates of the density of P inputs are not given within the study by Blackall *et al.* (2007). Other studies for other seabirds report rates as high as 114 tonnes N ha$^{-1}$ yr$^{-1}$ for Macaroni penguins *Eudyptes chrysolophus* (Riddick *et al.* 2012) to lower inputs of 1.0 tonne N ha$^{-1}$ yr$^{-1}$ for white-capped noddies *Anous minutus* (Schmidt *et al.* 2010). Comparatively, the density of guano-N input on Mingulay from puffins and skuas is thus relatively low in comparison to other studies, although relative comparisons are limited by both species and population density. The low nutrient input density for puffin and skuas on Mingulay is likely to be attributable to their low nesting density and relatively low nutrient input in relation to the larger seabird species, *e.g.* Northern gannet.

The deposition of guano and its effect on land is also dependent upon the receiving substrate. Bare-rock breeders, *e.g.* cliff-nesting common guillemots, are likely to have a larger proportion of guano washed away through rainfall or have N volatilised and lost as

N-$NH_3$, compared to vegetated colonies (Blackall *et al.* 2007). The $F_{\text{hab}}$ and $F_{\text{NV}}$ in this model take into consideration habitat type and the fraction lost through volatilisation and the sensitivity analysis showed these parameters to have little influence on the model output. Furthermore, the variation in nesting topography of puffins will influence deposition; steeper slopes are likely to receive less guano from aerial deposition as a greater proportion will fall directly into the sea. However, the studied puffin colony is relatively flat, so most guano is considered deposited onto land in relation to model parameters.

An unknown source of error is the assumption that seabirds are in nutrient balance, so that N and P intakes equal the N and P excreted in guano (Furness 1991). Whilst this is deemed reasonable for adults (Wilson *et al.* 2004a, 2004b), the validity of this assumption for chicks is unknown where N and P are likely to be incorporated into body mass during chick growth. Although the contribution of nutrients from chicks and fledglings is very much less than from adults, their influence on the total nutrient input can be construed as quite significant. Assuming a 50 % incorporation of nutrients into chick/fledgling growth (Wilson *et al.* 2004a) would reduce the total nutrient input by ~ 5.5 and 7.8 %, for puffins and skuas, respectively.

Only guano was considered as an input of nutrients onto Mingulay; however, it must be appreciated that seabirds can input nutrients in other forms. For example, nutrients can be further input through eggs (Siegfried *et al.*, 1978), feathers (Williams and Berruti, 1978; Smith, 2008), carrion (Ellis, 2005), drip from the nasal salt glands (Sobey and Kenworthy, 1979), pellets and carcasses of chicks and adults (Williams *et al.*, 1978). It is likely that the nutrient input from puffins, excluding guano, is relatively minimal, given very little remains of prey or carcasses were found within the colony (pers. obs.). Neither skuas nor puffins moult feathers while breeding, so deposition from feathers would be minimal, involving the occasional accidental loss of a few feathers. Given puffin productivity was estimated at 0.73, it can be surmised that 27% of eggs or chicks died and thus nutrients from this source could be considered as input. This would equate for the sub-colony to be 191 eggs or chicks, dependent upon developmental stage, calculated by taking 27 % of the number of the number of breeding pairs. Siegfried *et al.* (1978), from 12 Antarctic seabird species, estimated that 0.0099 kg N bird$^{-1}$ and 0.0076 kg P bird$^{-1}$ is input from lost and/or failed eggs. Assuming the work of Siegfried *et al.* (1978) is comparable to Northern hemisphere species and populations then the eastern puffin colony would receive

~ 1.9 kg N and 1.5 kg P per season from lost and/or failed eggs. Skuas, however, could be viewed as having a larger input of non-guano nutrients as a considerable quantity of prey remains were observed within territories (pers. obs.). This could thus represent a large source of nutrient input, which is not considered within this study. Furthermore, carcasses and eggs from failed breeding of skuas would again contribute to nutrient input; however, consumption of carcasses or eggs by scavenging skuas would lead to the introduction of error within the model by over-estimating nutrient input. The nutrient input from chicks of both species, which did not successfully fledge is not included within this model. Chick-rearing can take up to 44 days for puffins (Harris and Wanless 2011), so assuming that 27 % of the chicks die on the day of fledging (which could be considered itself overly-conservative) then this would contribute a maximum 3.7 % and 3.1 % more N and P, respectively. The productivity of skuas is not known on Mingulay and their contribution from unsuccessful fledglings, lost and/or failed eggs cannot be estimated. It can however be surmised that any nutrient input directly from guano onto Mingulay should not be considered as the total annual input but as a minimum.

The deposition of volatilised ammonia, either from within Mingulay or from the neighbouring island of Berneray (*c*. 700 m to the south; 26,000 razorbill and 37,000 common guillemots) can also be considered a large source of N input that is not considered within this model. Again, using the values of Wilson *et al.* (2004a) and scaling up their estimates of volatilised N for all breeding species on Mingulay results in the volatilisation of ~ 13.3 tonnes $NH_3$ $yr^{-1}$. This volatilised component is likely to be subtracted from the total island guano input (56.0 – 13.3 = 42.7 tonnes N $yr^{-1}$); however, a proportion of $NH_3$ will be re-deposited depending upon weather, source magnitude and local topography (Wilson *et al.* 2004a). Furthermore, Berneray, the neighbouring island to Mingulay is also estimated to produce 2.5 tonnes $NH_3$ $yr^{-1}$, which could also be deposited upon Mingulay. The exact fraction of guano which will be deposited onto the studied habitats of the puffin and skua colonies is unknown. Blackall *et al.* (2007) showed that at ~ 2 km from a seabird colony the ammonia emissions come close to zero. The studied puffin colony on the eastern side of Mingulay is ~ 2 km away from the majority of seabird population, although the skua population is within 2 km. It is therefore likely that the skua colony will include a larger fraction of volatilised N-$NH_3$, relative to the puffin sub-colony, although the difference between habitats is unknown (Wilson *et al.* 2004a).

Within the model, certain aspects of seabird ecology were not considered. Egg production costs were considered low and thus not incorporated into adult activity and maintenance requirements (Phillips *et al.* 1999). Specialisation of skuas in terms of their prey was not considered and an average value of a range of diets was considered given a lack of detailed diet data for Mingulay. Variation in diet between skua colonies (Furness 1987) restricts comparisons with other colonies. Separation of the season into different periods based upon breeding, *i.e.* pre-breeding and chick-rearing periods, was not considered within this model as they have been observed to have relatively little impact upon prior bioenergetics models (Phillips *et al.* 1999).

Male and female breeding puffins and skuas are estimated to deposit the same quantity of nutrient, however given the slight differences in size between the sexes there may be differences in nutrient deposition between sexes, which is not considered (Hamer and Furness 1991, Harris and Wanless 2011).

### 4.4.3 Non-seabird inputs

The input of N and P onto Mingulay from puffins and skuas represents a percentage of the total deposition of 42.7 tonnes N (excluding the volatilised component) and 9.3 tonnes P input across all seabirds. However, the magnitude of this input in relation to non-ornithogenic inputs is not considered. The following sections details the relative input of nutrients in comparison to other sources of nutrient deposition, such as biological nitrogen fixation and agricultural activities.

The main natural processes of N fixation arise from either lightning or a process of biological N fixation (BNF), dominated by bacteria in the soil or in symbiosis with leguminous plants (Galloway *et al.* 2004). On Mingulay for example, a 35 % cover of leguminous plants (*i.e. Trifolium* spp., unpubl. data) in the eastern puffin colony (assuming a mean area of 4 ha from the range 3.6 – 4.4 ha) could have a transfer rate of atmospheric N to reactive N from 1 x $10^4$ to 2 x $10^4$ mg N m-$^2$ (Galloway *et al.* 2004), which would result in the annual input by BNF of 140 to 280 kg. The maximum input is about half of the N from puffin guano in the studied colony. Considering annual BNF across the island (640 ha) and assuming half the island is heather moorland (with 4 % *Trifolium* spp. cover, pers. obs.) then N input from BNF would be 1 to 3 tonnes. Equally, with the same percentage cover of *Trifolium* for non-heather moorland habitat as the puffin colony, N input from BNF would be ~ 11 to 22 tonnes. The total input across all habitats on Mingulay thus equals 12 to 23 tonnes N, which exceeds the whole island input of N from puffins by more than double, assuming the maximum input from BNF. However, this input of BNF is approximately half of the total N input from all seabirds on Mingulay, assuming again the maximum input from BNF. Consideration must also be given to variation in the percentage cover of *Trifolium* spp. and also the input from other leguminous plants, *e.g. Lotus corniculatus*. Input from soil bacterial BNF is unknown and also input from lightning is unknown as rates of lightning were not quantified.

Input of N compounds onto Mingulay from anthropogenic sources is considered to be zero. Agricultural fertilization is no longer undertaken and the wet and dry deposition of N compounds onto Mingulay from external anthropogenic sources is considered conservatively minimal, if not zero, given its relative isolation. Non-seabird inputs of P arise primarily through weathering of primary and secondary minerals, which for this study is unknown (Frossard *et al.* 1995). Given that P is often limited and that there are very few non-seabird inputs of P then *in situ* production is considered minimal (Frossard *et al.* 1995).

In comparing the input of nutrients onto Mingulay with agricultural fertilization rates it can be shown that seabirds represent a significant factor in affecting the island environment. The maximum suggested input of N in fertilization for a range of agricultural land on largely organic soils is ~120 kg N ha$^{-1}$ (DEFRA 2010). However, given the considerable peat fraction within the skua colony the input from an agricultural aspect is likely to reduce to ~80 kg N ha$^{-1}$ (DEFRA 2010), which still falls within the range for intensive agricultural fertilization (60 to 400 kg N ha$^{-1}$) (Pearson and Stewart 1993, Young *et al.* 2010). For P the suggested concentration within fertiliser (in the form of phosphate) is ~ 53 to 113 kg P ha$^{-1}$ for soils which are considered relatively unresponsive to application and deficient, respectively. Above these values, the application of N and P is often considered in excess and damaging to the water environment and to the surrounding biodiversity (DEFRA 2010, Young *et al.* 2010). The results showed that N input from puffins exceeds the suggested maximum N application of 120 kg N ha$^{-1}$ (given the decreased peat content) by 113 to 139 % for peaty soil, using the range of estimated puffin colony areas. The input of P for the larger puffin colony size (4.4 ha), is estimated at 24 to 51 % of the suggested P application, whilst for the smaller estimated colony area (3.6 ha) the P input is 29 to 62 % of the suggested maximum P application. The N input from skuas is 14 to 22 % of the suggested maximum N application when considering a total colony area of 11.4 ha and a variable peat fraction. When considering the larger total colony area for skuas the N input is 9 to 14 % of the suggested maximum N application. The input of P for the larger skua colony size (18.8 ha), is estimated at 2 to 4% of the suggested P application, whilst for the smaller estimated colony area (11.4 ha) the P input is 3 to 7 % of the suggested maximum P application.

For skuas, the territory size used here is likely to be conservative and guano deposition is unlikely to be uniform across the territory with a large proportion of guano observed to be deposited proximal to the nest. Consequently, it is likely but unquantified that the nutrient input density is greater than calculated here for a smaller area in which guano is deposited.

Overall, the input of nutrients by puffins and skuas can be considered to be less than the production of N from BNF across Mingulay. However, consideration of the input of nutrients from all seabirds on Mingulay shows that their input is likely to be the largest source of nutrient onto Mingulay each year.

### 4.4.4 Conclusions

This study shows that the eastern puffin colony and the skua population through their guano alone deposit seasonally onto Mingulay an estimated 0.9 tonnes of N and 0.16 tonnes of P. This input represents a minimum density of approximately ~ 136 kg N ha$^{-1}$ yr$^{-1}$ and ~ 27 kg P ha$^{-1}$ yr$^{-1}$ for puffins. For skuas, this represents ~ 11 kg N ha$^{-1}$ yr$^{-1}$ and ~ 2 kg P ha$^{-1}$ yr$^{-1}$. In comparison to other colonies and for other seabird species, these inputs for N are comparatively low. However, when considering the input of nutrients on Mingulay from all seabirds, including the entire puffin population, then the estimated input is much greater at 42.7 tonnes N (excluding the fraction volatilised) and 9.3 tonnes P.

In relation to other sources of nutrient input such as biological nitrogen fixation from leguminous plants the input from puffins and skuas can be considered comparatively equal. However, the input from all seabirds on Mingulay is likely to far outweigh nitrogen fixation. Furthermore, the deposition of $NH_3$ from neighbouring islands and the re-deposition of $NH_3$ on Mingulay all add to the input of N by seabirds. It can therefore be considered that the input of nutrients onto Mingulay from seabirds including re-deposited $NH_3$ is likely to be the largest input of N annually. Given low concentrations of P naturally, the input of seabird nutrients is likely to represent a significant source; however the non-seabird input of P remains difficult to estimate.

The generality of this model could easily be extended by altering a few parameters, *e.g.* population size, to model nutrient input on other seabird-influenced systems. Improving estimates of sensitive model parameters is one area for increasing the accuracy of this model. Further research should focus upon the fate of deposited nutrients both within and proximal to seabird islands, as transported nutrients may well induce local changes to communities both directly and indirectly (Polis and Hurd 1996). Although outside the scope of this study, the seasonal input of ornithogenic nutrients onto Mingulay is likely to have significant impacts upon the recipient system (Mulder *et al.* 2011).

# Chapter 5

# The influence of Atlantic puffins *Fratercula arctica* and great skuas *Stercorarius skua* on Scottish islands

# Abstract

The input of nutrients onto island systems from seabirds can play an important role in driving terrestrial community dynamics. However, studies are limited by the appreciation of the wider influence which seabirds may exert on island food webs. In this study the effects of ornithogenic inputs on island food webs are tested by examining changes in plant community structure, plant productivity and the chemical content of grasses. Furthermore, to test whether seabird inputs flow throughout island food webs and into secondary consumers, samples of hair from rabbit and sheep are tested for their nitrogen stable isotope ratio. This study looks at colonies of Atlantic puffins *Fratercula arctica* and great skuas *Stercorarius skua* on three different islands around Scotland. The results of this study showed that seabirds are likely to alter plant community composition and puffins are observed to potentially increase plant productivity, relative to areas without seabirds. Chemical analyses showed that samples of a single species of grass, *Holcus lanatus*, and composite samples of grass were all significantly enriched in $^{15}$N and also had a higher N concentration within puffin and skua colonies, relative to areas without seabirds. Equally, rabbits and sheep found foraging within puffin colonies were also significantly enriched in $^{15}$N, relative to areas without seabirds. This study thus indicates for the first time the transfer of nutrients from seabirds into rabbits and sheep, via ornithogenic forage. The implications of this study have important consequences for the range of species possibly connected and dependent upon the temporal nutrient subsidy provided by seabirds. Although, not studied the flow of nutrients into herbivores may alter their productivity and behaviour, by the provision of improved forage. Overall, the results indicate that seabirds influence a range of species on Scottish islands and this could play a large role in influencing island food webs.

## 5.1 Introduction

The cross-scale interaction of nutrients and organisms between ecosystems can drive community dynamics and influence ecosystem processes (Knight *et al.* 2005, Peters *et al.* 2007, Bultman *et al.* 2014). The transfer of nutrients from the marine environment onto land represents a significant interaction, which can shape terrestrial communities (Croll *et al.* 2005, Ellis 2005). Nutrients are transferred onto land through primarily biotic vectors, such as seabirds and marine mammals, but also through abiotic deposition of organic material, *e.g.* from wind and tides (Polis and Hurd 1996, Havik *et al.* 2014).

Seabirds are one of the main biotic vectors responsible for transporting large quantities of nutrients onto land (Kolb *et al.* 2012). Seabirds forage over a large marine area and concentrate nutrients onto their nesting sites primarily in the form of guano but also through prey remains, eggs, feathers and carcasses (Siegfried *et al.* 1978, Kolb *et al.* 2012). This biotic deposition has been shown to enrich nitrogen (N) and phosphorous (P) content of local soil  and foliage, as well as altering diversity, enriching plant communities in $^{15}$N and influencing island consumer abundance (Sanchez-Piñero and Polis 2000, Polis *et al.* 2004, Ellis 2005, Ellis *et al.* 2006, Kolb *et al.* 2012). Furthermore, seabirds can physically disturb vegetation and soils, which alters plant composition and structure, and changes substrate chemistry and stability (Bancroft *et al.* 2005b, 2005a, Ellis 2005).

The effect of seabirds on altering soil chemistry, increasing primary productivity and concentrating foliar N content can influence surrounding communities by permeating throughout food webs (Harding *et al.* 2005, Fukami *et al.* 2006). For example, increased foliar N content, and thus nutritional quality, can lead to greater levels of herbivory (Mattson 1980). Increased vegetation quality can fuel communities of detritivores and herbivores (Sanchez-Piñero and Polis 2000), which in turn can benefit their predators (Stapp and Polis 2003). These studies demonstrate the importance of understanding how seabirds influence terrestrial ecosystem functioning. It is important to recognize the extent of trophic enrichment from seabirds by exploring and generalising current studies to other systems and species.

Most studies on the influence of nutrient input from marine to terrestrial systems have focussed upon insects and small mammals, in particular rodents (Stapp *et al.* 1999, Stapp 2002, Caut *et al.* 2012, Callaham *et al.* 2012), with few studies looking at the influence of seabirds on larger mammalian herbivores, such as ungulates. The only two known studies on ungulates document how seabirds support deer populations through provision of rich, ornithogenic pasture (Jakubas *et al.* 2008) and subsequent increased reproductive success (Iason *et al.* 1986), both as a result of guano-derived nutrient input. Furthermore, there is a disproportionately large number of studies focussing upon seabird trophic interactions at low latitude insular systems, *e.g.* islands in the Gulf of California (Polis and Hurd 1996, Anderson and Polis 1999, Sanchez-Piñero and Polis 2000, Wait *et al.* 2005, Ellis 2005), despite the considerably larger populations of seabirds at higher latitudes (Lloyd *et al.* 2010). There is therefore a need to explore how seabirds at high latitudes influence their environment and the extent to which their presence permeates the surrounding community.

The use of stable isotopes, *e.g.* $\delta^{15}$N, is a tool frequently used in ecology to explore trophic interactions and the flow of nutrients within ecological systems (Michener and Lajtha 2007). The study of $\delta^{15}$N values from different positions within trophic chains can elucidate the potential connections of nutrient and energy transfer, such as the direct predation of seabirds by rats (Stapp 2002) and the transfer of marine nutrients from shearwaters into vegetation and earthworms (Callaham *et al.* 2012).

In general, consumers assimilate the heavier $^{15}$N isotope preferentially to the $^{14}$N isotope of nitrogen leaving their tissues enriched in $^{15}$N, relative to that of their food (Hobson *et al.* 1994, Ayliffe *et al.* 2004, Passey *et al.* 2005). Consequently, herbivores feeding upon vegetation, which is itself enriched from seabird guano, should have hair enriched in $^{15}$N relative to herbivores feeding outside seabird-influenced areas. Rabbit *Oryctolagus cuniculus* and sheep *Ovis aries* are relatively confined to hefts or local home ranges (Myers and Poole 1963, Coulson *et al.* 1999, Devillard *et al.* 2008) and this behaviour allows for a natural comparison within an island of the stable isotope ratio of herbivores confined within seabird areas and those outwith.

The influence of seabirds on island communities is thus tested by studying the vegetation composition within and outwith seabird colonies. It is predicted that the presence of seabirds should influence floral diversity and increase primary productivity by the deposition of guano-derived nutrients. To test if primary productivity increases within an Atlantic puffin *Fratercula arctica* colony, relative to a control site, a manipulative experiment was established on Mingulay in the Outer Hebrides. Exclosures were established to examine how vegetation growth, as a proxy for primary productivity, is influenced by seabirds without the presence of grazing rabbits. Equally, if vegetation growth does increase within a seabird colony it might be expected that herbivore populations will be greater within the puffin colony, relative to control areas. To test this proposition, a separate study was established to look at how the numbers of rabbit droppings, as a proxy for population size, differed between a puffin colony and a control site (Wood 1988, Forys and Humphrey 1997, Palomares 2001).

