Causes and consequences of individual behavioural variability in a pelagic seabird



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Abstract

Individual differences in behaviour among wild animals have received increasing attention in the last few decades, accelerated by the development of higher-resolution, lighter and cheaper biotelemetry methods that provide unprecedented insights into individuals' behavioural tendencies. This thesis builds on earlier research to investigate the phenomenon of individual consistency in foraging behaviour in a pelagic seabird, the Manx shearwater (*Puffinus puffinus*), using biotelemetry data collected from five UK colonies by the Oxford Navigation Group since 2008.

Chapter 1 introduces key terms and definitions, and reviews the literatures of individuality in animal behaviour, particularly the causes and consequences of variability in space use and foraging, its implications for the role of learning and memory, and empirical support for the widespread occurrence of individual foraging site fidelity in seabirds. It concludes by outlining the analysis and predictions for Manx shearwaters for the following chapters.

Chapter 2 use simple characteristics of foraging trips extracted from GPS data collected at five UK colonies to describe the typical variability in foraging behaviour with respect to breeding stage and colony differences, as well as variation with age. Hypotheses as to the nature of variation between breeding stages and with age, informed by life history and cognitive expectations respectively, are explored, alongside commentary on possible explanations for colony differences.

Chapter 3 focusses on the Copeland dataset to investigate variability in foraging behaviour using the same metrics across individuals, and to quantify individual consistency in site use. We use a behavioural state classification algorithm and randomised site-comparison method to quantify the extent of individual foraging site fidelity, a composite measure of within-individual consistency and between-individual variability. We then investigate potential mechanisms relating to resource tracking, experience and physical constraints.

Chapter 4 discusses the overall conclusions, including the contribution of this dataset to understanding breeding stage variation in foraging behaviour, colony differences, individual repeatability and foraging site variability, and the likely role of learning and memory in foraging in this species, before outlining potential future research directions.

Chapter 1: Introduction & Review of Literature

1.1 Introduction

Within-species variation in behaviour is increasingly studied in wild animal populations for its evolutionary implications (Wolf and Weissing, 2012; Schradin, 2013; Bubac, Miller and Coltman, 2020) and a more detailed understanding of how individual animals interact with their environment (Sih *et al.*, 2012; Zwolak, 2018; Winberg and Sneddon, 2022). How behaviour varies within populations and over time is of interest for a more robust description of a species' life history (Burton *et al.*, 2011; Boyle, Sandercock and Martin, 2016; Wright *et al.*, 2019; Whittington *et al.*, 2022). Appreciation that differences at the individual level can be consistent across time (Dammhahn and Almeling, 2012) and can lead to predictions of how animals respond to environmental change (van Overveld and Matthysen, 2013; Spiegel *et al.*, 2015), conservation policies (Merrick and Koprowski, 2017) and scientific manipulation (Biro and Dingemanse, 2009; Roche, Careau and Binning, 2016) has led to increased interest in how they develop and in their role in different aspects of behaviour across different species.

Having a measure of the degree of individual variation in a population is also important in understanding that population's ecology in greater depth (Bolnick *et al.*, 2003; Violle *et al.*, 2012). Movement and space use are ecologically important, with consequences for foraging (Pyke, 2019), migration, dispersal and territory holding (Quinn and Brodeur, 1991; Putman *et al.*, 2011), interaction with conspecifics (Schlägel *et al.*, 2019) and disease dynamics (Fèvre *et al.*, 2006; Wilber *et al.*, 2022). Analysis of spatial behaviour is therefore valuable for investigating behavioural differences at the individual and sub-population levels (Hawkes, 2009; Shaw, 2020), and is increasingly feasible with biologging devices, a range of which are now available for use on free-ranging animals (Rutz and Hays, 2009; Whitford and Klimley, 2019).

Foraging behaviour has been a focal point of study in the behavioural ecology of animals, since as a "fundamental component of animal existence" (Stephens and Dunlap, 2008, p. 366), foraging represents a critical behaviour with relevance to all aspects of life history. Since the inception of the

field various approaches have been taken for predicting and analysing the movement of free-ranging animals in pursuit of food, whether based in classical optimal foraging theory (Stephens and Krebs, 1986; Mitchell and Powell, 2004) or more mechanistic modelling approaches such as those with roots in statistical physics (e.g. Lévy walks and Brownian motion; Gautestad and Mysterud, 2013). Recognition that underlying cognitive processes, as well as ecological and geographical constraints, mean animals do not merely behave like particles but tend towards more complex spatial distributions, has led to the development of increasingly complex models of animal foraging movements (Börger, Dalziel and Fryxell, 2008; Dalziel, Morales and Fryxell, 2008; Gautestad and Mysterud, 2010a, 2010b). In particular, these may take into account the accessibility of resources (Matthiopoulos, 2003), constraints of physiology and life history (Rosen, Winship and Hoopes, 2007; Malishev, Bull and Kearney, 2018) and cognitive influences like learning and memory (Stephens and Dunlap, 2008). The foraging strategies observed across taxa are a result of all these varying factors, and seem highly specific to the ecology and life history of any particular species.