To further examine how plants are influenced by seabirds, samples of grass (*Holcus lanatus* and composite samples) were collected and analysed for their N content and $\delta^{15}$N value. Given the enrichment of $\delta^{15}$N values across trophic levels and with the influence of seabirds (Mulder *et al*. 2011) this study aims to show an enrichment of N content and $\delta^{15}$N values within grasses in seabird colonies, relative to areas without seabirds. The study further aims to show the transfer of nutrients from ornithogenic grasses into mammalian herbivores, by sampling hair from rabbit and Soay sheep. Samples of hair are predicted to be more enriched from within seabird sites, relative to areas without seabirds.

This study was conducted on sites influenced by two seabird species in Scotland, the Atlantic puffin and the great skua *Stercorarius skua* (hereafter referred to as “puffin” and “skua”, respectively). The skua and puffin were chosen as these species represent two different nesting habits, surface and burrow nesters respectively, and the islands studied hold populations with accessible colonies. Studies were conducted and samples collected from three Scottish islands: Mingulay and Hirta (St. Kilda), Outer Hebrides, and Fair Isle, Shetland. All three islands are inhabited by populations of mammalian herbivores (rabbit on Mingulay and sheep on the latter two islands), which allows for exploration of the influence of seabirds indirectly on herbivores. The islands also hold significant populations of seabirds and all are listed as Special Protection Areas (SPAs) under the EC Birds Directive 2009/147/EC for their assemblage of seabirds.

# 5.2 **Methods**

## 5.2.1 Study area and sampling design

This study was conducted on three Scottish islands in 2011 and 2012. Details of each island including locations, underlying geology (given its influence upon surface soils; Jewell *et al.* 1974) and broad vegetation type are summarised in Table 5.1 and Figure 5.1.

Mingulay is found at the southern tip of the Outer Hebrides and Hirta forms part of the St. Kilda archipelago, west of the Outer Hebrides. Fair Isle is located between mainland Shetland and Orkney. These three islands were chosen because of their assemblage of seabirds and herbivores, their remoteness and lack of agricultural practice within study areas. The islands' remoteness and limited agricultural influence reduces the chance of large anthropogenic N input masking the influence of the seabirds. Anthropogenic N input can arise through agricultural practices, *e.g.* fertilization, and non-agricultural practices, *e.g.* sewage treatment, industry and transport, including aerial deposition of gaseous emissions (Blackall *et al.* 2008). The prevailing south-westerly winds reaching the three islands (Irvine 1968, Owen *et al.* 2004) will limit the aerial deposition of anthropogenic emission given limited land and industrial activity upwind. None of the islands received fertilization from agricultural influence. Fair Isle does have limited farming practices; however they are in the south of the island and comprise crofts, which will limit any influence on studied vegetation in the north of the island. The Village Bay on Hirta was last cultivated *c.* 1930 (Jewell *et al.* 1974) and is not considered to influence the study. Mingulay was deserted *c.* 100 years ago and has had, until recent times, sheep present (Buxton 1995); the vegetation is not considered to be influenced by anthropogenic activity either.

For each of the three islands, a seabird (SB, site where seabirds bred) and control site (CTRL, site with no or very few breeding seabirds) were established for both the puffin and the skua (except for Fair Isle where only puffins were studied). SB and CTRL sites had similar vegetation structure and composition, aspect, topography and slope (Table 5.1). There were three SB and CTRL sites for puffins. On Mingulay the SB site was located on the east of the island (56˚48' N, 07˚37' W) and the CTRL site *c.* 250 m west and further inland from the puffin colony (56˚49’ N, 07˚38’ W). On Hirta the puffin colony was located on the west of the island at Carn Mor (57˚48’ N, 08˚67’ W) and the CTRL site was the grassland of the Village (57˚48’ N, 08˚34’ W). On Fair Isle, the SB site was found at Roskillie (59˚32’ N, 01˚36’ W) and the CTRL site was *c.* 200 m south and inland, both on sheep-grazed, semi-improved grassland.

Unlike puffins that breed in dense colonies, skuas breed on individual territories. Therefore skua SB sites were individual territories and CTRL sites were determined as areas between territories but not within 15 m of the boundary of any known skua nest and loafing spot. Skua nests and loafing spots were identified through the presence of a nest cup (with territorial signs of occupation) and discarded prey remains or regurgitated pellets (Walsh *et al.* 1995). On Mingulay the main skua breeding area was found in the north-west of the island. On Hirta, the skuas bred on the col between Conachair and Mullach Mor (57˚49’ N, 08˚34’ W).

## 5.2.2 Vegetation

### 5.2.2.1 Sampling design

To compare the vegetation communities of sites occupied by seabirds and adjacent sites without seabirds the vegetation was studied using 1 $m^2$ quadrats.

On Mingulay, the puffin SB and CTRL site quadrats were arranged in transects. Each site, SB and CTRL, had four transects arranged perpendicular to the puffin colony’s cliff edge. The four transects at both the puffin colony and control site were arranged into two pairs with *c.* 100 m between pairs in the puffin colony and *c.* 40 m between pairs in the control site. The two transects within each pair were separated by *c.* 10 m and each of the transects’ five quadrats were separated by *c.* 15 m. The design of paired transects was done in order to combine an assessment of diversity with an additional experiment on the change in vegetation growth using exclosures (see below).

Diversity within the skua colony and its respective control site on Mingulay was assessed in randomized quadrats. Quadrats within skua territories were chosen by numbering each territory and randomly drawing territory numbers. Skua control quadrats were chosen by randomly determining bearings and distances from the study site centroid under the condition that the selected point was at least 15 m from the nearest known nest or loafing site. Fifteen metres was subjectively chosen in order to limit the influence of skuas on surrounding vegetation through, for example, concentrated deposition of guano or physical disturbance. The vegetation studies took place on Mingulay from early June to mid-July 2012 (puffin and skua area) and at the end of May 2013 (puffin area only).

On Hirta and Fair Isle, given time constraints, vegetation composition was not studied. However, vegetation was sampled using randomized quadrats in the puffin and skua SB and CTRL sites using random distances and bearings chosen from the site's centroid to place quadrats. Skua territories were sampled, following the same approach on Mingulay of randomly choosing numbered territories.

#### 5.2.2.2 Indices of diversity

The quadrats used were subdivided into 100 equal cells of 10 cm$^2$ each and the presence of every plant species was recorded in each cell. This produced a measure of abundance as percentage presence for each plant taxa. Individual plants overlapping cells were recorded separately in each cell. All plants recorded in the field were identified to the lowest taxonomic level reliably determined. Most plants were identified to species level; however some plants were only identified to the level of genus *e.g. Carex* and *Euphrasia* (see Appendix II for a full list of species observed). Identification of plants was aided by using field guides (Hubbard 1992, Rose and O'Reilly 2006, Poland and Clement 2009).

The presence of a species in each of the 10 cm$^2$ cells allows for the richness and abundance of a site's species to be calculated. Abundance and richness can be used together within one index to quantify diversity (Whittaker 1960). Simpson's index was chosen as the use of natural logs in alternative indices, *e.g.* the information statistic of the Shannon-Weiner index, emphasises rare species, whilst Simpson's index squares the relative abundance and gives more weight to more dominant species (Nagendra 2002, Magurran 2004). This weighting of Simpson's index is additionally applicable as the measure of abundance used within this study, *i.e.* frequency, will over emphasise rare species and put less weight on more dominant species. Simpson's index therefore does not exacerbate sampling limitations within the analysis, relative to the Shannon-Weiner index.

Diversity values were calculated using the following equations:

$D = 1 - \sum_{i=1}^{S} p_i^2$ Simpson's index (Equation 5.1)

$E_{1/D} = \frac{(1/D)}{S}$ Simpson's measure of evenness (Equation 5.2)

where $p_i$ is the proportion of occurrences in the $i^{th}$ species; $S$ is the number of species (Krebs 1999, Magurran 2004). For purposes of analysis and interpretation the complement of Simpson's index is used, *i.e.* 1-*D*.

#### 5.2.2.3 Vegetation sampling

Given the study's aim to explore nutrient transfer within island food webs, in particular from seabirds, into vegetation and into herbivores, grass samples were collected as grass is often the most selected forage material of sheep and rabbits (Fraser *et al.* 2009). Equally, the abundance and ubiquity of grass facilitates comparison between and within sites and islands. Grass samples were thus taken from quadrats in each SB and CTRL site on Mingulay (both puffin and skua colonies in 2011 and 2012), Hirta (both puffin and skua colonies in 2012) and Fair Isle (puffin colony in 2012). Samples were collected for analysis of N concentration and $\delta^{15}$N in relation to the presence of seabirds.

Samples of grass consisted of a composite sample and also of the species *Holcus lanatus* (Yorkshire Fog). A composite sample consisted of a sample of all the grass species within a quadrat. The mass of each grass species collected, for composite samples, was in approximate proportion to their abundance within each quadrat. Proportions of grass species were determined from measuring abundance in the field. Composite grass samples from Fair Isle and Hirta were however collected haphazardly as grass species' abundance was not recorded. A single species of grass was chosen to explore variation within a species between sites and between a single species and composite samples. *H. lanatus* was chosen because of its relative ubiquity between and within sites and islands and also because of the ease in identification from vegetative parts. Samples were not taken if they were observed to be covered in guano or other contaminants. Only the vegetative component of the grass was sampled, *i.e.* stems and leaves, to minimize variation in nutrient concentration between plant compartments (Wang and Schjoerring 2012, Szpak *et al.* 2013). Upon collection samples were stored in labelled bags in a cool environment before transport and storage at -20 º*C*. Samples were frozen on average five days after collection.

## 5.2.3 Herbivores

### 5.2.3.1 Exclosures

To understand the impact of seabird presence on the growth of above-ground biomass without the confounding effect of grazing, roofed exclosures were established in the puffin colony and its respective control site on Mingulay in 2012. Grazing exclosures in the puffin colony and control site comprised the same quadrats as the sampled vegetation quadrats. Two transects at each site consisted each of five square exclosures (1 m x 1 m and 0.3 m high and made from 1 inch diameter wire mesh). Each exclosure also had a paired quadrat next to it with no wire mesh exclosure (termed "open" quadrat) constituting the other two transects at each site. The open quadrat was positioned to minimize differences in vegetation within pairs.

To look at the change in growth over time the mean height of the vegetation was recorded from 10 evenly spaced measurements in every quadrat every four days from when the experiment was established on the 26th May 2012 until 5th July 2012 and then again from 19th May 2013 until 3rd July 2013. Four days was chosen as the sampling interval to balance observable change in grass growth with logistical constraints. Vegetation height was calculated by the height of the tallest vegetation connecting onto a rule pushed to the ground.

#### 5.2.3.2 Rabbit populations

To compare differences in rabbit population activity between the puffin SB and CTRL site on Mingulay rabbit droppings were counted, which is considered a relatively fast and reliable method for estimating rabbit population activity (Wood 1988, Forys and Humphrey 1997, Palomares 2001). To estimate rabbit activity four plots (2 $m^2$ each) were arranged evenly across two transects at both the puffin colony and its control site on Mingulay in 2011 and 2012. In 2011 each plot was cleared of rabbit droppings initially and then every day for 17 days the numbers of rabbit droppings were counted and then cleared from the 28th June until the 14th July. In 2012, rabbit droppings were counted for 8 days following the same procedure from the 4th July until the 11th July.

#### 5.2.3.3 Hair sampling

To understand if ornithogenic nutrients are transferred from vegetation to herbivores, hair samples were collected from sheep and rabbits in the puffin areas of Mingulay (2011 and 2012) and Hirta (2012). The proximity of SB and relevant CTRL sites was considered important for hair sampling as the distances between sites needed to be greater than the average home range of the sampled herbivores to increase the likelihood herbivores fed within the studied site. Samples of hair were tested for their $\delta^{15}$N values to understand if N from seabirds passes into vegetation and into herbivores.

On Hirta samples of wool were taken from the same quadrats as the samples of vegetation in the puffin colony and its respective control site. Wool samples were found discarded in or within 2 m from the quadrat. To reduce the probability of wool coming from the same sheep wool was sampled with maximal distance between quadrats and choosing samples of different fleece colour (Jewell *et al.* 1974, Clutton-Brock and Pemberton 2004).

On Mingulay, samples of rabbit fur were collected from within the puffin colony and from its control site. Samples were collected by cutting hair off dead rabbits obtained from either the on-going culling programme, or collecting recently dead individuals in both sites. Independence was ensured by removing the carcass after sampling.

### 5.2.4 Chemical analyses

Samples of grass were analysed for their N stable isotope ratio and N concentration. Samples of grass were prepared prior to analysis; they were visually inspected for contamination and only clean grass retained prior to despatch and freezing. Grass samples were not cleaned or stored in preservation agents as these chemicals may alter isotopic ratios (Quillfeldt *et al.* 2010, Michalik *et al.* 2012). Once thawed, grass samples were dried at 60 $^{o}$C for 48 hours (Olofsson *et al.* 2008, Bai *et al.* 2009). Dried grass samples were then homogenized to a fine powder using a SPEX 6700 liquid nitrogen freezer mill before being accurately weighed (*c.* 1.20 g) into individual tin cups ready for analyses of stable isotope ratios.

Hair samples, given their known surface residues, were washed in a 2:1 mixture of chloroform: methanol and then distilled water before air-drying on glass fibre filter paper (Wayland and Hobson 2001, Procházka *et al.* 2013). Hair samples were then cut with sterilized scissors before being accurately weighed (*c.* 0.70 g) into individual tin cups.

Plant and hair samples were then analysed for their $^{15}$N/$^{14}$N isotope ratios by continuous flow isotope ratio mass spectrometry (CF-IRMS) with a Costech ECS 4010 elemental analyser linked to a Thermo Scientific Delta V mass spectrometer at SUERC, East Kilbride. Laboratory analyses were conducted by Rona McGill, SUERC. The stable isotope ratios were expressed in $\delta^{15}$N values as parts per thousand (‰) according to

$$\delta^{15}N = [(^{15}N/^{14}N)_{sample} / ( ^{15}N/^{14}N)_{air} – 1] \text{ x } 1000 \text{ (‰)}$$

Internal standards are traceable to the international standard of AIR for N. Instrumental drift was corrected by means of the repeated measurement of two laboratory standards every 10 samples (alternating between gelatine and two isotopically distinctive alanines). Measurement errors were small with standard deviations on average 0.29 ‰ for N, based on repeat measurements of laboratory tryptophan.

To calculate the percentage weight of N, 4 different sized aliquots of a laboratory standard were analysed, either tryptophan or glutamic acid. The N content of the tryptophan (or glutamic acid) molecule is known and therefore how much N is represented by each aliquot of the standard can be determined. A calibration line is produced by plotting the peak area of N, at mass 28 (the peak is produced by the N gas in the mass spectrometer and mass 28 is the mass of a molecule of $N_2$ gas) for each tryptophan aliquot versus milligrams of N calculated for each aliquot, and this is used to estimate N content for all samples analysed on the same day as the calibration line. Percentage weight N is produced by dividing the mass of N within the sample by the sample’s initial mass.

### 5.2.5 Statistical analyses

Generalised linear mixed models (GLMM) were implemented to analyse the effect of seabird sites and presence on the species richness, Simpson’s diversity and evenness measures across SB and CTRL sites for both puffin and skuas. Seabird “sites” refers to either skua sites or puffin sites. The terminology “site” is used over species, as any models differentiating between species are confounded by site or habitat. An interaction was also included between both fixed effects. Year was included as a random effect to account for repeat measurements across sites. Models were run using a Gaussian error structure. Model structure: Index ~ seabird sites * seabird presence, random effect = year.

To measure similarity between communities percentage similarity ($P$; Equation 3) was used (Krebs 1999). $P$ is typically calculated between community samples; however multiple quadrats at each site on Mingulay allows for the mean and standard deviation of $P$ to be calculated. Mean values and standard deviation of $P$ were calculated by permuting the column order ($n$ = 10000) of each site's community matrix (where columns refer to quadrat and rows to species) before calculating each value of $P$.

$$P = \Sigma_i \, minimum \, (p_{1i}, p_{2i}) \qquad \text{Percentage similarity (Equation 5.3)}$$

where $P$ = percentage similarity between samples 1 and 2; $p_{1i}$ percentage of species $i$ in community sample 1; and $p_{2i}$, percentage of species $i$ in community sample 2.

Permutational multivariate analysis of variance (PERMANOVA) was used to determine any statistical effect of the presence of seabirds on plant community composition. The *adonis* function within the package 'vegan' of R was used for analysis on a Bray-Curtis similarity matrix with 999 iterations (Oksanen *et al.* 2008, R.Core-Team 2014). The Bray-Curtis index was used as it is relatively uninfluenced by species richness and sample size, whilst being insensitive to the abundance of the most dominant species (Wolda 1981, Magurran 2004). All PERMANOVA tests met the assumption of homogeneity between groups; detected using the *betadisper* routine also within the 'vegan' package (LeCraw *et al.* 2014).

To illustrate the vegetation composition of the different sites non-metric multidimensional scaling (NMDS) was used. NMDS was calculated based upon a Bray-Curtis similarity matrix (Bray and Curtis 1957). Analyses were undertaken using the *metaMDS* function within the 'vegan' package (Oksanen *et al.* 2008, R.Core-Team 2014). Ellipses of 95 % confidence intervals are plotted on the NMDS plot for each site. Distance between ellipses represents graphically the difference in community composition. Following Osland *et al.* (2011) and Jones *et al.* (2011) the number of dimensions within the NDMS analysis was determined in a step-down procedure comparing the number of dimensions against the final ordination stress, with stress as a measure of goodness of fit (Clarke 1993). For this model, two dimensions were selected given the low measure of stress ($< 0.15$) and the visual interpretability of two dimensions (Clarke and Ainsworth 1993, Legendre and Legendre 2012).

GLMMs were implemented with $\delta^{15}$N and N concentration (percentage weight) of grasses and hair samples as response variables. The fixed effects of seabird presence, island and seabird sites (the latter only for plant samples) were included initially with interactions between seabird presence and seabird sites. Seabird “sites” refers to either skua sites or puffin sites. The terminology “site” is used over species, as any models differentiating between species are confounded by site or habitat. A random effect of year was also included for the plant samples to account for repeated measurements over time at the same sites. Models were run using a Gaussian error structure. Model structure: nitrogen values ~ seabird presence * seabird site + island, random effect = year.

To model the difference in vegetation height between the puffin and control site and the effect of exclosure on vegetation over time, a GLMM with a Gaussian error structure was used. The response was the change in vegetation height at each time point from baseline measurements taken on the 26th May 2012. Fixed effects included seabird presence, exclosure and year. A three-way interaction between each of the fixed effects was also included. Random effects were included to account for the experimental structure and repeat measurements taken from the same quadrats. Model structure: seabird presence * exclosure * year, random effect = day of year/exclosure row.

To compare rabbit activity between sites with and without seabirds, numbers of rabbit droppings at puffin SB and CTRL sites on Mingulay were modelled in a GLMM with a Poisson error structure. The model used the number of droppings as the response variable whilst the fixed effects included seabird presence and year (2011 and 2012). An interaction between both fixed effects was also included.

Random effects within the model were incorporated to reflect the nested experimental design (transect/plot and day of year) to take into account repeat measures on the same plot. Model structure: seabird presence * year, random effects = transect/plot and day of year.

Significance is reported as $P < 0.05$ with statistical tests using a two-tailed test. Error values associated with mean values are standard deviation (SD), unless reported as standard error (SE). Model selection to produce the minimum adequate model (MAM) was determined by stepwise backwards removal of parameters from a fully parameterised model using maximum likelihood (ML). The significance of a fixed effect was determined by using likelihood ratio (LRT) chi-square tests between the GLMM and a GLMM excluding the fixed effect of interest (Pinheiro and Bates 2000, Miles 2010). Only significant terms are reported from model selection. MAMs were run using restricted maximum likelihood (REML) for presentation of model coefficients. To test differences between model groups *post-hoc* Tukey Honest Significant Difference tests are used. The functions *lmer* and *glmer* from the ‘lmerTest’ and ‘lme4’ package was used to implement Gaussian and non-Gaussian GLMMs, respectively (R.Core-Team 2014). The *glmer* function was adopted as, contrary to other functions, it allowed for multiple nested random effects with a non-Gaussian error structure. Model fit was assessed on the basis of normalised model residuals versus fitted values testing for heteroskedascity, low AIC values, a lack of over-dispersion and collinearity. All analyses are carried out in R *v*. 3.03 (R.Core-Team 2014).