There are, at least theoretically, circumstances where memory-informed foraging is not adaptive, such as when resources vary rapidly or when the costs of information retention outweigh its benefits (Stephens and Dunlap, 2008), or when resources vary entirely stochastically (Gautestad and Mysterud, 2013), in which cases random search strategies might be more efficient (Humphries *et al.*, 2012). However, for perhaps the majority of species, and certainly larger vertebrate species facing heterogeneous resource distributions, memory is often crucial for informing an individual's choices while foraging and therefore "a fundamental property of behaviour important to understanding complex processes" (Bracis *et al.*, 2015). Understanding both population-level distributions of foraging animals and the decisions of individuals is therefore best reached by incorporating memory into these models; not only can this extend our knowledge of foraging ecology, but by testing it against empirical data of foraging movements we can infer properties of the prey distributions animals are using, and infer something of the cognitive mechanisms they use in locating them. Indeed, as a behavioural domain, foraging "stands out as one of the simplest situations in which to seek an understanding of the ecological significance of learning and memory" (Stephens and Dunlap, 2008, p. 366).

Consistent intraspecific variation in foraging behaviour has been observed in many species (e.g. Wells and Wells, 1986; Ehlinger and Wilson, 1988; Davoren, Montevecchi and Anderson, 2003; Gurarie et al., 2022). This takes a variety of forms (discussed in more detail below) and can result from factors incidental to cognitive processes, like body size or sex (Austin, Bowen and McMillan, 2004; Beck *et al.*, 2007; Louis *et al.*, 2021), but in many cases arises via learning, whether about the spatial distribution and other predictable characteristics of prey resources (Greer, Gajdon and Nelson, 2015), or of foraging skills themselves (Dukas and Real, 1993; Warburton, 2003; Jaeggi *et al.*, 2010). While foraging specialisation, whereby individuals occupy a subset of the species' total niche width, either with respect to habitat use or diet (Bolnick *et al.*, 2003), represents one such example that might arise via a variety of processes, the related phenomenon of individual foraging site fidelity (IFSF), where individuals return repeatedly to the same foraging site over time, must be dependent on memory (where it can be demonstrated to be independent of social influence).

Central place foragers, those animals restricted to returning to a breeding site between foraging trips, have received special attention within the field of foraging theory (Orians and Pearson, 1979; Kacelnik, 1984; Wetterer, 1989), and, given the importance of travel and search time on reproductive success in these species (Clode, 1993), the ability to locate prey efficiently is thought to be especially significant given they may often be close to their physiological limits while provisioning (Burke and Montevecchi, 2009; Boyd *et al.*, 2016). As a group, they have also been subject to extensive empirical research revealing widespread occurrence of site fidelity, often at the individual level (e.g. in seabirds, Wakefield et al., 2015; Votier et al., 2017; Sztukowski et al., 2018; Michelot et al., 2021); though cf. (Courbin *et al.*, 2018); in pinnipeds, (Baylis *et al.*, 2012; Knox, Baylis and Arnould, 2018; Foo *et al.*, 2020; Iorio-Merlo *et al.*, 2022). Though not necessarily facing the same temporal constraints on movement as central place foragers, species exhibiting home ranges (i.e. whose general movement is spatially bound) present a related case, and much of the framework for modelling and interpreting home range behaviour may also inform study of central place foragers, particularly in the relevance of memory to site fidelity (Börger, Dalziel and Fryxell, 2008; Merkle, Fortin and Morales, 2014).

The repeatable characteristics of an individual's foraging behaviour therefore offer an insight into multiple aspects of a species' biology, from the nature of its trophic interactions to that of its cognitive abilities. Though highly studied in recent years, especially in temperate and polar regions (Ceia and Ramos, 2015), we still lack a detailed understanding of the foraging behaviour of seabirds, particularly pelagic species for whom direct observation even during the breeding season is essentially impossible. Biotelemetry studies are rapidly adding to our knowledge, but with an uneven species coverage (Bernard *et al.*, 2021) that increasingly reveals that findings (of e.g. foraging strategies like IFSF) are not generalisable even across closely related taxa, or in some cases even repeatable across studies of the same species (see Bartumeus et al., 2010; Courbin et al., 2018). The prevalence of individual variability should be of interest to researchers since its degree directly impacts the generalisability of descriptions of species' foraging behaviour, whether of diet, habitat use, or spatial distributions, all of which are important not just to scientific inquiries but also to practical applications such as in policy and conservation. Characterisation of the extent of individual-level variability in foraging strategies, especially in as yet un-investigated species and particularly of the contexts in which it arises, is therefore important for a more comprehensive understanding of the phenomenon and the foraging behaviour of seabird species in general.

Manx shearwaters (*Puffinus puffinus*) are long-lived, highly pelagic Procellariiform seabirds breeding across the North Atlantic (Brooke, 1990). As of 2004 the UK was estimated as holding around 90% of the global population (Newton, Thompson and Mitchell, 2004) and around half of these are found on Skomer Island in west Wales (Perrins *et al.*, 2019). Since 2004 the Oxford Navigation Group, among other research groups, has been tracking the at-sea movements of Manx shearwaters with bird-borne biologgers, mainly global positioning system (GPS) and light-level geolocation (GLS) devices. This work has been conducted variously across five different colonies in the Irish Sea (Skomer, Skokholm, Copeland, Lundy and Rum), which as a location itself accounts for a significant proportion of foraging activity in the species (Kober *et al.*, 2012). As a result, the group now has over 10 years of data on the movements of Manx shearwaters during migration and the over-wintering period, and the boreal summer breeding season. This offers a valuable opportunity for extensive investigation of the patterns

of at-sea behaviour in this species, and the quantification of behaviours previously observed informally through fieldwork. Previously, work by Dean (2012), Kirk (2016), and others used subsets of the dataset used here to look into some such aspects of Manx shearwaters' at-sea behaviour through GPS and GLS data respectively, providing important insights into the breeding and over-wintering behaviour of the species. However, these studies were limited to a subset of the five colonies now studied, and with more extensive and higher resolution data now available, there is new opportunity to investigate some of these behaviours, as well as additional questions of life history and learning.

While Kirk (2016) described notable within-individual consistency and between-individual variation in migration and over-wintering behaviours, this has not so far been studied in the breeding season. Consistency of individual space use during this period may be informative of both the mechanisms and functions of individual variation as well as contributing to our understanding of how these birds learn about their environment. The more recent, larger, multi-sensor datasets offer a valuable resource for investigating individual variation of free-ranging Manx shearwaters at the UK field sites. In addition, ringing efforts over recent decades at the Copeland Bird Observatory provide us with the ages of a relatively high proportion of individuals at the Copeland colony. Known-age individuals provide a case study for investigating learning (e.g. Wynn et al., 2022) as well as looking into inter-individual differences, where age may offer a powerful proxy for experience and therefore for studying the effects of learning and memory on behaviour (discussed in more detail in section 1.5 and Chapter 3).

Shearwaters are central place foragers (while breeding) and migrate annually, covering large distances in search of prey during both breeding and wintering seasons. During the breeding season (April-September) they are constrained to make repeated trips to and from the nest, and across their long lifespans they have extensive opportunity to learn details about the environment such as the locations of productive foraging areas and routes and cues for finding them. Given individual consistency in non-breeding season site use and migratory routes (Kirk, 2016), and the familiarity birds develop over their lifetimes with the foraging areas near their breeding colonies, individual variation in breeding season space use is plausible, yet has never been quantified for this species.

Likewise, between-colony effects on space use are only preliminarily understood (Freeman *et al.*, 2013), and though parental coordination during incubation and chick-rearing has been highly studied (e.g., Gillies et al., 2022), differences between the breeding stages themselves have not been described in detail.

As well as increasing our knowledge of the life history of Manx shearwaters, understanding the extent and causes of any variation among these factors may also reveal how flexible foraging behaviours are. Indeed, as they occupy a high trophic level these seabirds may be particularly vulnerable to environmental change and anthropogenic disturbance (Grémillet and Boulinier, 2009). Mortality through fishing bycatch and other threats have made the closely related Balearic shearwater the most endangered European seabird (Genovart *et al.*, 2016). As currently understood, Manx shearwaters do not suffer bycatch mortality, but in light of increasing anthropogenic disturbance and development across their UK foraging range (particularly in the Irish Sea), understanding how individuals and sub-populations habitually use different foraging areas might be an important tool for protecting them in future, and for informing practices for conserving others.

Beyond that, however, investigation of variability in space use is an avenue to understanding the mechanisms underlying the species' foraging behaviour and by extension, its foraging ecology. Below I present a review and discussion of literature investigating individual behavioural variability (1.2) in order to define terms and lay out the scope of this project within the wider field; in the context of movement ecology (1.3); and in detail that concerning individual variability in foraging behaviour and space use among central place foragers (1.4). Finally, I review the findings among seabirds in particular (1.5), and propose methods for investigating aspects of individual variation in at-sea behaviour in Manx shearwaters using available biotelemetry data, alongside predictions based on foraging theory and empirical results from comparable taxa.