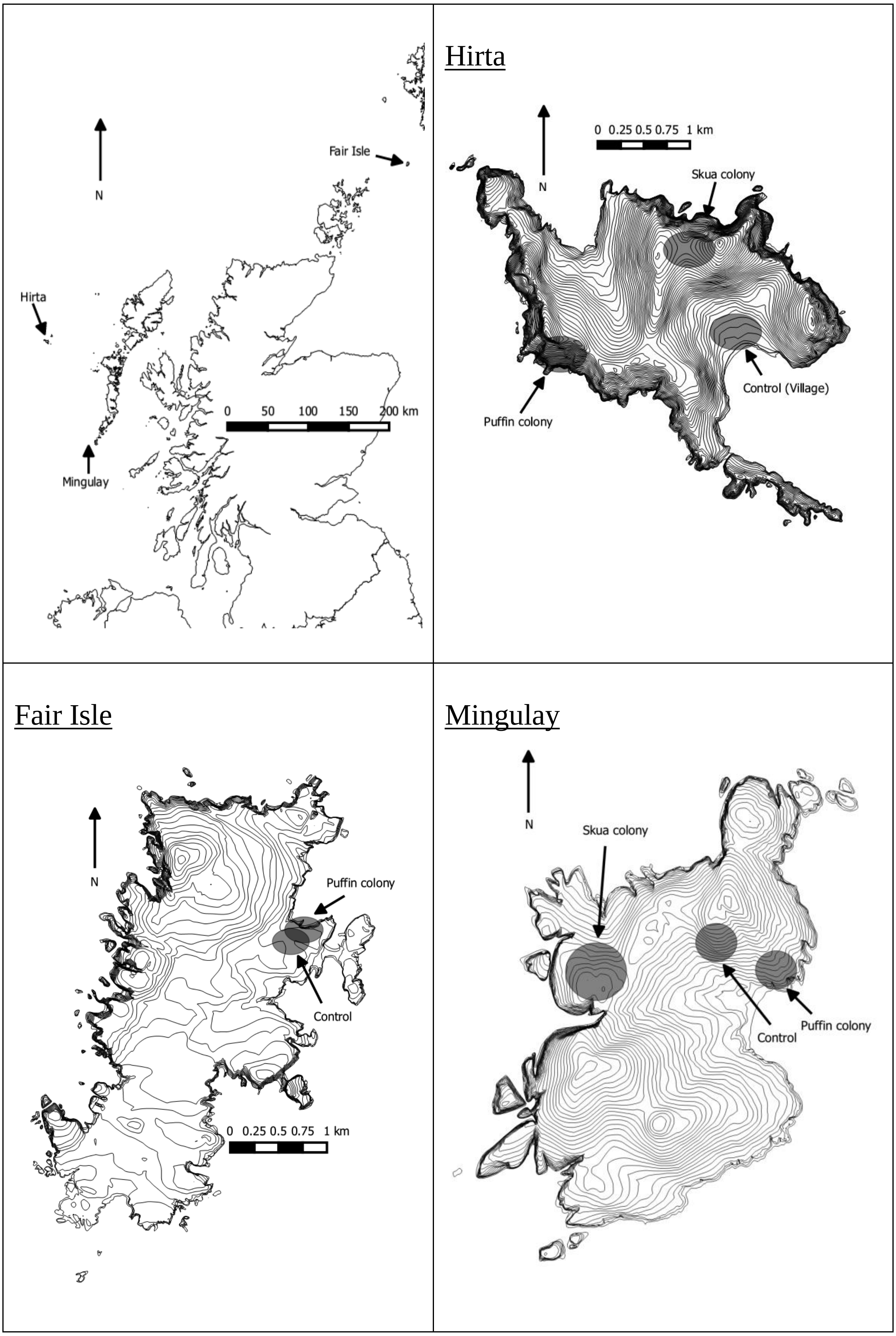

**Figure 5.1.** Location of the three islands where studies were conducted. Top left: UK overview of island locations. Shaded ellipses represent areas of study within islands. Control sites represent the control areas for puffin colonies. Skua colonies also include the control sites.

**Table 5.1.** Details of study islands.

| | Mingulay | Hirta | Fair Isle |
|---|---|---|---|
| Coordinates | 56$^{o}$, 48’ N, 07$^{o}$, 38’ W | 57$^{o}$ 49’ N, 08$^{o}$ 35’ W | 59$^{o}$ 31’ N, 01$^{o}$ 37’ W |
| Area (ha) | 640 | 670 | 768 |
| Geology* | Granite and Lewisian gneiss with superficial deposits of sand and gravel in the east. | Gabbro and granite formations | Predominantly sandstone formations |
| Vegetation | The skua colonies predominantly comprise an ungrazed, rank moorland assemblage of *Molinia caerulea*, *Carex* spp. and *Eriophorum* spp. although maritime communities can be found more coastally.<br>The puffin colonies generally comprise a mosaic of habitat, typically grazed, semi-improved *Festuca-Agrostis* communities, which in parts can be considered relatively species-rich. Again maritime species are more prevalent in closer proximity to the coast (Cheke & Reed, 1987; Proctor & Rafferty, 2004; this study). Both the SB and CTRL site were of similar terrain with southerly aspects. | The studied skua colony on the col of Conachair and Mullach Mor comprises predominantly bog communities; S*phagnum*, *Molinia* and *Eriophorum*. A transition of communities to higher ground sees wet heath dominate with *Calluna*, *Molinia*, *Potentilla*, *Deschampsia* and *Holcus* arising.<br>The puffin colony studied, Carn Mor, faces SE and is predominantly boulder scree interspersed with small swards of biotic grassland. *Holcus* predominates within this community with lesser amounts of *Poa*, *Agrostis* spp. and *Festuca rubra*.<br>The Village Bay, cultivated until the late 1990’s comprises a fertile sward of grazed *Holcus*/*Agrostis* grassland. *Festuca*, *Anthoxanthum* and *Poa* are also abundant (Jewell *et al.* 1974; this study). | The studied puffin colony at Roskillie faces NE, although the studied vegetation was on flat ground. The site consisted of semi-improved, grazed grassland with vegetated cliffs and coastal communities.<br>The puffin CTRL site consisted of grazed, flat, semi-improved grassland further inland from the puffin colony. Proximal to the CTRL site vegetation was of sub-maritime *C. vulgaris* and dry heath communities (Pritchard 1956; this study). |

*Geological data are sourced from the British Geological Survey ©NERC 2014.

# 5.3 **Results**

## 5.3.1 Community composition

On Mingulay 67 plant species or taxa, from 32 families, were identified in 121 sampling quadrats across all the sites and years (Appendix II).

On average, the puffin colony had lower species richness compared to the puffin CTRL site for both years. The skua territories also had lower species richness compared to the skua CTRL sites in 2012 (Table 5.2). There was a significant effect of the seabird site on the mean species richness between sites on Mingulay over time (LRT: seabird site, $\chi^2_1 = 64.74$, $P < 0.001$). The effect of seabird presence and an interaction between seabird presence and site were considered non-significant. The model coefficients estimate that the SB and CTRL site of the skuas are significantly less species rich with a difference of 8.8 species on average from the puffin SB and CTRL sites (site: $F_{1,98.7} = 84.79$, $P < 0.001$).

On average, the puffin colony had lower diversity (1-$D$) compared to the puffin CTRL site for both years. The skua territories also had lower diversity compared to the skua CTRL site in 2012 (Table 5.2). There was a marginally significant interaction between the seabird site and presence on the mean Simpson’s index (LRT: seabird species*presence; $\chi^2_1 = 3.84$, $P = 0.050$). The model output estimates that the skua sites (SB and CTRL) are significantly less diverse than the puffin sites and that there was a significant decrease in diversity with the presence of seabirds, relative to CTRL sites (site: $F_{1,117.0} = 557.6$, $P < 0.001$; seabird presence: $F_{1,117.0} = 8.57$, $P = 0.004$). *Post-hoc* Tukey tests show that there is a significant decrease in diversity from the skua CTRL sites to skua territories ($P = 0.017$) with a non-significant difference between the puffin SB and CTRL site.

On average, the puffin colony was less even compared to the puffin CTRL site for both years. The skua territories were also less even compared to the skua CTRL sites in 2012 (Table 5.2). There was a significant effect of seabird site and presence, with no significant interaction, on the mean Simpson’s evenness between sites on Mingulay over time (LRT: seabird site, $\chi^2_1 = 70.9$, $P < 0.001$; seabird presence, $\chi^2_1 = 5.23$, $P = 0.022$). Skua sites (SB and CTRL) were significantly less even than the puffin sites and there was a significant decrease in evenness with the presence of seabirds, relative to CTRL sites (site: $F_{1,17.61} = 112.0$, $P < 0.001$; seabird presence: $F_{1,117.0} = 5.22$, $P = 0.024$).

In 2012, the puffin colony had higher species richness and Simpson's index values and lower evenness compared to 2013, although the differences were not statistically different. Equally, in 2012, the puffin CTRL site had higher species richness and Simpson's index values and lower evenness compared to 2013, although the differences were again not statistically significant.

### 5.3.2 Inter-community comparisons

Two communities can have very similar values of diversity but consist of different species with similar richness and abundance (Jost 2010). Therefore, understanding the species difference between communities is of importance. The most abundant species or taxa (> 50 % presence) within the puffin colony in 2012 and 2013 were Bryophyta, *Thymus polytrichus, Festuca* spp., *Carex* spp. *Plantago lanceolata* and *H. lanatus*. The puffin control site was dominated by *Festuca* spp., *T. polytrichus*, Bryophyta, *Carex* spp., *Galium verum*, *P. lanceolata* and *Viola* spp.. The skua territories had noticeably different community compositions from the puffin colony, being dominated by mainly the grasses *Festuca* spp. and *H. lanatus*, whilst the skua control sites were dominated by *Festuca* spp., *Molinia caerulea* and *Potentilla erecta*. Species only within the puffin colony in 2012, relative to the control site were *Succisa pratensis*, *Poa compressa*, *Taraxacum* spp., *G. saxatilie* and *Bromus hordeaceus.* In 2013, the puffin colony contributed the species *Sagina procumbens*, *Sedum anglica* and *Koeleria macrantha*, relative to the puffin control site. In 2012, the skua territories contributed *Ophioglossum vulgatum*, *Cochlearia officinalis, S. anglica, G. saxatile*, *Ranunculus flammula*, *Armeria maritima* and *Primula vulgaris.*

Table 5.3 shows the mean percentage similarity ($P$) of species and abundance between sites. The most similar between site comparisons are the communities of the puffin SB and CTRL sites with ~ 0.7 similarity each year. The similarity between skua SB and CTRL sites was the next most similar at ~0.4. Confidence intervals can be created to test the null hypothesis that the difference between mean permutational percentage similarity values is zero. In comparing between puffin SB and CTRL sites over 2012 and 2013 there is a failure to reject the null hypothesis as the confidence intervals bound zero (95 % CI: -0.0008 to 0.0007); consequently it is concluded that there is no significant difference between percentage similarity over time between puffin SB and CTRL sites. In testing the difference between the mean percentage similarity of the puffin and skua SB and CTRL sites the null hypothesis is rejected that the mean difference is significantly different from zero (95 % CI: 0.0021 to 0.0064). It is therefore concluded that the difference between the puffin and skua SB and CTRL sites are significantly different.

Community composition was further shown to be significantly different between seabird sites and their respective control sites for both species and year (PERMANOVA; 2012, $\text{puffin}_{\text{SB-CTRL}}$, $F_{1,38} = 6.43$, $P < 0.001$; $\text{skua}_{\text{SB-CTRL}}$, $F_{1,39} = 13.91$, $P < 0.001$; 2013, $\text{puffin}_{\text{SB-CTRL}}$, $F_{1,38} = 6.50$, $P < 0.001$;). The ordination analysis (Figure 5.2) identified the four spatially distinct communities in 2012 using the Bray-Curtis similarity index. The distance between communities illustrates their difference and agrees with the results seen from the percentage similarity index with most similarity between puffin SB and CTRL, sites relative to skua sites.

There is a significant difference in grass species composition between communities on Mingulay (PERMANOVA; 2012, $\text{puffin}_{\text{SB-CTRL}}$, $F_{1,38} = 4.13$, $P = 0.006$; $\text{skua}_{\text{SB-CTRL}}$, $F_{1,39} = 26.36$, $P < 0.001$; 2013, $\text{puffin}_{\text{SB-CTRL}}$, $F_{1,38} = 4.13$, $P = 0.007$).

## 5.3.3 Chemical analyses

### 5.3.3.1 Plant nitrogen content

Samples of *Holcus lanatus* and composite grass samples from all three islands had a greater percentage weight of N within puffin and skua breeding areas, relative to control sites. The N content of *H. lanatus* from SB sites was greater by 0.71 % ± 0.25 SE relative to CTRL sites (seabird presence, $\chi^2_1 = 7.71$, $P = 0.005$; island, $\chi^2_1 = 0.94$, $P = 0.332$; site, $\chi^2_1 = 0.51$, $P = 0.476$; seabird presence*site, $\chi^2_1 = 2.96$, $P = 0.085$, Table 5.4). The effect of seabird presence on N content of the composite grass samples differed between seabird site (seabird presence*site, $\chi^2_1 = 6.06$, $P = 0.024$; island, $\chi^2_1 = 0.77$, $P = 0.380$). There was a significantly higher N content in samples from SB sites compared to the CTRL site for skuas (GLMM estimate; $\Delta_{\text{SkuaSB:SkuaCTRL}} = 0.91 \pm 0.17$ SE, $P = 0.001$) but not for puffins (GLMM estimate; $\Delta_{\text{PuffinSB:PuffinCTRL}} = 0.42 \pm 0.12$ SE, $P = 0.080$, Table 5.5). Enrichment in percentage weight of N between SB and CTRL sites across both species and island ranged from 0.05 to 1.31 and 0.36 to 0.94 for *H. lanatus* and composite samples, respectively (Table 5.6, Figure 5.3).

#### 5.3.3.2 Plant isotopic analyses

Samples of *Holcus lanatus* and composite grass samples from all three islands had a higher $\delta^{15}$N value within puffin and skua breeding areas, relative to control sites (Figure 5.3). The $\delta^{15}$N of *H. lanatus* was greater within the puffin SB site, relative to the CTRL site by 2.93 ‰ ± 1.02 SE ($P = 0.036$) and greater in the skua SB site relative to the CTRL site by 11.96 ‰ ± 1.56 SE ($P < 0.001$) (LRT: seabird presence*site, $\chi^2_1 = 19.42$, $P < 0.001$; island, $\chi^2_1 = 0.43$, $P = 0.513$). The effect of seabird presence on the $\delta^{15}$N signature of the composite grass samples differed between site and island (LRT: seabird presence*site, $\chi^2_1 = 5.86$, $P = 0.015$; island, $\chi^2_1 = 15.82$, $P < 0.001$). There was a significantly lower $\delta^{15}$N value from the skua SB to the skua CTRL site (GLMM estimate; $\Delta_{\text{SkuaSB:SkuaCTRL}} = -7.93 \pm 1.66$ SE, $P = 0.007$) and an insignificant difference from the puffin SB to the puffin CTRL sites (GLMM estimate; $\Delta_{\text{PuffinSB:PuffinCTRL}} = -3.47 \pm 1.40$ SE, $P = 0.151$). Hirta had significantly greater values of $\delta^{15}$N, relative to Fair Isle (GLMM estimate; $\Delta_{\text{Hirta:Fair Isle}} = 5.78 \pm 1.87$ SE, $P = 0.013$). There were no other significant differences between other pairs of islands.

#### 5.3.3.3 Hair isotopic analyses

Samples of hair had a greater $\delta^{15}$N signature in puffin colonies relative to control sites (Figure 5.3) with the difference dependent upon herbivore species (GLMM: seabird presence* herbivore, $\chi^2_1 = 12.35$, $P < 0.001$). Model estimates showed there to be a significant decrease in the $\delta^{15}$N signature from the puffin SB site to the puffin CTRL site when using wool (GLMM estimate; Hirta $\Delta_{\text{PuffinSB:PuffinCTRL}}$ = -5.28 ± 0.74 SE, $P < 0.001$) and a significant decrease from the puffin SB to the puffin CTRL site when using fur (GLMM estimate; Mingulay $\Delta_{\text{PuffinSB:PuffinCTRL}}$ = -1.79 ± 0.58 SE, $P$ = 0.020).

Across six sampling sites (SB and CTRL site at Hirta 2012 and Mingulay in 2011 and 2012 each) hair $\delta^{15}$N is positively correlated with the grass $\delta^{15}$N isotopic ratios found at the same area (Pearson's correlation = 0.989, $n$ = 6, $P < 0.001$).

### 5.3.4 Exclosures

In total, 6800 measurements of vegetation height were recorded over the two seasons. The results show an increase in vegetation height from baseline values when not grazed and that growth is greater in the puffin colony within the exclosures (Table 5.7). Equally, the difference in growth with the effect of exclosure varies between years (LRT: exclosure*seabird presence*year, $\chi^2_1 = 6.25$, $P = 0.012$, Table 5.8).

To simplify interpretation of the three-way interaction the change in vegetation height is analysed separately for each year (Table 5.8). The change in vegetation height is dependent upon seabird presence and the exclosure treatment in both years (LRT: 2012, exclosure*seabird presence, $\chi^2_1 = 6.68$, $P = 0.009$; 2013, $\chi^2_1 = 6.25$, $P < 0.001$). Vegetation was not significantly higher in the exclosures between the SB and CTRL site in 2012 (GLMM estimate; 2012 $\Delta_{\text{CTRL-Y:SB-Y}}$ = 2.03 ± 1.61 SE, $P$ = 0.587); however it was in 2013 (GLMM estimate; 2013 $\Delta_{\text{CTRL-Y:SB-Y}}$ = 13.74 ± 3.68 SE, $P$ = 0.002). There was no significant difference in the vegetation height in the open plots between SB and CTRL sites in either year. Across exclosure treatments there was significantly shorter vegetation in 2012 in the SB site, relative to the CTRL site (GLMM estimate; 2012 $\Delta_{\text{SB-CTRL}}$ = -3.86 ± 1.61 SE, $P$ = 0.017) but there was no significant difference in 2013.

## 5.3.5 Rabbit populations

Over the study period, rabbit dropping study plots were counted 200 times for the number of droppings present. The number of droppings is not dependent upon seabird presence with time, although it does differ between years and, although marginally non-significant, possibly with seabird presence (LRT: year, $\chi^2_1 = 20.69$, $P < 0.001$; seabird presence, $\chi^2_1 = 3.23$, $P = 0.072$). Retaining both seabird presence and year within the MAM model showed that there were more droppings in the puffin colony, relative to the control site and that there were more droppings in 2011, relative to 2012 (GLMM estimate; seabird presence $\Delta_{\mathrm{PuffinSB:PuffinCTRL}} = 0.34 \pm 0.18$ SE, $P = 0.059$; year $\Delta_{2011:2012} = -1.18 \pm 0.18$ SE, $P < 0.001$).

The mean numbers of droppings in the puffin SB site and CTRL site in 2011 were 65.65 ± 42.62 and 49.66 ± 41.54, respectively. The mean numbers of droppings in the puffin SB site and CTRL site in 2012 were 23.38 ± 24.20 and 16.94 ± 17.22, respectively.

**Table 5.2.** Mean (± SD) richness, diversity and evenness indices for plant data collected over two successive years at different locations on Mingulay.

| Location | Year | *N* | Mean species richness (*S*) | Simpson's index (1-*D*) | Simpson's measure of evenness ($E_{1/D}$) |
|---|---|---|---|---|---|
| Puffin SB | 2012 | 20 | 25.10 (± 2.45) | 0.92 (± 0.01 ) | 0.49 (± 0.05 ) |
| | 2013 | 20 | 23.10 (± 1.68) | 0.91 (± 0.01) | 0.51 (± 0.05 ) |
| Puffin CTRL | 2012 | 20 | 25.65 (± 2.08 ) | 0.93 (± 0.01) | 0.53 (± 0.08 ) |
| | 2013 | 20 | 23.10 (± 2.25) | 0.92 (± 0.1) | 0.53 (± 0.07 ) |
| Skua SB | 2012 | 21 | 12.48 (± 3.25) | 0.77 (± 0.07 ) | 0.38 (± 0.06 ) |
| Skua CTRL | 2012 | 20 | 13.45 (± 3.46) | 0.81 (± 0.05) | 0.41 (± 0.05 ) |

**Table 5.3.** The plant community mean percentage similarity between sites. Zero represents complete dissimilarity, whilst 1 indicates complete similarity. Values in parentheses are SD.

| Site | Puffin SB 2013 | Puffin CTRL 2012 | Puffin SB 2012 | Skua SB 2012 | Skua CTRL 2012 |
|---|---|---|---|---|---|
| Puffin CTRL '13 | 0.697 (± 0.058) | 0.724 (± 0.071) | 0.697 (± 0.060) | 0.279 (± 0.069) | 0.307 (± 0.083) |
| Puffin SB '13 | - | 0.687 (± 0.050) | 0.724 (± 0.070) | 0.295 (± 0.069) | 0.311 (± 0.088) |
| Puffin CTRL '12 | - | - | 0.696 (± 0.059) | 0.260 (± 0.068) | 0.309 (± 0.085) |
| Puffin SB '12 | - | - | - | 0.291 (± 0.068) | 0.310 (± 0.088) |
| Skua SB '12 | - | - | - | - | 0.411 (± 0.127) |

**Table 5.4.** Model coefficients for the nitrogen content of Composite and Holcus samples.

| Parameter | Estimate | SE | df | *t* | *P* |
|---|---|---|---|---|---|
| *Composite* | | | | | |
| Intercept | 2.11 | 0.27 | 1.16 | 7.94 | 0.059 |
| Seabird presence | 0.42 | 0.12 | 124.00 | 3.42 | 0.001 |
| Site | -0.27 | 0.14 | 124.21 | -1.97 | 0.051 |
| Seabird presence * Site | 0.49 | 0.21 | 124.18 | 2.36 | 0.020 |
| | | | | | |
| *Holcus lanatus* | | | | | |
| Intercept | 1.86 | 0.19 | 2.61 | 9.71 | 0.004 |
| Seabird presence | 0.71 | 0.25 | 27.09 | 2.89 | 0.007 |

**Table 5.5.** Model coefficients for the nitrogen stable isotope ratio of Composite and Holcus samples.

| Parameter | Estimate | SE | df | *t* | *P* |
|---|---|---|---|---|---|
| *Composite* | | | | | |
| Intercept | -0.37 | 1.64 | 9.60 | -0.23 | 0.827 |
| Island: Kilda | 5.78 | 1.87 | 9.13 | 3.09 | 0.013 |
| Island: Mingulay | 0.93 | 1.73 | 9.28 | 0.54 | 0.605 |
| Seabird presence | 3.48 | 1.40 | 7.96 | 2.48 | 0.038 |
| Site | 1.38 | 1.57 | 8.1 | 0.88 | 0.406 |
| Seabird presence * Site | 4.46 | 2.17 | 8.40 | 2.06 | 0.072 |
| | | | | | |
| *Holcus lanatus* | | | | | |
| Intercept | 0.01 | 0.73 | 26.00 | 0.01 | 0.994 |
| Seabird presence | 2.95 | 1.01 | 26.00 | 2.91 | 0.007 |
| Seabird site | 0.96 | 1.37 | 26.00 | 0.70 | 0.491 |
| Seabird presence * Site | 9.01 | 1.86 | 26.00 | 4.85 | 0.001 |

**Table 5.6**. The mean (± SD) nitrogen concentration and $\delta^{15}$N of *Holcus lanatus* and composite samples across the three study islands. Values for Mingulay are averaged over 2011 and 2012. Values in parentheses are sample size.

| | *Holcus lanatus* | | | | | | Composite | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Island | Puffin | | | Skua | | | Puffin | | | Skua | | |
| | SB | CTRL | Δ | SB | CTRL | Δ | SB | CTRL | Δ | SB | CTRL | Δ |
| Percentage N concentration | | | | | | | | | | | | |
| Fair Isle | 2.44 ± 0.30 (5) | 2.39 ± 0.37 (5) | 0.05 | - | - | - | 2.43 ± 0.27 (5) | 2.34 ± 0.54 (5) | | - | - | - |
| Hirta | - | - | - | - | - | - | 2.37 ± 0.31 (13) | 1.79 ± 0.12 (13) | 0.58 | 2.13 ± 0.37 (6) | 1.66 ± 0.49 (6) | 0.47 |
| Mingulay | 2.56 ± 1.21 (6) | 1.72 ± 0.11 (5) | 0.84 | 2.71 ± 0.68 (5) | 1.40 ± 0.06 (4) | 1.31 | 2.52 ± 0.97 (27) | 2.16 ± 0.40 (28) | 0.36 | 2.87 ± 0.71 (14) | 1.93 ± 0.39 (22) | 0.94 |
| $\delta^{15}$N | | | | | | | | | | | | |
| Fair Isle | 3.37 ± 0.53 (5) | 0.24 ± 0.51 (5) | 3.13 | - | - | - | 2.85 ± 0.75 (5) | -0.11 ± 1.17 (5) | 2.96 | - | - | - |
| Hirta | - | - | - | - | - | - | 11.48 ± 2.19 (13) | 4.55 ± 1.75 (13) | 6.93 | 12.83 ± 1.90 (6) | 6.74 ± 3.14 (6) | 6.09 |
| Mingulay | 2.61 ± 2.56 (6) | -0.22 ± 0.54 (5) | 2.83 | 12.93 ± 4.97 (5) | 0.96 ± 1.07 (4) | 11.97 | 2.99 ± 2.97 (28) | 0.94 ± 1.73 (27) | 2.05 | 10.92 ± 3.07 (22) | 1.23 ± 2.69 (14) | 9.69 |

**Table 5.7.** The change in vegetation growth within and outwith (open) exclosures over time, ± SD. Values correspond to the mean difference (cm) of repeat measurements from the baseline measurements across the season in 2012.

| | 2012 | | | 2013 | | |
|---|---|---|---|---|---|---|
| | Exclosure | Open | Δ | Exclosure | Open | Δ |
| Puffin SB | 25.39 ± 19.82 | 7.69 ± 11.13 | 17.7 | 62.15 ± 29.94 | 8.63 ± 11.36 | 53.88 |
| Puffin CTRL | 23.36 ± 19.48 | 11.55 ± 11.98 | 11.81 | 48.41 ± 24.55 | 13.05 ± 7.67 | 35.36 |

**Table 5.8.** Model coefficients for the change in vegetation height with the effect of exclosures

| Parameter | Estimate | SE | df | *t* | *P* |
|---|---|---|---|---|---|
| *Three-way interaction* | | | | | |
| Intercept | 8.24 | 2.99 | 20.20 | 2.76 | 0.012 |
| Site: SB | -3.86 | 1.93 | 562.30 | -2.00 | 0.046 |
| Exclosure: Yes | 11.81 | 1.93 | 562.30 | 6.11 | 0.000 |
| Year: 2013 | 13.46 | 3.53 | 344.90 | 3.82 | 0.000 |
| Site: SB * Year: 2013 | -0.56 | 3.46 | 562.30 | -0.16 | 0.872 |
| Site: SB * Exclosure: Yes | 5.89 | 2.73 | 562.30 | 2.16 | 0.031 |
| Exclosure: Yes * Year: 2013 | 23.55 | 3.46 | 562.30 | 6.81 | 0.000 |
| Site: SB * Exclosure: Yes * Year 2013 | 12.26 | 4.89 | 562.30 | 2.51 | 0.012 |
| | | | | | |
| *2012* | | | | | |
| Intercept | 11.55 | 3.09 | 13.60 | 3.74 | 0.002 |
| Site: SB | -3.86 | 1.61 | 385.00 | -2.41 | 0.017 |
| Exclosure: Yes | 11.81 | 1.61 | 385.00 | 7.36 | 0.001 |
| Site: SB * Exclosure: Yes | 5.90 | 2.27 | 385.00 | 2.60 | 0.010 |
| | | | | | |
| *2013* | | | | | |
| Intercept | 13.05 | 3.14 | 89.38 | 4.16 | 0.001 |
| Site: SB | -4.42 | 3.65 | 175.00 | -1.21 | 0.228 |
| 0Exclosure: Yes | 35.36 | 3.65 | 175.00 | 9.68 | 0.001 |
| Site: SB * Exclosure: Yes | 18.15 | 5.16 | 175.00 | 3.52 | 0.001 |

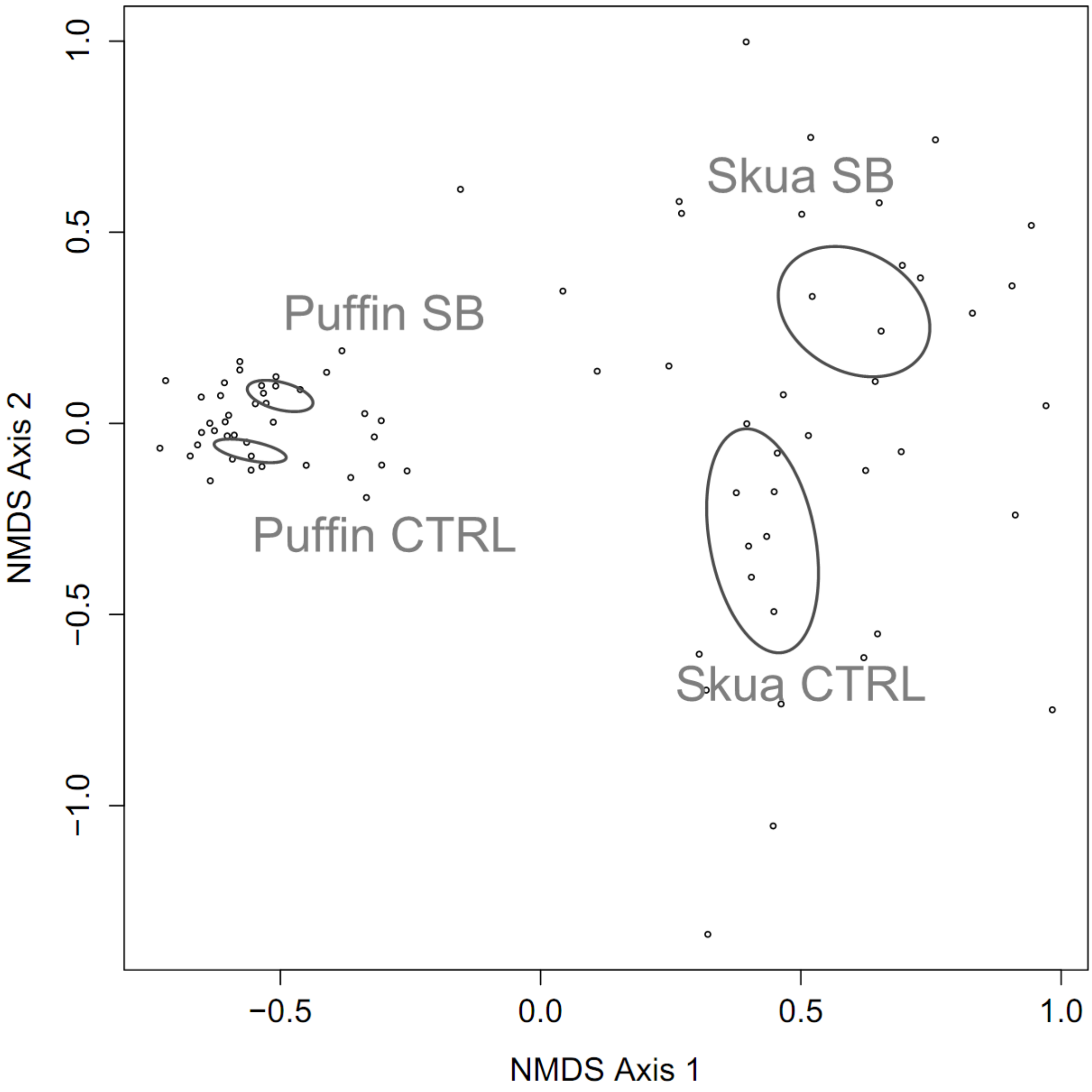

**Figure 5.2.** NMDS plot of community plant data between sites in 2012 produced using a Bray-Curtis similarity matrix. Ellipses represent 95 % confidence intervals for each sites plant community composition. SB = seabird sites, CTRL = control sites. Points represent quadrats. Stress = 0.13. k = 2.

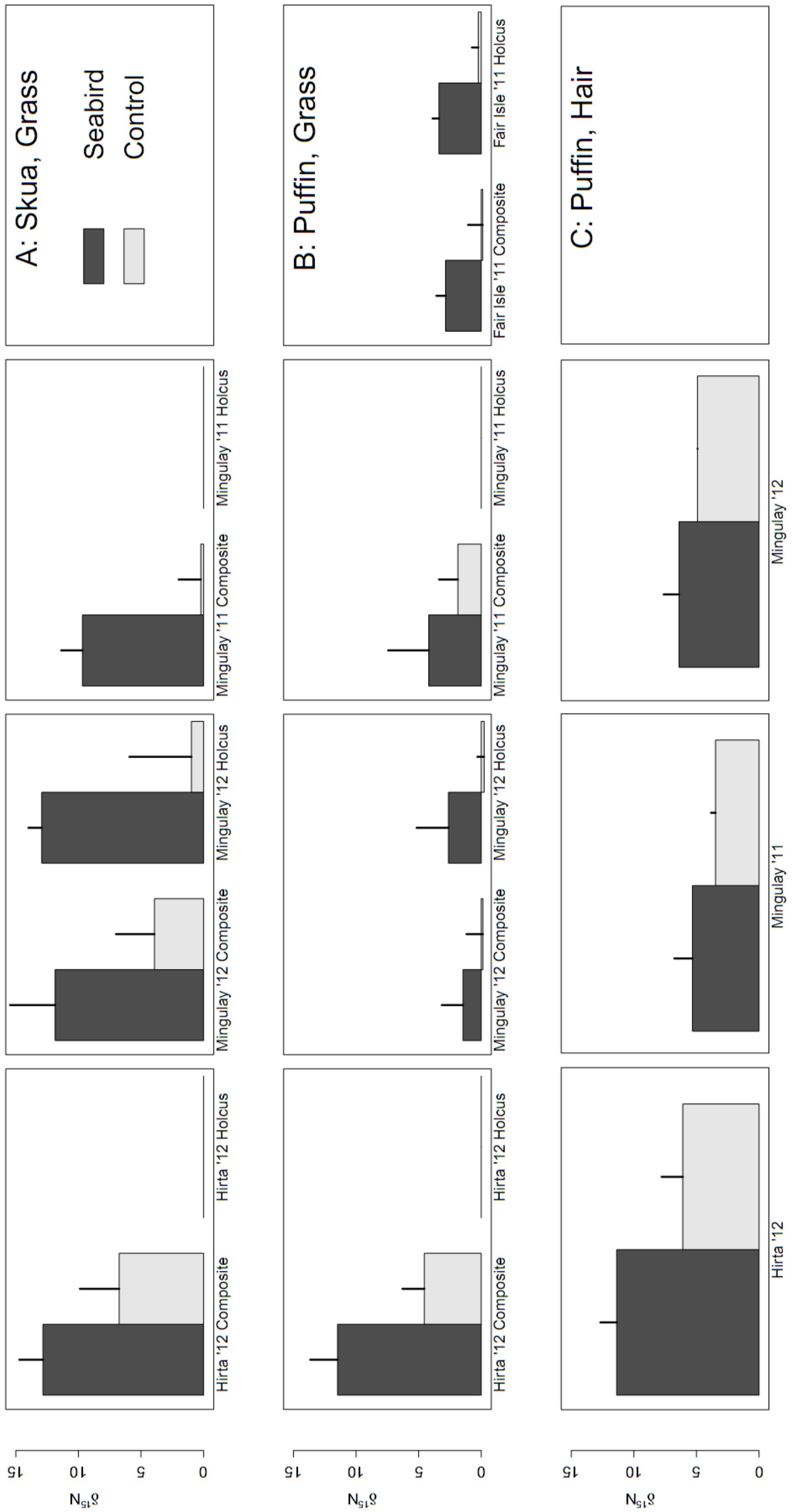

**Figure 5.3.** Mean (± SD) values of $\delta^{15}$N of grass samples and hair samples from within and outwith seabird colonies on islands over time. A) Samples of grass collected from skua colones; B) Samples of grass collected from puffin colonies; C) Samples of wool and fur from Hirta and Mingulay, respectively.

## 5.4 **Discussion**

This study shows that the presence of puffins and skuas at their breeding colonies influences both primary producers and indirectly secondary consumers. Seabirds influenced both the chemical and physical parameters of colony vegetation, relative to control areas. Plants within seabird colonies had increased values of $\delta^{15}$N and percentage weight of N, relative to control areas. The increased values of $\delta^{15}$N were also visible in herbivores in SB sites suggesting nutrient transfer from seabirds to herbivores, indirectly through vegetation.

Community composition in seabird colonies was shown to be, overall, significantly different from CTRL areas. Indices of diversity were in all cases lower within SB sites, relative to CTRL sites for both puffins and skuas. The differences for these indices were not significant, except for skuas using Simpson's D. This study shows that as diversity decreases in seabird colonies the evenness of a community also decreases suggesting greater proportional abundance of some species, relative to others. The results of PERMANOVA and NMDS further illustrate the differences in communities both between seabird species and between SB and CTRL sites.

Variation in community composition between species and SB and CTRL sites is however attributable to many factors, *e.g.* grazing regime, soil conditions, nutrient input, competition and other biotic and abiotic variables (Clutton-Brock and Pemberton 2004, Newman 2006, Mulder *et al.* 2011). Disentangling contributing factors influencing community composition from the effect of seabirds is difficult. The relative comparison between SB and CTRL sites provides one way in which to control for the effect of seabirds. The intrinsic difference between SB and CTRL sites is one limitation in the comparison of community composition and the effect of seabirds.

The association of particular plant species to seabirds does provide one way for the relative effect of seabirds to be understood. For example, some species are often associated with seabirds, as a result of their affinity for guano-derived nitrogen, their tolerance to disturbance and ability to competitively exclude less tolerant species and also their evolved mechanisms for transportation by birds (Ryan and Watkins 1989, Hill *et al.* 1999, Wait *et al.* 2005, Ellis 2005, Rajakaruna *et al.* 2009).

One species found in greater abundance in both puffin and skua SB sites, relative to CTRL sites, was *Holcus lanatus*. *H. lanatus* was found predominantly surrounding puffin burrow entrances and on skua loafing spots in luxuriant growth (pers. obs.); analogous to the "shearwater greens" of Callaham *et al.* (2012). The abundance and relative dominance of *H. lanatus* is probably due to its fast growth rate in response to N fertilisation (Poorter and Pothmann 1992). The abundance of two other nitrophilous species *Poa annua* and *Rumex acetosa* (Gillham 1956) within skua SB sites was also quite noticeable, in relation to skua CTRL sites. Equally, *Urtica dioica* and *Cirsium* spp. were locally abundant within the puffin colony (though by chance *U. dioica* was not found within quadrats). These two former ruderal species were not often found outside the puffin colony, except on disturbed ground as in the old village settlement on Mingulay (pers. obs.). The exclusion of more woody and herbaceous perennials, *e.g.* Ericaceae, in favour of herbaceous ruderals and annual species, is a relationship found across the world on sites influenced by seabirds (Croll *et al.* 2005, Ellis 2005).

The effect of grazing could explain the variation in community composition within the puffin colony and also between puffins and skuas. The greater diversity in the puffin sites, relative to the skua sites, could be influenced by grazing, which is known to increase species richness at moderate intensity (Proulx and Mazumder 1998, Virtanen and Crawley 2010). The absence of grazing in the skua colony suggests that the variation in diversity observed is likely to be attributable to the presence of skuas and/or site selection for nesting. The relative contribution of skua presence or initial site selection on the difference in community composition is difficult to interpret; however, future work could look at community composition where the history of colony growth is well known.