1.2 Individual variation in behaviour: key concepts and definitions

1.2.1 Background

Early evolutionary and ecological studies of behaviour treated individual conspecifics as interchangeable units, with equivalent behavioural capacities and niche occupancy (Vandermeer, 1972). Optimisation theories in particular view animal behaviour as maximising a fitness-related currency under a particular trade-off, and though this does not necessarily exclude the potential to model inter-individual variation, it has often assumed one optimum for all species members (see Carter et al., 2013). During the same period, nonetheless, there have been observations and consideration of variability *per se* (Bell, 2006); more holistic views of animal behaviour, which take into account the increasing evidence of differences in behaviour between individual conspecifics, see that for many species individuals constitute only a portion of the niche width of the species as a whole (Bolnick *et al.*, 2003), and consistently vary in their behaviour along a number of trait axes (Réale *et al.*, 2007). Theoretical underpinnings of this view run along a number of lines, influenced by fields as disparate as ecological niche theory (Bolnick *et al.*, 2003; Dall, Houston and McNamara, 2004) and research on personality in human and non-human animal psychology (Gosling and John, 1999; Gosling, 2001). The emerging picture is of widespread, consistently divergent behavioural patterns between individuals that exist in behaviours relevant to multiple life history traits. Reconciling such a picture, of variation consistently maintained across a population, with natural selection and its tendency to reduce variation is not a new concern (Harley, 1981; Hines, 1987), and numerous approaches have been taken to explaining persistent inter-individual differences. Various avenues are discussed here as relevant to this thesis, focussing later on concepts and definitions relating to the study of individual variability in foraging behaviour and space use in particular.

If behavioural variation arises randomly, either as a result of random developmental events or through the cumulative effects of differing experiences during an animal's life, then we may not need further explanation for it. If the latter was the case, we might expect behaviour to diverge by chance among ageing individuals. Alternatively, behavioural differences fixed through early developmental events

might canalise behaviour in young animals, such that differences between individuals do not much vary over the course of their lifetime. However, if these random differences between individuals affect their fitness, they will be subject to selection. How extensive the role of selection is in shaping within-generation variation is little understood, though certain recent studies suggest selection among juvenile animals can play a significant role in reducing variation among behavioural traits (e.g. migratory orientation in common terns *Sterna hirundo*, Wynn *et al.*, in review; compensation for wind drift in black kites *Milvus migrans*, (Sergio *et al.*, 2022) . However, at least theoretically, any adaptation that can reduce the likelihood of an individual's fitness being negatively affected by such random events might have an advantage. The above scenarios of external or developmental events affecting an animal's behaviour then constitute *developmental plasticity* (Stamps, 2016), and are interesting as an organism's evolved plastic response to its environment, alongside life-long flexibility in the form of *phenotypic plasticity* (Piersma and Drent, 2003). However, for these to contribute to variation between individuals, they must be affecting individuals differently. Where these differences are non-random, we come back to the original question: why might animals behave consistently differently to one another?

First to consider is how we are expecting behavioural differences to manifest themselves in individuals, i.e. how they develop, as this will inform us as to how they are being maintained. This of course depends on the trait being studied, but in general, the easiest dichotomy to draw is between innate or genetic differences and those arising during an organism's lifetime. The former may be genetic tendencies towards certain patterns of behaviour (and therefore heritable), though they might also result from irreversible developmental effects. Evidence from human personality research suggests a relatively high proportion of certain behavioural traits' variance across populations can be explained by genetic factors (Plomin *et al.*, 2016), and though this has received less attention in non-human animal studies, there is some evidence of the same phenomenon in other species, including great tits (*Parus major*), sticklebacks (*Gasterosteus aculeatus*), bighorn sheep (*Ovis canadensis*) and chimpanzees (*Pan troglodytes*), as reviewed by van Oers et al. (2005). However, this does not of

course hold for all behavioural traits, and equally does not negate the possibility of environmental and developmental influences on behavioural tendencies.

On the other hand, differences emerging during the animal's lifetime might be the result of learning from experience, or of specific environmental factors interacting with the animal's development. How learning influences behaviour is well understood in many ways in some species, but is presumably only relevant to certain behavioural traits; not all behaviours can be influenced by learning, and some traits are more malleable to learning than others. The distinction between innate and learnt behaviours is in reality not so clear, as an individual's learning process is also affected by heritable factors. Another source of influence is the social or cultural environment an animal experiences while learning the relevant behaviour (Heyes and Galef, 1996; Galef and Laland, 2005; Van Schaik, 2010).

That consistent between-individual variation is observed may suggest there are advantages to different modes of behaviour. If individuals behave differently they might experience less intraspecific competition for food resources. Indeed, the opportunities for behavioural differences to be beneficial are most apparent in foraging, where individuals stand to gain by not overlapping in the food they seek to exploit. This is the basis of individual specialisation, the idea that individuals occupy some portion, but not all, of the population's niche width (Bolnick *et al.*, 2003), thought to at least temporarily reduce competition among individuals (Bolnick *et al.*, 2010; Araújo, Bolnick and Layman, 2011). Individual specialisation is often thought of as a product of learning (assumed by some optimal foraging theory approaches), but the reality may be a complicated interplay between constitutional disposition (genetic or environmentally determined), social or cultural factors, and learning from experience (Araújo, Bolnick and Layman, 2011).