The observed community within skua SB sites is statistically different from the surrounding vegetation and the composition agrees with other seabird-influenced communities (Croll *et al.* 2005, Ellis 2005). Therefore it seems probable that skuas do influence vegetation, but it is possible that the sites are selected for a particular composition or position. Equally, the effect of skuas is likely to become more pronounced over time. Skuas can repeatedly use the same nesting site (Sjúrður Hammer, pers. comm.), which could lead to more ornithogenic vegetation with time. The skua colony on Mingulay has only recently grown from 13 pairs in 1998 to its current 76 pairs in 2013 (The National Trust for Scotland, unpubl. data). It is therefore possible that the skua SB sites chosen could represent relatively new territories, which may not exhibit the more pronounced cumulative impacts of skuas. Equally, the effect of puffins may become more pronounced over time with continual nutrient deposition and burrow excavation. Puffins on the island of Grassholm, for example, nested at such density that over time they eroded away their own colony (Harris and Wanless 2011). The nesting density of puffins on the studied colony on Mingulay is considered low at ~ 0.05 apparently occupied burrows (AOBs) $m^{-2}$ (pers. obs., Chapter 3), in relation to other colonies, which can average ~ 0.5 - 1 AOB $m^{-2}$ (Harris and Wanless 2011). The influence of puffins on the studied colony on Mingulay is therefore considered relatively minimal in relation to other colonies, although their effect on land could increase with time and cumulative impacts.

Overall, the communities observed for both puffins and skuas appear to have relatively different compositions, which differ with seabird species and CTRL site. The association and abundance of nitrophilous species within SB sites suggest the regular input of nutrients, which support a community influenced in part by seabirds. Understanding the choice of site by skuas and the intrinsic difference between SB and CTRL sites are some limitations though in discussing the effect of seabirds on vegetation. In general, the variation in community composition within seabird colonies caused by seabird nutrient input and physical disturbance provides increased spatial heterogeneity, which over an island scale will increase diversity. However, when considering the chemical differences between SB and CTRL sites the effect of seabirds on vegetation becomes more apparent.

Although the degree of influence seabirds can have on a community can be difficult to exactly interpret the chemical analyses on grasses provide a more compelling argument for the influence of seabirds on vegetation. The N content and $\delta^{15}$N values of samples of *Holcus lanatus* in SB sites were on average greater than CTRL areas, indicating assimilation of nutrients from seabirds (Mulder *et al.* 2011). The analysis of composite samples is confounded by the aggregation, and taxonomic differences between grass species (Szpak *et al.* 2013). However, the increased N content and $\delta^{15}$N values of composite samples in SB sites, relative to CTRL sites, across three islands, two years and two seabird species suggests that seabirds do influence a range of grass species. Although sources of N were not analysed for their $\delta^{15}$N values, the numerous studies supporting increased $\delta^{15}$N values in seabirds and guano suggests an ornithogenic source influencing vegetation in seabird colonies (Mulder *et al.* 2011, Szpak *et al.* 2013). The magnitude of the increase of $\delta^{15}$N values varies with seabird species.

Skuas were shown to enrich samples of *H. lanatus* between SB and CTRL sites by ~ 12 ‰, which assuming a difference between trophic levels of ~ 3 ‰, suggests that grass could be receiving N from ~ 4 trophic levels higher (Minagawa and Wada 1984, Bilby *et al.* 2003). Puffins were estimated to only enrich *H. lanatus* between SB and CTRL sites by ~ 3 ‰. The range of N isotope values for *H. lanatus* within this study are for both seabirds species relatively low in comparison to the influence of shearwaters and petrels on *H. lanatus* in New Zealand (Jones 2010). The difference though in isotopic enrichment between SB and CTRL sites could perhaps be explained in part by variation in diet between puffins and skuas (Ellis *et al.* 2006). Puffins typically feed upon the relatively low trophic level sandeel (*Ammodytes* spp.; Harris and Wanless 2011), whilst skuas can feed upon a range of prey associated with higher trophic levels *e.g.* seabirds and whitefish, as observed on both Mingulay and Hirta (pers.obs., Chapter 4; Miles 2010). The particularly high $\delta^{15}$N values of SB composite samples on Hirta suggest that puffins may feed upon higher trophic level prey. However, it is more likely that the boulder scree which the puffins inhabit at Carn Mor promotes volatilisation of guano, which in turn can increase the $\delta^{15}$N value (Wilson *et al.* 2004a). Volatilisation and subsequent fractionation of guano upon vegetated surfaces, as is applicable for all other sites studied, is considered relatively less (Sutton *et al.* 1995, Wilson *et al.* 2004a). Guano, when deposited in particular on rock surfaces, can readily volatilise into ammonia with a greater fraction of the lighter isotope of $^{14}$N being lost over the heavier $^{15}$N (Wilson *et al.* 2004a, Ellis *et al.* 2006). This fractionation upon the boulder scree may explain the higher $^{15}$N values observed, although there may be a suggestion of density-dependent processes given that Carn Mor is substantially larger than any other colony studied (Harris and Wanless 2011). There will also be an influence from the input of nutrients from other seabirds in the Carn Mor colony, *e.g.* Manx shearwaters *Puffinus puffinus* and Leach’s storm-petrels *Oceanodroma leucorhoa*. Concomitant with this isotopic increase in SB sites was the greater percentage weight of N within puffin and skua SB sites; a pattern present in both *Holcus lanatus* and composite grass samples. The enrichment of $\delta^{15}$N and the increased N concentration is also observed in other studies (Anderson and Polis 1999, Maron *et al.* 2006, Fukami *et al.* 2006) and suggests that N is limiting within SB colonies and that vegetation exploits higher concentrations of N as a result of seabird presence (Hannan *et al.* 2007). Equally, the variation in both percentage weight of N and $\delta^{15}$N values within an island highlights the spatial variation in the effect of seabirds on islands (Caut *et al.* 2012). The relatively high $\delta^{15}$N values in the CTRL site on Hirta also suggests some input of nutrients from seabirds, relative to Mingulay and Fair Isle. This increased $\delta^{15}$N value may have arisen due to the relatively small population of seabirds, which inhabit the village bay. The village bay holds small populations (< 25 "pairs") of Northern fulmar *Fulmarus glacialis,* European storm-petrels *Hydrobates pelagicus*, with both great skuas and Arctic skuas *Stercorarius parastiticus* nesting nearby (Prior 2013).

Further variation in N concentration and $\delta^{15}$N values can arise within different parts of the plant and over time in relation to growth stage (Szpak *et al.* 2013). This variation is minimized by sampling over the same period in time and only sampling above-ground vegetative parts of grasses. $\delta^{15}$N can also be influenced by mean annual temperature and precipitation (Szpak *et al.* 2013); however changes are often observed over global scales and unlikely to occur over the relatively small scales of this study (Amundson *et al.* 2003).

Elevated N concentration within vegetation is often associated with greater nutritional quality and this can lead to higher levels of herbivory (Mattson 1980, Iason *et al.* 1986, White 1993). The increased $\delta^{15}$N value of sheep and rabbit hair found within puffin colonies, relative to CTRL sites, suggests that the input of nutrients by puffins can be traced into secondary consumers. Accordingly, the proportional difference between $\delta^{15}$N values of composite grass samples from SB and CTRL sites is reflected in the $\delta^{15}$N values of hair samples between Mingulay and Hirta. For example, the difference in $\delta^{15}$N values of wool is much larger than samples of fur, from the puffin colony to the CTRL site and the same difference is observed in the $\delta^{15}$N values of composite grass samples. This difference lends further support to the transfer of nutrients from seabirds to herbivores. A similar study also showed that the $\delta^{15}$N values of dietary plants predicted bone collagen $\delta^{15}$N values in kangaroos (Murphy and Bowman 2006), suggesting that consumption of plants will affect further herbivore tissue. The enrichment of secondary consumers from consumption of ornithogenic vegetation has also been found in other studies (Stapp *et al.* 1999, Stapp and Polis 2003, Caut *et al.* 2012); although to the author's knowledge, nutrient transfer from seabirds to rabbits and sheep is not documented. Given the use of enriched N vegetation by herbivores, as identified by nitrogen stable isotopes, it is possible that this will alter foraging behaviour or increase reproductive success (Iason *et al.* 1986, Jakubas *et al.* 2008). The behaviour or reproductive success of rabbits and sheep within this study was not however measured.

The increased value of $\delta^{15}$N within sheep hair relative to rabbit hair could be explained in part by their difference in anatomy. Rabbits are hindgut fermenters and sheep are foregut fermenters (Illius and Gordon 1992). This disparity in digestion influences $\delta^{15}$N values with foregut fermenters having relatively higher $\delta^{15}$N values compared to hindgut fermenters, although the difference is also species dependent (Sponheimer *et al.* 2003).

A limitation with the collection of discarded sheep hair is the consideration that samples are not independent from each other and could have been transported into the sites from another area. The distinct $\delta^{15}$N values of sheep wool between SB and CTRL sites suggests however spatial segregation of sheep based upon different values of $\delta^{15}$N forage. It therefore seems likely that the sheep in either SB or CTRL site were subject to, on average, different grazing areas across the growth of the hair. Given that sheep are often hefted to particular areas over time (Coulson *et al.* 1999) this result is thus expected. The possibility that the wool samples were not independent is one limitation, although the chance of this was reduced by sampling with maximal distance and choice of fleece colour between samples. Rabbits were all sampled from independent individuals. The serial formation of hair from temporal assimilation of nutrients lends samples of hair to be considered a composite of the nutrients ingested over a course of time. This serial formation has allowed for the exploration of temporal variation in diet by separating hair strands into sections (Ayliffe *et al.* 2004, Cerling *et al.* 2006). Growth of the fleece primarily occurs between June and August with a reduction in growth over winter (Clutton-Brock and Pemberton 2004). It is therefore conceivable that the $\delta^{15}$N value of wool is reflective of the assimilation of seabird-derived nutrients, as both wool and grass are grown at approximately the same time. Rabbits, conversely, have hair both in and out of the growth phase, at the same time (Rony *et al.* 1953). There is a suggestion though that the growth of rabbit hair is more predominant in spring, rather than winter (Rony *et al.* 1953). Accordingly, the samples of hair from rabbits could also be considered to be consistent with the assimilation of seabird-derived nutrients in vegetation. Given sheep are most likely to eat grass during summer the samples obtained (both *Holcus lanatus* and composite samples) are reflective of their diet (Clutton-Brock and Pemberton 2004). Rabbits on Mingulay grazed most species in the studied areas, leaving typically only relatively indigestible species, *e.g. Juncus* spp., *Carex* spp. and *Cirsium* spp. (pers. obs.). Although, both graminoid and dicotyledon species were grazed, the effect of seabirds is predicted to influence all plant species, although the magnitude of effect on each species is unknown.

The transfer of nutrients from seabirds to plants to herbivores suggests that herbivore populations could benefit from the presence of seabirds (Iason *et al.* 1986). The exclosure experiment showed that vegetation height was greater, when not grazed, over both years within the puffin colony. Increased productivity and an increased N concentration as a result of seabird nutrient input is a response often found in seabird colonies (Sanchez-Piñero and Polis 2000, Reich *et al.* 2001, Maron *et al.* 2006). Given equal grazing levels it can be assumed that the greater productivity in the puffin colony provides additional forage material for herbivores, which can influence survival (Clutton-Brock and Pemberton 2004). Equally, the higher quality forage material provided by skuas within their territories could also provide nutritional material for grazing sheep, in an otherwise relatively unpalatable sward (Virtanen and Crawley 2010). However, whether sheep are tolerated feeding within skua territories within the breeding season is debateable (Furness 1987). The provision of better quality forage in seabird colonies outside the breeding season could certainly infer nutritional benefit for herbivores (Clutton-Brock and Pemberton 2004).

With further regard to the indirect influence of puffins on rabbits the exclosure experiment showed that grass was grazed to a similar height over both years across the SB and CTRL sites. This would indicate that grazing pressure is likely to be equal over sites and time. There were a greater number of rabbit droppings in the puffin colony, compared to the control site, although the difference was not significant. This would suggest that there is perhaps greater rabbit activity in the puffin colony, although variation in other factors between the puffin colony and the control site could confound the results. Differences between sites could include the differential use of habitat within the control site over the wider landscape outside of the studied area as well variation in predation rates and parental care (Mattson 1980, von Holst *et al.* 2002, Rodel *et al.* 2008).

The generality of these findings are likely to be applicable to other ground-nesting seabird species, *e.g. Larus* spp. and *Sterna* spp.. However, as with this study, the effect that these species will have on land is dependent upon colony size and nesting density (Ellis *et al.* 2006, Jovani *et al.* 2008). As colonies become larger and nesting density increases their effect on local vegetation will increase. At high nesting density the effect of seabirds on increased primary productivity is likely to reverse and the toxic effects of guano and increased physical disturbance could limit growth of vegetation (Fangmeier *et al.* 1994, Sanchez-Piñero and Polis 2000). The cumulative effect of all seabird populations will be much larger than the isolated effects of puffins and skuas. The volatilisation and deposition of ammonia ($NH_3$) derived from guano could be considerable and its effect is likely to influence surrounding communities (Wilson *et al.* 2004a, Blackall *et al.* 2008). However, the lower percentage weight of N within grasses of CTRL sites suggests that deposition of volatilised N-$NH_3$ is not as important as localised deposition from seabirds in the colony. With changing populations of seabirds their effect on land could potentially alter whole food webs by variation in primary productivity, diversity and those species linked to seabird-derived resources.

Many studies have shown that there is a positive correlation between elevated soil N concentration and plant N concentration as a result of seabird presence (Anderson and Polis 1999, Maron *et al.* 2006). It can therefore be assumed that the soils on the islands in this study will likely be enriched in N in the presence of puffins and skuas. This influence, besides influencing plants and herbivores, will probably affect a range of below-ground communities from microbes (Wright *et al.* 2010) to invertebrates (Callaham *et al.* 2012). Run-off of nutrients from the seabird colonies could also impact coastal marine communities (Polis and Hurd 1996). The impact of puffins and skuas and the deposition of nutrients could also permeate into small rodents (as on Carn Mor, Hirta with the field mouse *Apodemus sylvaticus*, unpubl. data, Tom Black) and even insectivorous passerines by an increase in the abundance of their prey (Polis and Hurd 1995, Kolb *et al.* 2012, Cross *et al.* 2014). With regards to the islands sampled in this study all three islands hold populations of the winter wren *Troglodytes troglodytes*, which could all be considered genetically different (Shannon *et al.* 2014). The viability of resident insectivorous passerines could be dependent upon the abundant insect prey associated with seabird colonies. Overall, it seems to be likely that the effect of seabirds on island food webs is widespread. However, more work is needed to explore the temporal effects of seabirds on island food webs from periods, for example, outside the breeding season (Caut *et al.* 2012).

In conclusion, the cross-scale interaction of seabirds is observed to influence vegetation in seabird colonies and indirectly influence herbivores feeding in relation to seabird colonies. Puffins and skuas are likely to decrease plant diversity on Mingulay, resulting in greater proportional abundance of those species more tolerant to nutrient deposition and physical disturbance. This altered community composition created by seabirds will increase both spatial heterogeneity and diversity on an island scale. Separating the relative factors responsible for driving diversity is however difficult. Puffins and skuas both increase the percentage weight of N within grasses in seabird colonies and $\delta^{15}$N values indicate that these nutrients originate from seabirds. The increased $\delta^{15}$N value within mammalian hair also indicates the transfer of nutrients from seabirds indirectly across trophic levels via grazing. This provision of ornithogenic nutrients could alter the behaviour and increase reproductive success of herbivore communities. These results suggest that the effect of seabirds is far reaching within island food webs and that many other species may be dependent upon the temporal resource supplied by seabirds.

# Chapter 6

# Isotopic analysis of island House Martins *Delichon urbica* indicates marine provenance of nutrients

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# Abstract

The presence of one of the largest colonies of House Martins in Europe on the small island of Stora Karlsö, Sweden, led us to investigate the source of their food by analysis of stable isotopes of carbon and nitrogen. Carbon isotopic values of House Martin nestlings were the same as those of Common Guillemot nestlings fed on marine fish, but differed from local Collared Flycatcher nestlings fed on woodland insects. We infer that these House Martins fed their chicks almost exclusively on insects that had used nutrients derived from seabirds, indicating a dependence on the presence of a large seabird colony. We suggest by extension that some populations of island passerines of high conservation importance may also be dependent on nutrient subsidies from seabird colonies.

## 6.1 Introduction

Trophic cascades have been documented for a wide range of terrestrial and marine ecosystems, resulting from a growing understanding of energy flows and species interactions within systems (Pace *et al.* 1999). Such studies can explain factors influencing the structure and function of ecosystems and contribute towards an increased understanding of the role of human actions in shaping such dynamics (Shurin *et al.* 2002, Nyström *et al.* 2012). Recent studies of trophic cascades across ecosystems (Knight *et al.* 2005) highlight a number of issues associated with complex management of cross-scale dynamics (Cash *et al.* 2006). In particular, the effect of human actions on aquatic systems may be more significant when compared to terrestrial systems (Shurin *et al.* 2002). This sensitivity in aquatic systems may result in significant changes to consumer populations if perturbed. This disturbance could then propagate throughout aquatic environments and also influence terrestrial systems, which are subsidized by aquatic trans-boundary input (Kolb *et al.* 2010b). The trans-boundary input of nutrients is an increasingly recognised example of such cross-scale dynamic (Layman *et al.* 2012), which can have significant impacts upon recipient communities (Ellis 2005, Young *et al.* 2010, Caut *et al.* 2012).

In this study, we focus on seabirds as an important link in cross-scale dynamics. Seabirds have particularly been shown to influence insular systems where they breed (Mulder *et al.* 2011, Caut *et al.* 2012) by bringing onto land large quantities of nutrients through prey remains, eggs, feathers, carcasses and especially through deposition of guano (Siegfried *et al.* 1978). Nitrogen-rich guano frequently influences terrestrial systems (Ellis 2005), but it can also influence surrounding coastal waters through nutrient run-off (Bosman & Hockey 1986, Kolb *et al.* 2010b, 2010a). These marine subsidies may subsequently influence coastal communities, resulting in elevated nutrient levels, algal production and insect density (Bosman and Hockey 1986, Kolb *et al.* 2010a). Consequently, these subsidies may again feedback onto islands by terrestrial consumers feeding upon organisms who are themselves supported by nutrient run-off from seabird colonies.

We specifically investigated nitrogen and carbon stable isotopes, a commonly used tracer of nutrient transfer between food webs (Inger and Bearhop 2008), and focussed on feathers in terrestrial passerine House Martin *Delichon urbica* nestlings to trace seabird-derived nutrients. An individual's dietary selection can be inferred from the isotope signal of the feathers for the period over which they were grown and irrigated with blood (Forero and Hobson 2003, Pearson *et al.* 2003). Nitrogen isotopes indicate the trophic level at which animals were feeding, whilst isotopes of carbon differ in relative abundance between marine and terrestrial/freshwater ecosystems and thus indicate the source of carbon (Inger and Bearhop 2008). Breeding House Martins typically feed on flying terrestrial or freshwater insects within about 0.75 km of the nest, with an average foraging range of 0.45 km (Bryant and Turner 1987, Forrester *et al.* 2007). The abundant insect community often associated with seabird colonies (Sanchez-Piñero and Polis 2000, Kolb *et al.* 2010a) potentially represents a large, marine-derived prey source for such aerial insectivorous passerines. This study focuses upon an unusually large and expanding House Martin colony situated above a large and also expanding seabird colony in the Baltic Sea. To our knowledge, there are no published examples of nutrient transfer to passerines from seabirds. We thus test the hypothesis that House Martins on Stora Karlsö are strongly associated and dependent upon changes in the Baltic marine food web, mediated through ornithogenic insect prey rather than terrestrial autochthonous insects.

## 6.2 Methods

The Swedish island of Stora Karlsö (57°17'N, 17°58'E) in the Baltic Sea, *c.* 6.5 km off the west coast of Gotland (Figure 6.1) holds most of the breeding Common Guillemot *Uria aalge* population in the Baltic, with about 10,000 pairs nesting on limestone cliffs on the east coast, as well as large numbers of Razorbills *Alca torda* (Kadin *et al.* 2012). A lighthouse situated on top of the main seabird cliff provides nest sites for a colony of House Martins, comprising 150 pairs in 2013. To determine the extent to which seabirds influence the diet of terrestrial passerines, feathers were collected from nestlings of Common Guillemots, House Martins and Collared Flycatchers *Ficedula albicollis*. Feathers were analysed for the stable isotope ratios of nitrogen and carbon. Common Guillemot nestlings are fed entirely on small fish from the Baltic Sea (Kadin *et al.* 2012), thus representing a isotopic endpoint for a marine diet. Collared Flycatcher nestlings in the population sampled are fed with woodland caterpillars (Veen *et al.* 2010), representing the isotopic endpoint for the terrestrial diet. Variation in isotope values of carbon and nitrogen of House Martin nestling feathers, relative to Collared Flycatcher and Common Guillemot feathers, could thus be attributed to the indirect influence of ornithogenic prey.

Single feathers (tertials) were collected from one House Martin nestling from each of 16 nests on the lighthouse at Stora Karlsö between 30 June and 5 July 2013. Single feathers (primary coverts) were collected from each of 15 Common Guillemot nestlings captured below the cliff at Stora Karlsö as they fledged on 30 June 2013. Single feathers (tertials) were collected from one Collared Flycatcher nestling from each of 23 nest boxes (30 km from the House Martin colony) on Gotland from 23 to 25 June 2013. Cleaning or preservation agents may alter isotopic ratios (Quillfeldt *et al.* 2010). Consequently, feathers were collected, visually inspected for contamination and only clean feathers retained, and feathers were stored dry prior to analysis (Michalik *et al.* 2012). In the laboratory, feather barbs from a sample were cut from the rachis with sterilized scissors and weighed accurately (*c.* 0.7 mg) into individual tin cups for isotopic analysis. Carbon and nitrogen isotopes were analysed by continuous flow isotope ratio mass spectrometry (CF-IRMS) with a Costech ECS 4010 elemental analyser linked to a Thermo Scientific Delta V mass spectrometer. The stable isotope ratios were expressed in $\delta$ values as parts per thousand (‰). Internal standards are traceable to the following international standards, AIR for nitrogen and PeeDee Belemnite for carbon. Instrumental drift was corrected by means of the repeated measurement of two laboratory standards every 10 samples (alternating between gelatine and two isotopically distinctive alanines). Errors were small with standard deviations less than 0.04% for carbon and 0.15% for nitrogen, based on repeated measurements of lab tryptophan.

## 6.3 **Results**

Feathers analysed for $\delta^{15}$N and $\delta^{13}$C exhibited a range of isotopic values between species and individuals (Figure 6.2). Mean values ± se (and range) of $\delta^{15}$N for each species were: House Martin = 9.51 ± 0.06 (9.12 - 9.92), Collared Flycatcher = 8.35 ± 0.10 (7.75 – 9.87) and Common Guillemot = 14.39 ± 0.10 (13.82 – 15.33). Mean values ± SE (and range) of $\delta^{13}$C for each species were: House Martin = -20.06 ± 0.13 (-20.99 – -19.22), Collared Flycatcher = -23.74 ± 0.09 (-24.43 – -22.90) and Common Guillemot = -20.03 ± 0.05 (-20.49 – -19.70). There was a significant segregation in isotope values of feathers between species (MANOVA: Wilk's lambda = 0.002, $F_{2,51}$ = 571.6, $P < 0.001$; Figure 6.2) and both nitrogen and carbon isotopes contributed significantly to the difference between species (ANOVA: $\delta^{15}$N, $F_{2,51}$ = 541.4, $P < 0.001$; $\delta^{13}$C, $F_{2,51}$ = 1155.9, $P < 0.001$). *Post-hoc* Tukey's tests showed a significant difference in the $\delta^{15}$N between all three species ($P < 0.001$). The *post-hoc* tests for $\delta^{13}$C showed that, although there were significant differences between the pairs Collared Flycatcher-Common Guillemot and Collared Flycatcher-House Martin ($P < 0.001$), the difference between House Martin and Common Guillemot was not significant ($P = 0.967$). When comparing the difference in mean isotopic values between species, the largest differences are seen for nitrogen (6.04 ‰ between Collared Flycatcher and Common Guillemot, Table 6.1). Concomitant with the Tukey's test results, the smallest observed difference was -0.04‰ between the carbon isotope samples of House Martin and Common Guillemot.

**Table 6.1.** The difference in isotope values between pairs of species. Values in parentheses are lower and upper confidence intervals.

| Species comparison | Δ $\delta^{15}$N (‰) | Δ $\delta^{13}$C (‰) |
|---|---|---|
| Collared Flycatcher - Common Guillemot | 6.04 (5.73, 6.35) | 3.71 (3.38, 4.04) |
| Collared Flycatcher - House Martin | 1.16 (0.86, 1.47) | 3.67 (3.35, 3.99) |
| House Martin - Common Guillemot | 4.88 (4.55, 5.22) | -0.04 (-0.39, 0.32) |

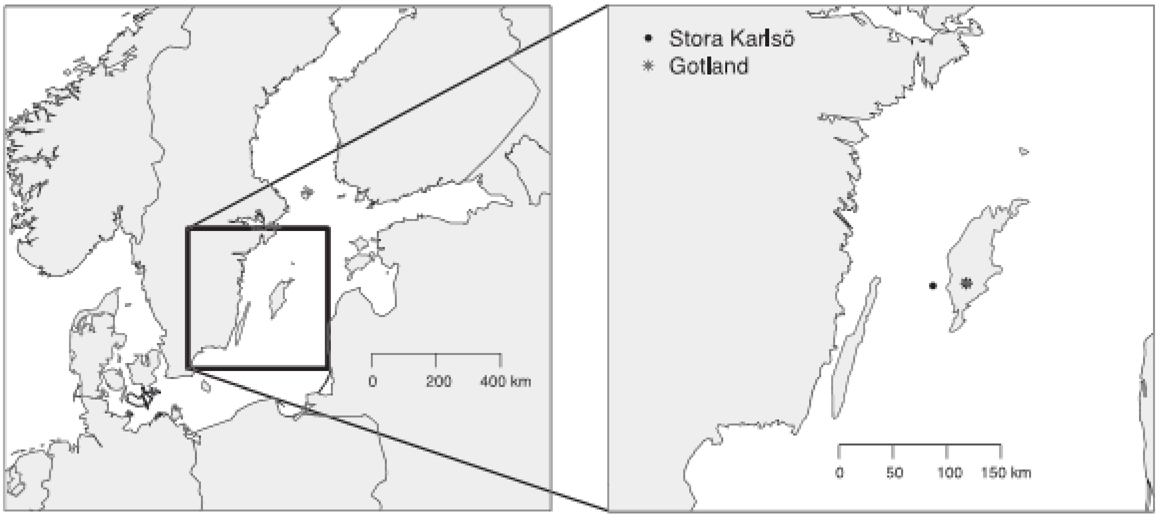


**Figure 6.1.** Location of the sampling sites in the Baltic Sea.

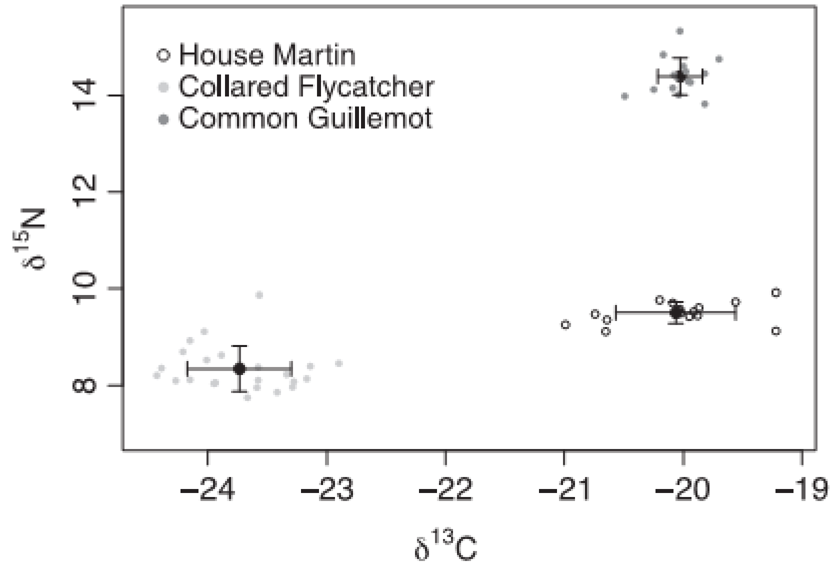


**Figure 6.2.** Stable isotope values in solid black symbols (‰, mean ± SD) for bird feathers. Scattered points around the means represent the individual samples for each species.

## 6.4 **Discussion**

We observed significant segregation in both nitrogen and carbon isotope values between the feathers of the three bird species (Figure 6.2). In particular, the carbon isotopic value of the ‘terrestrial’ House Martin was almost identical to that of the marine Common Guillemot, indicating a clear dependence of marine nutrients on the terrestrial bird species. The segregation of each species’ feathers by its isotope values is related to $\delta^{13}$C and $\delta^{15}$N variation in the diet; Common Guillemots feed predominantly on Sprats *Sprattus sprattus* (Kadin *et al.* 2012), Collared Flycatchers feed on a terrestrial-based (woodland) insect population and House Martins feed on an insect population, for which the carbon isotope value in chick feathers indicates is essentially 100% subsidized by marine nutrients most likely to be made available through seabirds.

The link between the observed nitrogen and carbon isotope values of House Martins and Common Guillemots is most likely to be through a marine prey source. It is most probable that the insect population which House Martin feed upon comprises adult Chironomidae (Håkan Elmqvist and Yngve Brodén, pers. comm.). Chironomidae emerge from coastal environments in the Baltic Sea where they are often found at much higher densities in proximity to seabird colonies (Kolb *et al.* 2010a). Chironomidae larvae near to seabird colonies are also found to have enriched $\delta^{15}$N values, reflecting their potential use of ornithogenic nutrients, which have been transported to coastal environments (Kolb *et al.* 2010b, 2012). Adult Chironomidae live for not more than a few days on average and do not feed extensively (Armitage *et al.* 1995), which would result in their stable isotope values reflecting that of the seabird-derived nutrients assimilated during larval development .

There are, to our knowledge, no previous examples of ornithogenic allochthonous input influencing insectivorous passerines, and relatively few examples of how nutrients can be traced from trans-boundary input into insectivorous passerines. Examples of allochthonous input traced into passerines include Tree Swallows *Tachycineta bicolor* in western Canada containing sewage-derived nitrogen as a result of feeding on emergent aquatic insects influenced by riverine sewage input (Wayland and Hobson 2001), and Winter Wrens *Troglodytes troglodytes* enriched in $\delta^{15}$N as a result of feeding on invertebrates, which in turn feed on salmon carcasses in North America (Christie *et al.* 2008). Furthermore, *Cinclodes* spp. of South America exhibit marine signatures when strongly associated with foraging in coastal environments compared to inland species of the same genus (Sabat and del Rio 2002). In contrast, isotopic signatures of different insectivorous passerine species, when uninfluenced by marine or anthropogenic inputs, appear to be consistent in their stable isotope values, in particular for $\delta^{13}$C (Hobson 1999). This consistency of stable isotope values between species also supports the use of a different insectivorous passerine species as a control sample in our study.

There is the possibility that observed differences in carbon values between the two insectivorous species could be attributed to other factors influencing carbon isotope ratios besides House Martins feeding on ornithogenic insects; however these factors are considered unlikely given the difference in magnitude. For example, $\delta^{13}$C values vary between plants with different photosynthetic pathways, *i.e.* C3, C4 or CAM. Given that plant species on both Stora Karlsö and Gotland are predominantly C3 plants, the enrichment of $^{13}$C observed in C4 or CAM plants is unlikely to contribute to the enriched signature of House Martins from herbivorous insect prey sources (Rubenstein and Hobson 2004). Both Stora Karlsö and Gotland are also at similar altitudes and latitudes thus the effect of these factors on carbon isotopic ratios will not influence the results. The use of sulphur isotopes ($^{34}$S/$^{32}$S) in identifying the origin of the House Martins’ prey is another potential tool to determine whether nutrients are derived from either a marine or terrestrial source (Hobson *et al.* 1999). However for this study the feathers sampled were not of sufficient mass to be analysed for both sulphur and nitrogen and carbon isotopic analysis.

The significant increase in $^{15}$N between Collared Flycatcher and House Martin also suggests the latter are feeding on more enriched $^{15}$N prey, attributed to the input of seabird nutrients. However, the $\delta^{15}$N values of House Martins are considerably lower than those of Common Guillemot chicks. This is not surprising, firstly as seabirds excrete nitrogen that is depleted relative to the ingested food (Bird *et al.* 2008), and secondly, as nutrient run-off into coastal waters would likely result in a lowering of the $\delta^{15}$N values due to dilution during transportation and within the Baltic Sea. This in turn would result in less enriched $\delta^{15}$N values of Chironomidae larvae and thus House Martins, relative to Common Guillemots.

An alternative prey source for House Martins may be terrestrial arthropods, which are often found in high abundance when feeding upon ornithogenic detritus (Polis and Hurd 1995, 1996, Sanchez-Piñero and Polis 2000). Bird *et al.* (2008) inferred that the nitrogen signature of ammonia was especially depleted since guano nitrogen signature was not dramatically different from that of the birds' food. This suggests that the nitrogen taken up by insects feeding within the seabird colony could be derived from ammonia rather than from the uric acid component of excreta.

House Martins breed throughout much of Europe, but their colonies are typically of fewer than five pairs and only about 1% of colonies hold more than 30 pairs (Cramp 1988). In much of the suitable habitat in Europe, nesting density of House Martins is typically around one to two pairs per km$^2$ (Cramp 1988), so Stora Karlsö (an island of 2.5 km$^2$ with 170 pairs of House Martins in 2013) represents an unusually high breeding density for this species. House Martin numbers in the lighthouse colony increased from 23 pairs in 1984 to 41 in 1998, 51 in 2005 and 150 in 2013 (Länsstyrelsen 2006, unpubl. data). This increase contrasts with an estimated 30-49% decline in House Martins throughout Sweden over a 30-year period (Ottvall *et al.* 2009). Colony specific population parameters of Common Guillemots, including adult survival (Österblom *et al.* 2004) and breeding success (Kadin *et al.* 2012) are consistently high, and indicate, together with census counts at Stora Karlsö (JHS unpubl. data) a substantial increase in the Common Guillemot population. Counts of Razorbills, the other large population of sprat feeding seabird on Stora Karlsö, also show a marked increase during recent years (Länsstyrelsen. 2006). Previous studies indicate strong links between the dynamics of several Common Guillemot population parameters and the dynamics of the sprat stock (Österblom *et al.* 2006, Kadin *et al.* 2012). It is likely that the growth of the Guillemot population has been enabled by a dramatic increase in the Baltic Sea sprat stock, in turn affected by overfishing of its main predator cod *Gadus morhua* and changing climatic conditions (Casini *et al.* 2008, 2009). Overfishing of cod can have profound effects on entire marine food webs – examples include effects on pelagic fish stocks, zooplankton, phytoplankton and nutrients in the Scotian Shelf (Frank *et al.* 2005), and potentially also phytoplankton biomass in the Baltic Sea (Casini *et al.* 2009). We speculate that the increasing numbers in the House Martin colony on Stora Karlsö may be a consequence of the large and increasing Common Guillemot population (in turn substantially affected by marine ecosystem dynamics), through the provision of an abundant coastal insect prey subsidy derived from nutrient run-off into coastal waters from the adjacent seabird colony.

The $\delta^{15}$N and especially the $\delta^{13}$C values of House Martin nestling feathers indicate that seabirds play an important role in the transfer of nutrients from the marine environment into this local population. Other island populations of insectivorous birds may also be influenced by the presence of seabirds. For example, the St Kilda Wren *T. t. hirtensis* (Miles 2011) and the Fair Isle Wren *T. t. fridariensis* (Aspinall and Aspinall 2011) occur at remarkably high local densities, especially on the sea cliffs (Forrester *et al.* 2007), which hold internationally important populations of seabirds. Their numbers may be dependent on nutrient inputs to these islands from seabirds. There is thus a need to further understand the degree of dependence of other passerine species and populations on seabird subsidies, in particular in the context of declining seabird populations (Caut *et al.* 2012). We argue that such cross-scale dynamics represent an interesting challenge for agencies defining their management mandate by traditional ecosystem boundaries.

# Chapter 7

# General Discussion

## 7.1 Summary of main findings

This final chapter brings together the results of this thesis and discusses them in the context of two broad categories: monitoring the Atlantic puffin using time-lapse photography (Chapters 2 – 3), and the influence of seabirds on islands (Chapters 4 -6).

This study has demonstrated that the Atlantic puffin can be monitored remotely from time-lapse photography; however there are limitations which warrant further study. In general, the use of cameras for monitoring puffins allows high temporal resolution data to be collected on the numbers of puffins over time with very little human intervention. Manual methods for determining such resolution of attendance are likely to require significant costs of time, labour and exposure to often harsh conditions in remote locations. Adaptations to hardware could relatively easily adapt camera systems to remotely collect data without human intervention, except for installation and collection of cameras.

Data derived from time-lapse photography can be used to provide a detailed insight into puffin attendance, across different temporal scales. Installation of multiple cameras also allows for consideration of the variation in attendance between and within colonies. Understanding how attendance varies has important consequences for refining periods of manual monitoring, inferring productivity and also as a stand-alone approach for estimating population size.

Understanding how puffin attendance varies over a daily and seasonal scale can lead to a more appropriate timing of when counts should be undertaken; cameras installed early in the season could be used to predict periods of high attendance, which could be used to standardise counts of puffins. However, the feasibility of this approach was not tested in this study and is an avenue for further work.

Combining high temporal resolution data with variables known to influence attendance provides further knowledge on the variability of puffin attendance. For example, using only data extracted from photographs showed that predator presence decreased puffin attendance. By relating attendance to other variables, *e.g.* weather or tidal stage, their effect on attendance can also be understood in detail. This study showed that puffin attendance decreased with spring and neap tides, decreased with increasing wind speeds and was not influenced by temperature. However, there are methodological limitations which require further consideration.

Whilst understanding attendance patterns is of importance in reflecting local conditions and productivity (Gaston and Nettleship 1982, Anker-Nilssen 2010) and also for refining periods of manual counts, there is also the potential for the use of photography as a stand-alone approach. The results of this study showed that high temporal resolution data can capture much higher counts of puffins on land, which show a positive and significant relationship with population size. However, the variability that can be introduced from having different photographic intervals or study durations between cameras requires the need for standardised sampling intensity. There is also the possibility to monitor puffins by plotting the positions of puffins over time with the assumption that clusters of puffin may infer an occupied burrow. Overall, the use of time-lapse photography is not suggested as a replacement to monitor puffins, rather as an additional tool for detailed exploration of puffin attendance and for deriving indices of population size, in particular locations. Where access to puffin colonies is impossible then counts of puffins from photography may be of use to infer population size. However, to use photography to monitor puffins requires further work in increasing sample size, considering edge effects and producing a better understanding of the relationship between counts of puffins and the population size.

With a detailed understanding of population size the influence of seabirds on land can be more fully understood. The result of this study showed that seabirds input vast quantities of nutrients onto land in one breeding season. Whilst this study is confined to one island, the methodology and broadly the results are applicable to all islands with seabird populations.

The input of nutrients onto islands was shown in this study to influence a broad range of species. The physical presence of seabirds and their nutrient input onto islands around Scotland resulted in the formation of relatively different plant communities, often with the presence of species associated with high nitrogen input. The influence of seabirds for this study was most noticeable in the upland moorland of Mingulay where skua territories had distinctly different vegetation without any influence of grazing. Skua territories were dominated by the lush growth of grasses in contrast to the surrounding relatively rank heather community. The chemical composition of grasses in both the puffin and skua colonies was also shown to be significantly different from control areas. Grasses from seabird colonies had significantly higher $\delta^{15}$N values and N concentration, compared to control areas, which is indicative of nutrients being derived from seabirds. Whilst this observation of higher $\delta^{15}$N values in plants is well studied in the literature, this study further demonstrated that seabird nutrients pass into secondary consumers. Hair samples from rabbit and sheep found within puffin colonies had significantly higher values of $\delta^{15}$N, compared to samples of hair from control areas. This would indicate that rabbits and sheep are deriving their nutrients in part from seabirds. This observation is to the author's knowledge the first demonstration of nutrients being transferred from seabirds to rabbit or sheep, via ornithogenic forage.