Alternatively, we can envisage evolutionary scenarios in which broader behavioural differences are maintained. Firstly, though perhaps least applicably, differences might accumulate between sub-populations due to drift, regardless of their fitness (dis)advantages; for instance in sparse metapopulations with small and semi-isolated sub-populations with little gene flow. Secondly, divergent selection might push a population to extremes in a trait where they represent mutually exclusive strategies for solving a particular problem (see Wolf et al., 2007). We might expect to see

this behavioural distribution in cases of incipient speciation, perhaps accompanying other drivers of reproductive isolation or contributing to it directly. Where the fitness benefits of one strategy depend on the prevalence of the other, seen in socially competitive scenarios as described by game theory's hawk and dove games (Maynard Smith and Price, 1973; Maynard Smith, 1982), frequency-dependent selection may maintain a mix of phenotypes (well established for instance in aposematism, mimicry and crypsis; Endler, 1988; Mallet and Joron, 2003; McKinnon and Pierotti, 2010).

These mechanisms rely on a static environment, in which the payoffs from adopting different behavioural strategies – i.e. the fitness advantage of behaving in a certain way – are fixed. In reality, this is rarely the case, especially for more behaviourally complex animals. Many animals exploit temporally and spatially unpredictable resources, the quantities and locations of which might vary with changes in season or climate, in population density, or in the behaviour of other animals. Any temporally heterogeneous environment may therefore favour the maintenance of variation with respect to foraging behaviour over time, and favour individual specialisation and behavioural variation between individuals (Mangel, 1991). Strategies for exploiting specific resources become more and less profitable with changes in the resources' availability over time periods longer than a generation. Observing a population at a single snapshot in time, as we do, may, in this scenario, therefore show a mix of strategies as a legacy of past environmental change. Given an environmental variability capricious enough that it promotes the changing fortunes of each strategy enough to ensure none go to fixation, but regular enough that none go to extinction either, over longer periods variation in behaviour will be maintained.

Yet even within a generation, any animal exploiting temporally heterogeneous resources must have a way of locating and estimating the benefits of different ones. Dall and Cuthill (1997) explain how the need for accurate estimates of the payoffs of food resources biases against generalist strategies, both at the individual and genotypic levels. A generalist is at an advantage when environmental fluctuations render a specialist's resource unusable, as it is able to exploit a variety of them, which, if independent, provide insurance against environmental change. However, using multiple resources incurs a greater *information cost* in terms of sampling them all often enough to maintain reliable estimates of their

payoffs, in order that the animal might make the best-informed decisions about which resources to exploit at any one time. This is an extension of the general 'cost of flexibility' envisaged to generalism: a generalist, in keeping the ability to use multiple resources, is inevitably less efficient at exploiting any single resource than the relevant specialist (Futuyma and Moreno, 1988). Over generations too, a generalist genotype – one exhibiting plasticity – may be liable to accumulate more deleterious mutations, as in each manifestation it can only be subject to selection on the niche instance in which it finds itself, rather than all that its generalism might allow (Dall and Cuthill, 1997). Despite this, generalism at the genotypic level has been proposed as a way to mitigate the effects of temporal environmental variation on fitness, in the form of genetic 'bet-hedging' (Gillespie, 1977) or 'developmental instability' (Simons and Johnston, 1997), though little is known about the mechanisms that might underlie these processes. Regardless of the genetic underpinnings, specialisation of individuals on particular resources remains a candidate mechanism for the maintenance of behavioural variation within a population.

It is still often thought that the behavioural variation within species is non-adaptive, merely noise surrounding an adaptive average (Dall, Houston and McNamara, 2004), and that studying individual variation requires justification of how such variation could be maintained if it is adaptive. However, as Dall and colleagues point out, evidence that this behavioural variance is "often distributed in a non-random manner, along particular axes" (Dall, Houston and McNamara, 2004) suggests that it must have ecological and evolutionary consequences, as otherwise it would have been eliminated. The evidence of consistent differences between individuals in traits relevant to fitness is mounting in diverse taxa: to date stable individual variation in some trait has been found in gastropods, crustaceans, insects, fish, reptiles, amphibians, birds and mammals (for reviews, see Bolnick et al., 2003; Réale et al., 2007), with individual specialisation noted for a total of 189 species as of 2011 (Araújo, Bolnick and Layman, 2011). However, it is worth noting that publication bias towards positive results is likely skewing this picture in the favour of strong individual differences, and a more nuanced view might be yet to emerge.