Furthermore, a novel study on passerines demonstrated that ornithogenic nutrients deposited on an island in the Baltic Sea were incorporated into house martin chicks. This transfer of nutrients is likely to arise through the feeding of house martins on emergent Chironomidae, which had incorporated ornithogenic nutrients from the guano leached into surrounding waters underneath seabird colonies.

Together these studies on the influence of seabirds on islands extend our understanding of how seabirds exert bottom-up dynamics on insular food webs.

## 7.2 Conservation issues and further work

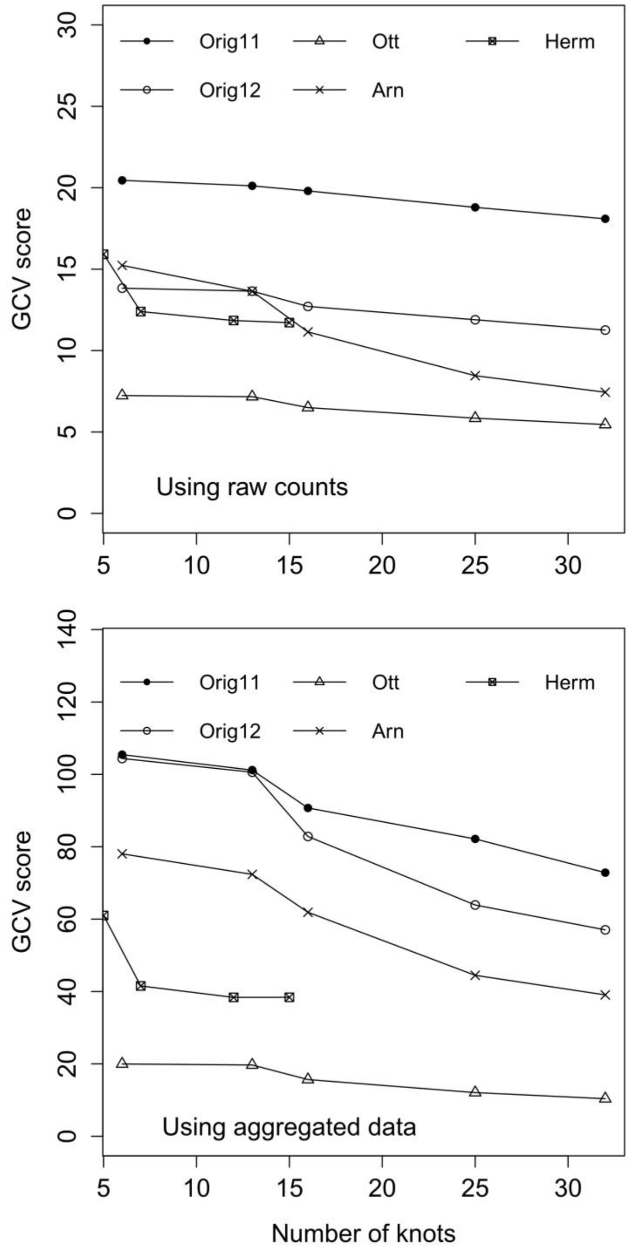
Determining the population size of seabirds is critical for understanding the response of seabirds to both natural and anthropogenic change and furthermore for targeting effective management of populations. The difficulty in monitoring the Atlantic puffin is still not fully overcome; however the use of time-lapse photography provides an additional tool to supplement existing schemes in those locations which are currently inaccessible. Equally, the use of time-lapse photography for monitoring colonial seabirds is likely to have far reaching consequences for a range of species (Huffeldt and Merkel 2013). The use of photography in general could be used to study a range of seabird behaviour and components of breeding success, *e.g.* productivity, although for puffins more work is needed (Anker-Nilssen 2010, Lorentzen *et al.* 2012). Photography could also be used to develop indices of disturbance by enumerating predator presence or observing human disturbance within photographs.

The lack of an automated approach to counting puffins is a main factor limiting the use of this method currently. When puffins can be automatically detected and counted accurately then the viability of a photographic method will increase. As technology further improves, time-lapse photography may be replaced by video, where a frame by frame analysis provides continual coverage across the season (Dickinson *et al.* 2008). There is overall a need to develop a monitoring programme using time-lapse photography to look into its validity in detecting long-term changes in population size and further work on how it compares to current methods.

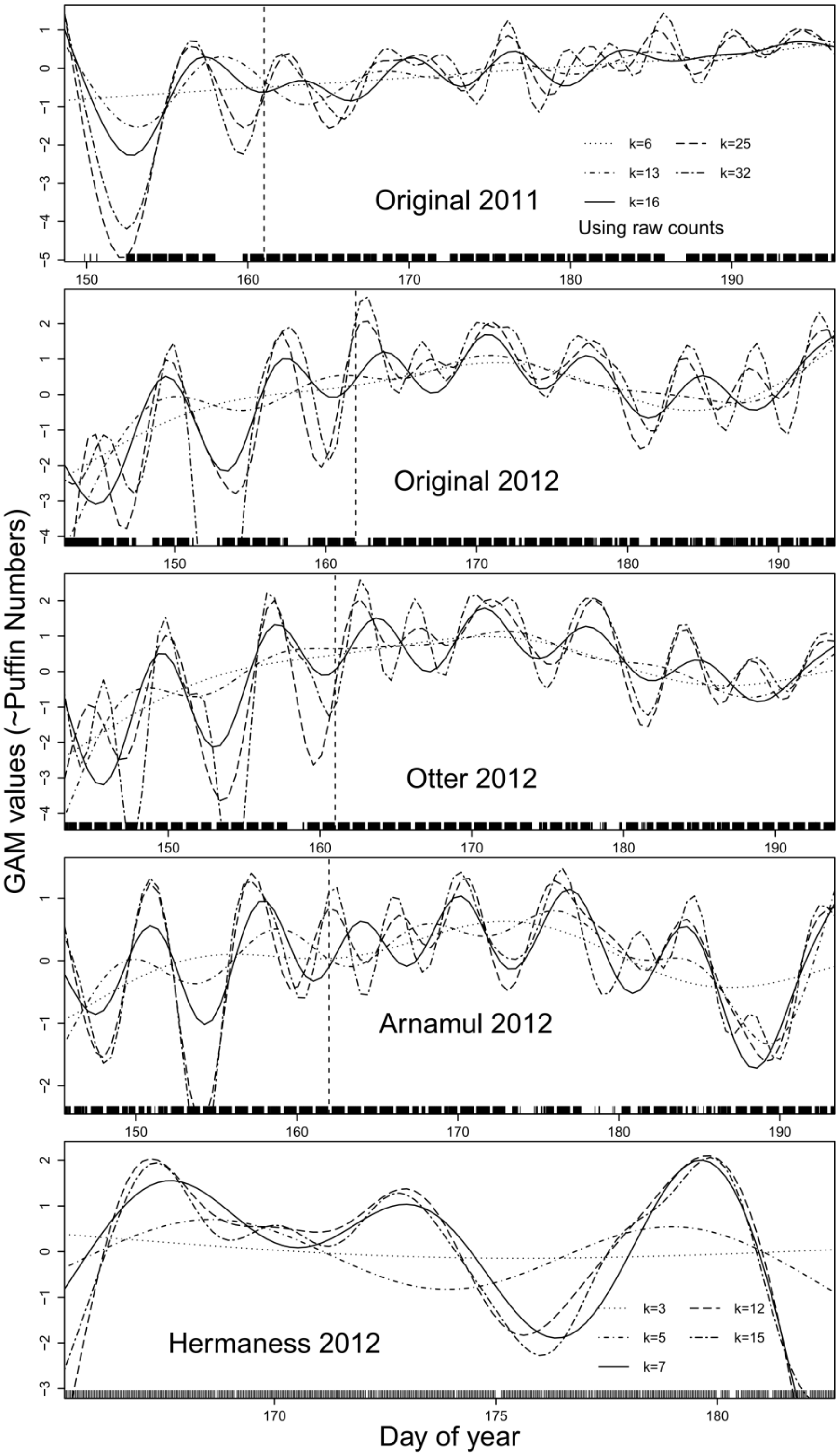
With an increasing understanding of the size of a population comes further awareness of the extent to which seabirds influence terrestrial systems. This study demonstrates that seabirds deposit large quantities of nutrients onto land, which as exemplified by Mingulay, is likely to outweigh the *in situ* production of nutrients. Changes in seabird populations either from natural or anthropogenic cause could quite possibly have wider impacts on island food webs than perhaps previously considered. This study has demonstrated that nutrients from seabirds travel through island food webs and influence species not necessarily associated with seabirds directly, *e.g.* sheep, rabbits and a migratory passerine species. Equally, this study has only considered limited avenues of seabird influence. The vast quantities of nutrients deposited on land by seabirds combined with their physical disturbance and the introduction of novel species from seed dispersal are all important areas with which to research further. Equally, the transfer of ornithogenic nutrients may increase productivity or alter behaviour of grazing animals and this is not considered in this study. Given the contentious association between skuas and grazing animals the benefit these seabirds may actually exert on grazers requires further work. It is also important to note that large quantities of nitrogen are likely to be leached out of island systems and into surrounding systems: either terrestrial, freshwater or marine. Exploring the fate of nitrogen post-deposition may reveal how trans-boundary movement influences neighbouring systems. Removal of a seabird population could result in large scale shifts in community structure. Finally, species tied to island habitats during the breeding season may be closely linked with seabird populations, which raise important concerns governing how management and conservation of seabird populations influences island food webs.

# APPENDIX I

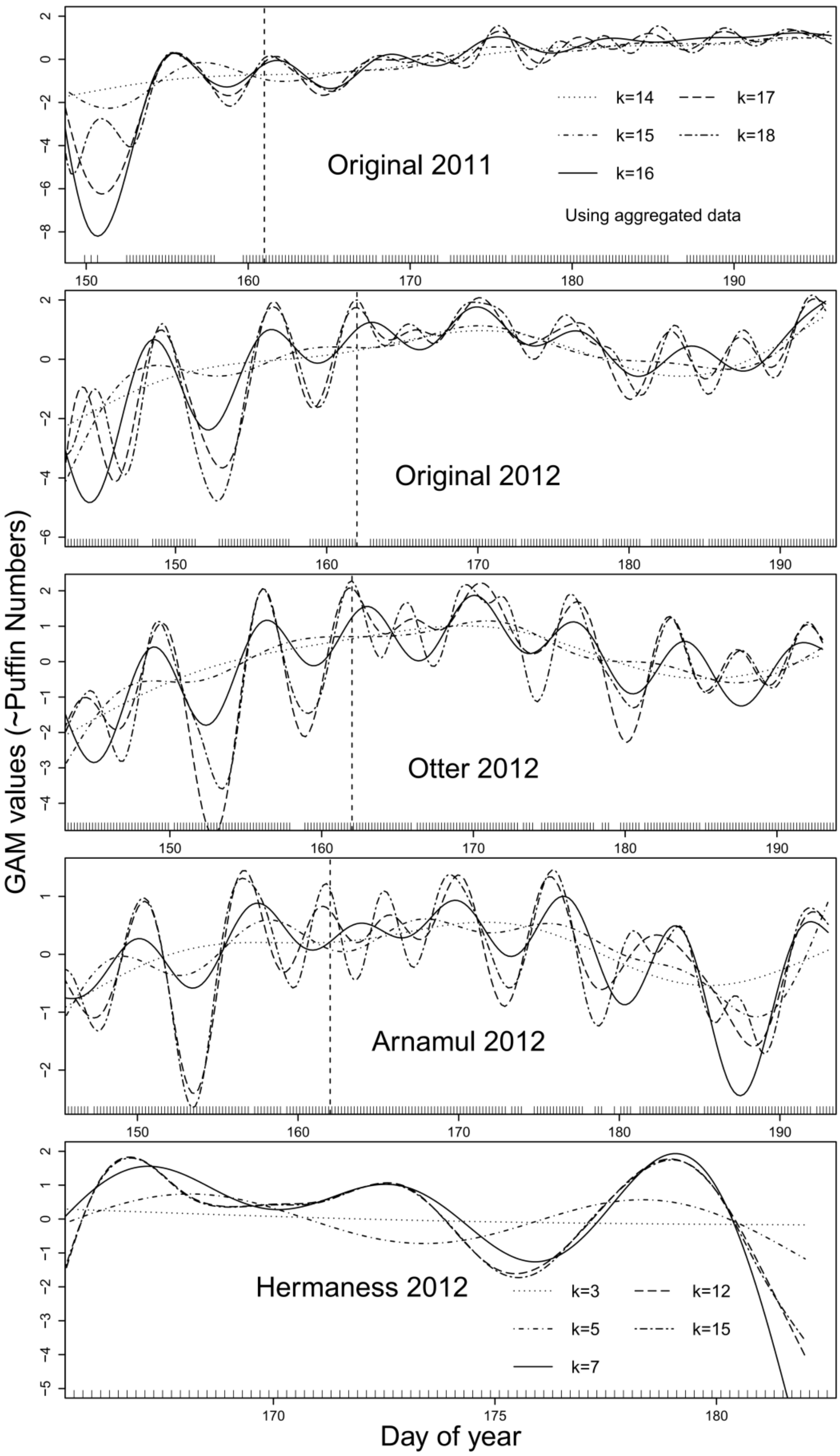
## Generalised additive models



**A:** Generalised cross-validation (GCV) scores for each colony with different numbers of knots, using (top) raw counts and (bottom) aggregated data into five ~5-h daily periods.



**B:** Predicted GAM values with varying numbers of knots (k), derived from the raw counts of puffins observed for each colony. The small, vertical dashes going along the x-axis (rug plot) represent the density of observations over time. Note the different x-axis scales. The x-axis scale, vertical line and number of knots are as Figure 2.6.



**C:** Predicted GAM values with varying degrees of freedom derived from the aggregated number of puffins into daily periods over time. The rug plot represents the density of observations over time. Note the different x-axis scales. The x-axis scale, vertical line and number of knots are as Figure 2.6

# APPENDIX II

# Abundance and list of plant species on Mingulay

Total abundance data for combined quadrats from each site and species on Mingulay over time. P = Puffin; S = Skua; SB = Seabird and Ct = Control

| Species | Species' code | P SB 2013 | P Ct 2013 | P SB 2012 | P Ct 2012 | S SB 2012 | S Ct 2012 |
|---|---|---|---|---|---|---|---|
| *Achillea millefolium* | Ach_mil | 437 | 493 | 335 | 417 | 0 | 0 |
| *A. capillaris* | Agr_cap | 65 | 269 | 58 | 225 | 114 | 84 |
| *A.stolonifera* | Agr_stol | 120 | 139 | 334 | 327 | 510 | 142 |
| *Anagallis tenella* | Ana_ten | 245 | 789 | 395 | 869 | 0 | 5 |
| *Anthoxanthum odoroatum* | Ant_odo | 243 | 108 | 127 | 171 | 48 | 122 |
| *Armeria maritima* | Arm_mar | 0 | 0 | 0 | 0 | 1 | 0 |
| *Bellis perennis* | Bel_per | 55 | 83 | 26 | 112 | 0 | 0 |
| *Bromus hordeaceus* | Bro_hor | 0 | 0 | 38 | 0 | 0 | 0 |
| Bryophyta | Moss | 2000 | 1828 | 1834 | 1870 | 81 | 354 |
| *Calluna vulgaris* | Cal_vul | 0 | 7 | 0 | 13 | 12 | 163 |
| *Carex* spp. | Car_spp | 1678 | 1366 | 1677 | 1670 | 268 | 686 |
| *Centaurea nigrans* | Cen_nig | 121 | 318 | 86 | 316 | 0 | 0 |
| *Centaurium pulchellum* | Cen_pul | 0 | 0 | 25 | 2 | 0 | 0 |
| *Cerastium fontanum* | Cer_fon | 43 | 1 | 14 | 19 | 65 | 3 |
| *Cirsium arvense* | Cir_arv | 0 | 3 | 0 | 5 | 0 | 0 |
| *Cochlearia officinalis* | Coc_off | 0 | 0 | 0 | 0 | 12 | 0 |
| *Dactylorhiza fuchsii* | Dac_fus | 0 | 1 | 0 | 0 | 0 | 1 |
| *D. incarnata* | Dac_inc | 0 | 0 | 0 | 0 | 0 | 1 |
| *D.maculata* | Dac_mac | 0 | 0 | 0 | 0 | 0 | 3 |
| *Equisteum* spp. | Equ_spp | 0 | 3 | 0 | 0 | 0 | 0 |
| *Erica cinerea* | Eri_cin | 0 | 0 | 0 | 0 | 1 | 3 |
| *E. tetralix* | Eri_tet | 0 | 0 | 0 | 0 | 5 | 69 |
| *Eriophurum angustifolium* | Eri_ang | 0 | 0 | 0 | 0 | 74 | 131 |
| *Euphrasia* agg. | Eup_agg | 89 | 73 | 331 | 230 | 0 | 0 |
| *Festuca* spp. | Festuca | 1910 | 1998 | 2000 | 2000 | 1851 | 1919 |
| *Galium saxatile* | Gal_sax | 0 | 10 | 8 | 0 | 21 | 0 |
| *G. verum* | Gal_ver | 641 | 610 | 813 | 1234 | 0 | 0 |
| *Holcus lanatus* | Hol_lan | 1082 | 893 | 860 | 635 | 1067 | 159 |
| *Hydrocotyle vulgaris* | Hyd_vul | 0 | 40 | 0 | 48 | 0 | 0 |
| *Juncus spp.* | Jun_spp | 0 | 0 | 0 | 0 | 0 | 4 |
| *Koeleria macrantha* | Koe_mac | 4 | 0 | 200 | 47 | 7 | 9 |
| *Leontodon autumnalis* | Leo_aut | 0 | 0 | 0 | 0 | 0 | 2 |
| *Linum catharticum* | Lin_cat | 40 | 153 | 274 | 428 | 0 | 0 |
| *Lotus corniculatus* | Lot_cor | 394 | 785 | 305 | 652 | 0 | 0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Luzula campestris* | Luz_cam | 359 | 288 | 263 | 291 | 304 | 47 |
| *Molinia caerulea* | Mol_cae | 10 | 46 | 0 | 0 | 69 | 1261 |
| *Myosotis* spp. | Myo_spp | 0 | 0 | 0 | 0 | 0 | 1 |
| *Nardus stricta* | Nar_str | 0 | 6 | 0 | 39 | 15 | 101 |
| *Narthecium ossifragum* | Nar_oss | 0 | 0 | 0 | 0 | 0 | 31 |
| *Ophioglossum vulgatum* | Oph_vul | 77 | 1 | 23 | 18 | 1 | 0 |
| *Pedicularis sylvatica* | Ped_syl | 0 | 0 | 0 | 0 | 0 | 1 |
| *Plantago coronopus* | Pla_cor | 806 | 502 | 671 | 551 | 30 | 20 |
| *P. lanatus* | Pla_lan | 1141 | 1391 | 957 | 1189 | 38 | 101 |
| *P.maritima* | Pla_mar | 451 | 120 | 385 | 69 | 110 | 202 |
| *Poa compressa* | Poa_com | 0 | 0 | 1 | 0 | 0 | 0 |
| *P. pratensis* | Poa_pra | 120 | 27 | 171 | 60 | 265 | 3 |
| *Polygala serpyllifolia* | Pol_ser | 0 | 0 | 0 | 7 | 0 | 8 |
| *P. vulgaris* | Pol_vul | 0 | 0 | 6 | 4 | 0 | 0 |
| *Potentilla erecta* | Pot_ere | 0 | 63 | 0 | 119 | 590 | 1029 |
| *Primula vulgarus* | Pri_vul | 0 | 0 | 0 | 0 | 4 | 0 |
| *Prunella vulgaris* | Pru_vul | 662 | 637 | 541 | 712 | 0 | 0 |
| *Pteridium aquilinum* | Pte_aqu | 0 | 3 | 0 | 5 | 0 | 0 |
| *Ranunculus flammula* | Ran_fla | 0 | 0 | 0 | 0 | 7 | 0 |
| *R. repens* | Ran_rep | 16 | 25 | 10 | 8 | 0 | 0 |
| *Rumex acetosa* | Rum_ace | 0 | 0 | 0 | 1 | 37 | 1 |
| *Sagina procumbens* | Sag_pro | 0 | 0 | 0 | 0 | 25 | 1 |
| *Salix repens* | Sal_rep | 0 | 0 | 0 | 0 | 10 | 115 |
| *Scilla verna* | Sci_ver | 296 | 1 | 285 | 2 | 36 | 21 |
| *Sedum anglica* | Sed_ang | 1 | 0 | 0 | 0 | 5 | 0 |
| *Senecio jacobea* | Sen_jac | 117 | 128 | 140 | 116 | 0 | 0 |
| *Succisa pratensis* | Suc_pra | 0 | 0 | 6 | 0 | 19 | 152 |
| *Taraxacum* spp. | Tar_spp | 0 | 0 | 1 | 0 | 37 | 2 |
| *Thymus polytrichus* | Thy_pol | 1986 | 1839 | 1978 | 1884 | 13 | 111 |
| *Tricophorum cespitosum* | Tri_ces | 0 | 0 | 0 | 0 | 0 | 80 |
| *Trifoium spp.* | Tri_spp | 699 | 485 | 664 | 522 | 170 | 82 |
| *Viola* spp. | Vio_spp | 316 | 1054 | 349 | 1102 | 32 | 100 |
| *Vetch* spp. | Vet_spp | 0 | 3 | 0 | 17 | 0 | 0 |

# APPENDIX III

# Isotopic analysis of island House Martins *Delichon urbica* indicates marine provenance of nutrients

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Short communication

# Isotopic analysis of island House Martins *Delichon urbica* indicates marine provenance of nutrients

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The presence of one of the largest colonies of House Martins in Europe on the small island of Stora Karlsö, Sweden, led us to investigate the source of their food by analysis of stable isotopes of carbon and nitrogen. Carbon isotopic values of House Martin nestlings were the same as those of Common Guillemot *Uria aalge* nestlings fed on marine fish, but differed from local Collared Flycatcher *Ficedula albicollis* nestlings fed on woodland insects. We infer that these House Martins fed their chicks almost exclusively on insects that had used nutrients derived from seabirds, indicating a dependence on the presence of a large seabird colony. We suggest by extension that some populations of island passerines of high conservation importance may also be dependent on nutrient subsidies from seabird colonies.