In some cases, *individual behavioural variability* (IBV) correlates with age, sex, or other class identity factor, but referred to here and throughout is the residual variance left unexplained when these factors have been taken into account. Below I review various approaches to studying IBV, including defining relevant terms and concepts to contextualise those chosen in this study against the wider field.

1.2.2 The study of individual behavioural variation in animals

Research into individual behavioural variation is diverse and has led concurrently in three somewhat separated directions: *individual niche specialisation*, *personality* (and *behavioural syndromes*), and division of labour within collective groups of individuals, as in eusocial insect societies or group hunting (Carneiro *et al.*, 2017). For this thesis, the first two are relevant, though each are to an extent a lens through which to see the more fundamental phenomenon of variation between individuals.

Réale et al. (2007), identified two useful questions for studying IBV, which approach the topic from functional and mechanistic directions. The first, “Do trait differences play an ecological or evolutionary role?”, highlights the importance of studying behavioural variation in an ecological/evolutionary framework; the second, “Why do we observe between-individual variation in behaviour in natural populations?” focusses on the possible underlying mechanisms while developing methodologies for and interpreting the results of these studies.

In the past decade, much work has been done to standardise the field’s use of statistics, terminology, and behavioural assay methods (as well as biologging techniques: see 1.3.2). As a consequence, there is now an extensive literature on the perceived best practices for studying individual variation in behavioural traits, both in conceptualising and quantifying it. The following discussion summarises the relevant developments to be used in this thesis, while tying it to ecological/evolutionary concepts and mechanistic explanations.

Studying behavioural variation

For differences in behaviour to be of interest, researchers usually require them to be stable over time and context; that is, an individual will show consistent behaviour in the domain studied, which is different from other individuals' behaviour, or the population average, but consistent to itself when tested at other times and in multiple contexts. However, in reality individuals can also differ in their degree of consistency – their own variability about their behavioural mean. From this arises the concept of predictability: "within-individual behavioural variation in the same environment" (Cleasby, Nakagawa and Schielzeth, 2015). How predictable an animal is depends on the similarity of any measurement of its behaviour to other measures of the same behaviour. This can only be interpreted when put in the context of others' behaviour from the same population. Using predictability to study individual variation can make cross-study comparisons easier if it provides a standardised measure. It is also significant as highly repeatable traits are most responsive to natural selection (Dingemanse and Dochtermann, 2013).

Many methods for estimating individual predictability exist but not all are comparable across studies, or populations, either for lack of standardisation or because they do not account for the differences between populations in within- and between-individual consistency (Cleasby, Nakagawa and Schielzeth, 2015). Mixed effects models are a common tool for partitioning these sources of variation – individual- and population-level variance – since they allow estimation of between- and within-individual variances directly (Dingemanse and Dochtermann, 2013). A typical model would account for the variation explained by broad identity categories such as sex, age or population subset (here, colony), and then focus on the residual variance as that potentially attributable to individual differences in behaviour (though some of this residual variance will be due to random environmental effects, or noise introduced by measurements). Fitting individual ID as a random effect then gives a measure of the proportion of residual variance, that not explained by fixed factors, which can be attributed to which individual it comes from. Hierarchical and double-hierarchical generalised linear models ((D)HGLMs) are also frequently used as they can model variation in variances, as well as in means (Cleasby, Nakagawa and Schielzeth, 2015).

This approach is analogous to Bolnick et al.'s (2003) method for partitioning the population niche among individuals: an individual's 'niche occupancy' can be calculated as a proportion of that expressed by the whole population. As an ecological tool, this is useful for assessing the impact for example of individual specialisation – an instance of individual behavioural differences. More recently, this one-dimensional measure has been extended to multiple niche dimensions (i.e. food sources and environmental conditions), specifically in the context of seabird ecology (Bonnet-Lebrun et al., 2018; see 1.4).

In addition to getting a reliable estimate of individual variation at any one time (or over the timepoints of the study), we need to understand how this develops over longer timescales for a full picture of how individual differences arise, are maintained, and affect evolution. This requires understanding how robust they are to changes in an animal's age and environment, and ideally whether it has a heritable basis, though the latter is usually out of reach for studies of wild populations, especially of long-lived species. In practice, examining how behaviour changes with age may allow similar questions to be answered.

Personality

The application of this term from human psychology (Gosling, 2001) to animal behaviour is older than might be expected, with investigations of "typical personality patterns" in dolphins (*Tursiops truncatus*) and chimpanzees (*Pan troglodytes*) at least as early as the 1960s and '70s (Kellerman, 1966; Buirski, Plutchik and Kellerman, 1978). A general definition, and one approximating the many uses across the field, is that *personality* (or *temperament*) refers to inter-individual differences in certain behaviours that are stable over time and across different behavioural contexts (Réale *et al.*, 2007). However, this masks some semantic and conceptual issues in how the term is often used, and some examination of what is meant by it is helpful to clarify its use. It is also notably similar to what is usually meant by 'individual differences' alone in other fields, not always accompanied by the term *personality*. There

is also substantial opposition to its use as an explanatory rather than descriptive framework (Beekman and Jordan, 2017) and in more recent years seems to be receding as an approach to understanding IBV in behavioural ecology, in favour of more mechanistic and functional explanations.