**Keywords:** Common Guillemot, food webs, passerines, stable isotope analysis.

Trophic cascades have been documented for a wide range of terrestrial and marine ecosystems, resulting from a growing understanding of energy flows and species interactions within systems (Pace *et al.* 1999). Such studies can explain factors influencing the structure and function of ecosystems and contribute towards an increased understanding of the role of human actions in shaping such dynamics (Shurin *et al.* 2002, Nyström *et al.* 2012). Recent studies of trophic cascades across ecosystems (Knight *et al.* 2005) highlight a number of issues associated with complex management of cross-scale dynamics (Cash *et al.* 2006). In particular, the effect of human actions on aquatic systems may be more significant than on terrestrial systems (Shurin *et al.* 2002). This sensitivity in aquatic systems may result in significant changes to consumer populations if perturbed. This disturbance could then propagate throughout aquatic environments and also influence terrestrial systems, which are subsidized by aquatic trans-boundary input (Kolb *et al.* 2010b). The trans-boundary input of nutrients is an increasingly recognized example of such cross-scale dynamics (Layman *et al.* 2012), which can have significant impacts upon recipient communities (Ellis 2005, Young *et al.* 2010, Caut *et al.* 2012).

In this study, we focus on seabirds as an important link in cross-scale dynamics. Seabirds have been shown to influence insular systems where they breed (Mulder *et al.* 2011, Caut *et al.* 2012) by bringing onto land large quantities of nutrients through prey remains, eggs, feathers, carcasses and especially the deposition of guano (Siegfried *et al.* 1978). Nitrogen-rich guano frequently influences terrestrial systems (Ellis 2005), but it can also influence surrounding coastal waters through nutrient run-off (Bosman & Hockey 1986, Kolb *et al.* 2010a,b). These marine subsidies may subsequently influence coastal communities, resulting in elevated nutrient levels, algal production and insect density (Bosman & Hockey 1986, Kolb *et al.* 2010a). Consequently, these subsidies may again feed back onto islands by terrestrial consumers feeding upon organisms that are themselves supported by nutrient run-off from seabird colonies.

We specifically investigated nitrogen and carbon stable isotopes, a commonly used tracer of nutrient transfer between food webs (Inger & Bearhop 2008), and focused on feathers in terrestrial House Martin *Delichon urbica* nestlings to trace seabird-derived nutrients. An individual's dietary selection can be inferred from the isotope signal of the feathers for the period over which they were grown and irrigated with blood (Forero & Hobson 2003, Pearson *et al.* 2003). Nitrogen isotopes indicate the trophic level at which animals were feeding, while isotopes of carbon differ in relative abundance between marine and terrestrial/freshwater ecosystems and thus indicate the source of carbon (Inger & Bearhop 2008). Breeding House Martins typically feed on flying terrestrial or freshwater insects within about 0.75 km of the nest, with an average foraging range of 0.45 km (Bryant & Turner 1987, Forrester & Andrews 2007). The abundant insect community often associated with seabird colonies (Sanchez-Piñero & Polis 2000, Kolb *et al.* 2010a) potentially represents a large, marine-derived prey source for such aerial insectivorous passerines. This study focuses upon an unusually large and expanding House Martin colony situated above a large and also expanding seabird colony on a small island in

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the Baltic Sea. To our knowledge, there are no published examples of nutrient transfer from seabirds to passerines. We thus test the hypothesis that House Martins on Stora Karlsö are strongly associated with and dependent upon changes in the Baltic marine food web, mediated through ornithogenic insect prey rather than terrestrial autochthonous insects.

## METHODS

The Swedish island of Stora Karlsö (57°17′N, 17°58′E) in the Baltic Sea, *c.* 6.5 km off the west coast of Gotland (Fig. 1), holds most of the breeding Common Guillemot *Uria aalge* population in the Baltic, with about 10 000 pairs nesting on limestone cliffs on the east coast, as well as large numbers of Razorbills *Alca torda* (Kadin *et al.* 2012). A lighthouse situated on top of the main seabird cliff provides nest-sites for a large colony of House Martins, numbering 150 pairs in 2013. To determine the extent to which seabirds influence the diet of terrestrial passerines, feathers were collected from nestlings of Common Guillemots, House Martins and Collared Flycatchers *Ficedula albicollis*. Feathers were analysed for the stable isotope ratios of nitrogen and carbon. Common Guillemot nestlings are fed entirely on small fish from the Baltic Sea (Kadin *et al.* 2012), thus representing an isotopic endpoint for a marine diet. Collared Flycatcher nestlings in the population sampled are fed on woodland caterpillars (Veen *et al.* 2010), representing the isotopic endpoint for the terrestrial diet. Variation in isotope values of carbon and nitrogen of House Martin nestling feathers, relative to Collared Flycatcher and Common Guillemot feathers, could thus be attributed to the indirect influence of ornithogenic prey.

Single feathers (tertials) were collected from one House Martin nestling from each of 16 nests on the lighthouse at Stora Karlsö between 30 June and 5 July 2013. Single feathers (primary coverts) were collected from each of 15 Common Guillemot nestlings captured below the cliff at Stora Karlsö as they fledged on 30 June 2013. Single feathers (tertials) were collected from one Collared Flycatcher nestling from each of 23 nest-boxes (30 km from the House Martin colony) on Gotland from 23 to 25 June 2013. Cleaning or preservation agents may alter isotopic ratios (Quillfeldt *et al.* 2010). Consequently, feathers were collected, visually inspected for contamination (only clean feathers were retained) and stored dry prior to analysis (Michalik *et al.* 2012). In the laboratory, feather barbs from a sample were cut from the rachis with sterilized scissors and weighed precisely (*c.* 0.7 mg) in individual tin cups for isotopic analysis. Carbon and nitrogen isotopes were analysed by continuous flow isotope ratio mass spectrometry (CF-IRMS) with a Costech ECS 4010 elemental analyser linked to a Thermo Scientific Delta V mass spectrometer. The stable isotope ratios were expressed in $\delta$ values as parts per thousand (‰). Internal standards are traceable to the following international standards, AIR for nitrogen and PeeDee Belemnite for carbon. Instrumental drift was corrected by means of the repeated measurement of two laboratory standards every 10 samples (alternating between gelatine and two isotopically distinctive alanines). Errors were small with standard deviations less than 0.04% for carbon and 0.15% for nitrogen, based on repeated measurements of laboratory tryptophan.

## RESULTS

Feathers analysed for $\delta^{15}$N and $\delta^{13}$C exhibited a range of isotopic values between species and individuals (Fig. 2). Mean values ± 1 se (and range) of $\delta^{15}$N for each species were: House Martin = 9.51 ± 0.06 (9.12–9.92), Collared Flycatcher = 8.35 ± 0.10 (7.75–9.87) and Common Guillemot = 14.39 ± 0.10 (13.82–15.33). Mean values ± 1 se (and range) of $\delta^{13}$C for each species were: House Martin = −20.06 ± 0.13 (−20.99 to −19.22), Collared Flycatcher = −23.74 ±

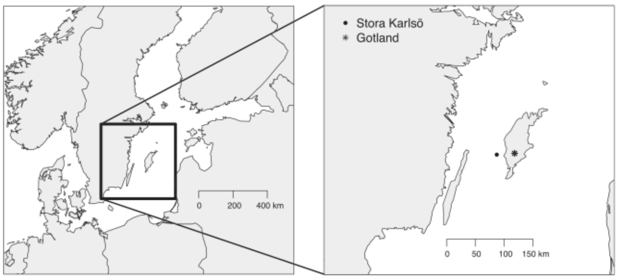

**Figure 1.** Location of the sampling sites in the Baltic Sea.

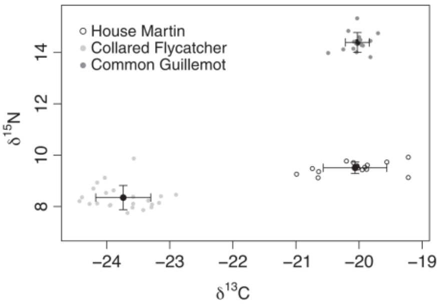

**Figure 2.** Stable isotope values in solid black symbols (‰, mean ± 1 sd) for bird feathers. Scattered points around the means represent individual samples for each species.

**Table 1.** The difference in isotope values between pairs of species

| Species comparison | Δ $\delta^{15}$N (‰) | Δ $\delta^{13}$C (‰) |
|---|---|---|
| Collared Flycatcher–Common Guillemot | 6.04 (5.73, 6.35) | 3.71 (3.38, 4.04) |
| Collared Flycatcher–House Martin | 1.16 (0.86, 1.47) | 3.67 (3.35, 3.99) |
| House Martin–Common Guillemot | 4.88 (4.55, 5.22) | −0.04 (−0.39, 0.32) |

Values in parentheses are lower and upper 95% confidence intervals.

0.09 (−24.43 to −22.90) and Common Guillemot = −20.03 ± 0.05 (−20.49 to −19.70). There was a significant segregation in isotope values of feathers between species (multivariate analysis of variance (MANOVA): Wilks' lambda = 0.002, $F_{2,51}$ = 571.6, $P < 0.001$; Fig. 2) and both nitrogen and carbon isotopes contributed significantly to the difference between species (analysis of variance (ANOVA): $\delta^{15}$N, $F_{2,51}$ = 541.4, $P < 0.001$; $\delta^{13}$C, $F_{2,51}$ = 1155.9, $P < 0.001$). *Post hoc* Tukey tests showed a significant difference in $\delta^{15}$N between all three species ($P < 0.001$). The *post hoc* tests for $\delta^{13}$C showed that, although there were significant differences between the pairs Collared Flycatcher–Common Guillemot and Collared Flycatcher–House Martin ($P < 0.001$), the difference between House Martin and Common Guillemot was not significant ($P = 0.967$). When comparing the difference in mean isotopic values between species, the largest differences were seen for nitrogen (6.04‰ between Collared Flycatcher and Common Guillemot, Table 1). Concomitant with the Tukey test results, the smallest observed difference was −0.04‰, between the carbon isotope samples of House Martin and Common Guillemot.

## DISCUSSION

We observed significant segregation in both nitrogen and carbon isotope values between the feathers of the three bird species (Fig. 2). In particular, the carbon isotopic value of the 'terrestrial' House Martin was almost identical to that of the marine Common Guillemot, indicating a clear dependence of the terrestrial bird species on marine nutrients. The segregation of each species' feathers by its isotope values is related to $\delta^{13}$C and $\delta^{15}$N variation in the diet; Common Guillemots feed predominantly on Sprats *Sprattus sprattus* (Kadin *et al.* 2012), Collared Flycatchers feed on a terrestrial-based (woodland) insect population, and House Martins feed on an insect population, for which the carbon isotope value in chick feathers indicates is essentially entirely subsidized by marine nutrients, most likely made available through seabirds.

The link between the observed nitrogen and carbon isotope values of House Martins and Common Guillemots is most likely through a marine prey source. It is most probable that the insect population that House Martins feed upon comprises adult Chironomidae (H. Elmqvist and Y. Brodén, pers. comm.). Chironomidae emerge from coastal environments in the Baltic Sea where they are often found at much higher densities in proximity to seabird colonies (Kolb *et al.* 2010a). Chironomidae larvae near to seabird colonies are also found to have enriched $\delta^{15}$N values, reflecting their potential use of ornithogenic nutrients, which have been transported to coastal environments (Kolb *et al.* 2010b, 2012). Adult Chironomidae live for not more than a few days on average and do not feed extensively (Armitage *et al.* 1995), which would result in their stable isotope values reflecting that of the seabird-derived nutrients assimilated during larval development.

There are, to our knowledge, no previous examples of ornithogenic allochthonous input influencing insectivorous passerines, and relatively few examples of how nutrients can be traced from trans-boundary input into insectivorous passerines. Examples of allochthonous input traced in passerines include Tree Swallows *Tachycineta bicolor* in western Canada containing sewage-derived nitrogen as a result of feeding on emergent aquatic insects influenced by riverine sewage input (Wayland & Hobson 2001), and Eurasian Wrens *Troglodytes troglodytes* enriched in $\delta^{15}$N as a result of feeding on invertebrates, which in turn feed on salmon carcasses in North America (Christie *et al.* 2008). Furthermore, *Cinclodes* spp. of South America exhibit marine signatures when strongly associated with foraging in coastal environments compared with inland species of the same genus (Sabat & del Rio 2002). In contrast, isotopic signatures of different insectivorous passerine species, when uninfluenced by marine or anthropogenic inputs, appear to be consistent in their stable isotope values, in particular for $\delta^{13}C$ (Hobson 1999). This consistency of stable isotope values between species also supports the use of a different insectivorous passerine species as a control sample in our study.

There is the possibility that observed differences in carbon values between the two insectivorous species could be attributed to other factors influencing carbon isotope ratios besides House Martins feeding on ornithogenic insects; however, these factors are considered unlikely given the difference in magnitude. For example, $\delta^{13}C$ values vary between plants with different photosynthetic pathways, i.e. C3, C4 or CAM. Given that plant species on both Stora Karlsö and Gotland are predominantly C3 plants, the enrichment of $^{13}C$ observed in C4 or CAM plants is unlikely to contribute to the enriched signature of House Martins from herbivorous insect prey sources (Rubenstein & Hobson 2004). Both Stora Karlsö and Gotland are also at similar altitudes and latitudes and thus the effect of these factors on carbon isotopic ratios will not influence the results. The use of sulphur isotopes ($^{34}S/^{32}S$) in identifying the origin of the House Martin prey is another potential tool to determine whether nutrients are derived from a marine or a terrestrial source (Hobson *et al.* 1999). However, for this study the feathers sampled were not of sufficient mass to be analysed for both sulphur and nitrogen and carbon isotopic analysis.

The significant increase in $^{15}N$ between Collared Flycatcher and House Martin also suggests the latter are feeding on more enriched $^{15}N$ prey, attributed to the input of seabird nutrients. However, the $\delta^{15}N$ values of House Martins are considerably lower than those of Common Guillemot chicks. This is not surprising, firstly as seabirds excrete nitrogen that is depleted relative to the ingested food (Bird *et al.* 2008), and secondly, as nutrient run-off into coastal waters would probably result in a lowering of the $\delta^{15}N$ values due to dilution during transportation and within the Baltic Sea. This in turn would result in less enriched $\delta^{15}N$ values of Chironomidae larvae and thus House Martins, relative to Common Guillemots.

An alternative prey source for House Martins may be terrestrial arthropods, which are often found in high abundance when feeding upon ornithogenic detritus (Polis & Hurd 1995, 1996, Sanchez-Piñero & Polis 2000). Bird *et al.* (2008) inferred that the nitrogen signature of ammonia was especially depleted, as the guano nitrogen signature was not dramatically different from that of the birds' food. This suggests that the nitrogen taken up by insects feeding within the seabird colony could be derived from ammonia rather than from the uric acid component of excreta.

House Martins breed throughout much of Europe, but their colonies are typically of fewer than five pairs and only about 1% of colonies hold more than 30 pairs (Cramp 1988). In much of the suitable habitat in Europe, the nesting density of House Martins is typically around one to two pairs per km$^2$ (Cramp 1988), so Stora Karlsö (an island of 2.5 km$^2$ with 170 pairs of House Martins in 2013) represents an unusually high breeding density for this species. House Martin numbers in the lighthouse colony increased from 23 pairs in 1984 to 41 in 1998, 51 in 2005 and 150 in 2013 (Hedgren & Kolehmainen 2006, Länsstyrelsen 2006). This increase contrasts with an estimated 30–49% decline in House Martins throughout Sweden over a 30-year period (Ottvall *et al.* 2009). Colony-specific population parameters of Common Guillemots, including adult survival (Österblom *et al.* 2004) and breeding success (Kadin *et al.* 2012), are consistently high, and indicate, together with census counts at Stora Karlsö (Hedgren & Kolehmainen 2006), a substantial increase in the Common Guillemot population. Counts of Razorbills, the other large population of sprat-feeding seabirds on Stora Karlsö, also show a marked increase during recent years (Länsstyrelsen 2006). Previous studies indicate strong links between the dynamics of several Common Guillemot population parameters and the dynamics of the Sprat stock (Österblom *et al.* 2006, Kadin *et al.* 2012). It is likely that the growth of the Guillemot population has been enabled by a dramatic increase in the Baltic Sea Sprat stock, in turn affected by overfishing of its main predator Cod *Gadus morhua* and changing climatic conditions (Casini *et al.* 2008, 2009). Overfishing of Cod can have profound effects on entire marine food webs – examples include effects on pelagic fish stocks, zooplankton, phytoplankton and nutrients in the Scotian Shelf (Frank *et al.* 2005), and potentially also phytoplankton biomass in the Baltic Sea (Casini *et al.* 2009). We speculate that the increasing numbers in the House Martin colony on Stora Karlsö may be a consequence of the large and increasing Common Guillemot population (in turn substantially affected by marine ecosystem dynamics), through the provision of an abundant coastal insect prey subsidy derived from nutrient run-off into coastal waters from the adjacent seabird colony.

The $\delta^{15}N$ and especially the $\delta^{13}C$ values of House Martin nestling feathers indicate that seabirds play an important role in the transfer of nutrients from the marine environment to this local population. Other island populations of insectivorous birds may also be influenced by the presence of seabirds. For example, the St Kilda Wren *Troglodytes troglodytes hirtensis* (Miles 2011) and the Fair Isle Wren *Troglodytes troglodytes fridariensis* (Aspinall & Aspinall 2011) occur at remarkably high local densities, especially on the sea cliffs (Forrester & Andrews 2007), which hold internationally important populations of seabirds. Their numbers may be dependent on nutrient inputs to these islands from seabirds. There is thus a need to understand better the degree of dependence of other passerine species and populations on seabird subsidies, in particular in the context of declining seabird populations (Caut *et al.* 2012). We argue that such cross-scale dynamics represent an interesting challenge for agencies defining their management mandate by traditional ecosystem boundaries.

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