As explained by Kaiser and Müller (2021), much of the confusion over the use of the personality concept applied to animals arises when it is confounded with its meaning in humans, and from a lack of clarity in the many different terms used within personality research. Distinguishing between *personality traits* and *personality in general*, they argue that by properly separating the two researchers can better use the concept in animal behaviour research. For a given behaviour, an individual animal can act in a way that compares with the actions of its conspecifics, labelled its *behavioural type.* These are objects of measurement and exist only as empirical measures of whatever tests have been applied by the study in question.

From behavioural types, i.e. the existence of individual differences in a certain behaviour that are stable across time and contexts, researchers infer *personality traits*. As they are inferred from patterns, rather than directly observed from instances of behaviour, a good way of thinking of personality traits is as dispositions towards certain patterns of action (Kaiser and Müller, 2021), which is how they are usually interpreted in biological research (Réale *et al.*, 2007). By measuring many personality traits in several individual animals of a group, a picture of the animals' *personality in general* is constructed (the concept usually thought of when the word 'personality' is used in a human context). Where personality traits are expressed along a continuum, *personality in general* is by contrast binary: an animal either has a personality in general or it does not.

Since it is an empirical question whether or not a species exhibits personality in general, or indeed specific personality traits, the phenomenon of personality cannot be hypothesised as a description of behaviour until inter-individual differences in the behaviour have been thoroughly established. Many studies attempt, in addition, to explain behavioural variation with personality concepts, which in the context of the above discussion is tautological and which has contributed substantially to the decline in its use (Beekman and Jordan, 2017). Perhaps a better way to use personality concepts is to examine correlations between behavioural types (as *behavioural syndromes*; Sih et al., 2004), in order

to suggest mechanisms that are likely to explain the existence of inter-individual differences in general. This is appropriate where robust inter-individual differences in the study behaviour have already been demonstrated, and where there is a species-specific reason for expecting the personality trait in question to be linked to it, in a way that has ecological validity. However, it is then an open question whether 'personality' is a useful term to add to the field, as it is then interchangeable with 'behavioural syndrome'. For this work, the latter term is preferred and the personality framework is avoided and reference to 'individual behavioural variation' is made as relevant to the trait in question. 'Personality trait' can be replaced with 'behavioural trait' without any loss of explanatory power and indeed with the loss of substantial confusion.

Regardless of their age or sex, humans differ consistently in their expression of five personality traits (Gosling and John, 1999), though there is increasing evidence that these traits are not stable across cultures (Henrich, 2020). In other animals, studies have repeatedly found consistency in a number of traits in a wide range of taxa, including fearfulness/reactivity, exploration, sociability, aggression, activity and risk-taking/dominance (Gosling, 2001; Dall, Houston and McNamara, 2004). There are many hypotheses as to the evolutionary causes and consequences of the emergence of stable differences in behaviour – for instance, resulting from cost-benefit trade-offs (see Carter et al., 2013), or favouring the evolution of cooperation (Fishman, 2003). However, until the heritability of such differences is better understood these are difficult to test (Dall, Houston and McNamara, 2004).

The lasting disconnect between personality research and other instances of studying individual differences has left duplicated explanations of essentially the same phenomena. Increasingly personality traits, assayed in captive individuals, are correlated with differences in other more naturalistic behaviours, and there has been increased effort to integrate research between the two fields. For instance, work in mouse lemurs (*Microcebus murinus*) supports the idea that behavioural traits estimated in captivity can reliably indicate animals' behaviour in the wild (Dammhahn and Almeling, 2012). Indeed, this work directly related behavioural traits to fitness via differences in reproductive potential, a route others are increasingly taking to explain certain traits (Wolf *et al.*, 2007; Dammhahn, 2012). Wherever 'personality' is invoked in behavioural studies there are multiple

considerations to testing that the proposed trait assay is valid, especially when carrying it out in a new study species. However, many studies assume a test's validity from its use in other species and do not check for convergent and discriminant validities or reliability, nor use multiple tests to quantify a single trait, all factors required by the standards of the field (Gosling, 2001; Carter *et al.*, 2013). Using appropriate tools (such as PCA) for interpreting tests, and designing appropriate measurements and measurement situations, are also crucial and often overlooked.

Behavioural syndromes and mechanistic bases

If using personality to explain individual differences in behaviours is tautological, it might still be used to identify trends in how individuals' behaviour differs. This is also true of behavioural syndromes, which arguably have much more potential to implicate mechanisms underlying behavioural differences. *Behavioural syndromes* are "suites of correlated behaviours" in the same way that life-history syndromes refer to suites of correlated life-history traits (Sih *et al.*, 2004). For example, great tits (*Parus major*) show different tendencies to explore their environment, and those that explore 'fast' are also more likely to be aggressive and dominant (Verbeek, Boon and Drent, 1996), neophobic and their behaviour routine-based (Verbeek, Drent and Wiepkema, 1994). From a description of which traits are correlated and how, these last authors propose a mechanism: that this IBV stems from "differences in the way in which information concerning the environment is collected and dealt with". Behavioural syndromes are in this way more useful tools for understanding behavioural variation than personality (in general or trait-wise) alone. Arguably, they add something conceptually to an explanatory framework for behavioural consistency, particularly by positing mechanistic links between traits and therefore correlated trait values, as described below, which may answer questions of how variation is maintained (i.e. via trade-offs between related traits).

Links between the traits mentioned above have been identified in numerous species and relate to a broader theory about how behavioural traits correlate with life-history trade-offs, first conceptualised as a 'proactive-reactive axis' or variation in 'coping style' (Koolhaas *et al.*, 1999). Ricklefs and Wikelski

(2002) further argued for integration of behaviour and physiology into theories of life history trade-offs; their basis was that organisms' responses to their environment are constrained by the allocation of finite resources, that they therefore alternately enter physiological states to achieve different functions, and that these states might be modulated by demographic effects, such as the individual's expected future reproduction. Overall, this would lead to the correlation of many behavioural and life-history traits, which, they argued, were mediated through endocrinal mechanisms. Following the 'fast-slow continuum' concept from life history theory – correlating reproductive rate, development and lifespan – a similar observation of differences at the sub-population level gave rise to the 'pace-of-life syndrome' (Réale *et al.*, 2010), that suggested a raft of behaviours, physiological mechanisms, and life history traits to be linked. Ricklefs and Wikelski (2002) described a similar idea, a so-called 'nexus' of behaviour, physiology and life-history, which provides another framework for thinking about intraspecific differences, and particularly for hypothesising about the potential mechanisms underlying differences in behaviour and their evolutionary role. Endocrinal mechanisms in particular are receiving increased attention (e.g. Wilson et al., 2019).

Considering competing allocation for different tasks leads to the theory of an exploration-exploitation continuum. This approach combines predictions from optimal foraging theory (Charnov, 1976) that animals should allocate time in and between patches in relation to patch quality and distribution, with the fact that no animal can have complete information about all patches in the environment at once (Stephens and Krebs, 1986); a trade-off between information gathering (exploration) and foraging (exploitation) is therefore inevitable (Kramer and Weary, 1991; Cohen, McClure and Yu, 2007; Eliassen *et al.*, 2007; Mehlhorn *et al.*, 2015). Position on this continuum might depend on current and expected future fitness (discussed below), intrinsic morphological or physiological factors that affect energetic requirements or competitive ability, social hierarchy, or even cognitive ability to learn from and remember environmental information. Because it integrates multiple factors across behaviour, physiology and life-history, this concept fits well with other explanations of behavioural syndromes and with empirical work showing correlation between exploration and other traits.

Individuals' approach to 'risk' has been hypothesised as the common factor explaining the correlation of these traits; using a combination of individual-based modelling and a game-theoretic approach, (Wolf *et al.*, 2007) argued that behavioural syndromes involving behavioural traits associated with risk emerge due to the trade-off between exploration and reproduction. Whenever individuals in a population have differing fitness expectations (residual reproductive value), those with less will be more risk-prone. Thus behavioural differences may be a consequence of expected fitness differences between individuals, or a result of selection on exploratory tendencies. However, empirical work to support this is still lacking. Moiron, Laskowski and Niemelä (2020) conducted a meta-analysis to examine how the among-individual component of behavioural variation explained the impact of 'risky' behaviours on mortality. As Wolf *et al.*'s was, their basis was the prediction of life history theory that individuals solve the trade-off between current and future reproduction differently (Stearns, 1992), and this manifests in between-individual differences in behaviour. Yet, Moiron and colleagues found that there was no negative relationship between behaviour and survival, and so no evidence for the association of risky behaviours with higher mortality.

A more species-specific approach to understanding the causes of individual differences in behaviour is likely more productive. Though behavioural syndromes offer a useful mechanistic basis for explaining some aspects of IBV as described above, they (and particularly the exploration-exploitation continuum) have proved limited in empirical studies and are especially difficult to link with learning. In this work, behavioural syndromes will be used as a supporting conceptual approach to understand aspects of trait covariation but not as an organising method outright. A final example in support of this approach to using the behavioural syndrome concept as a prompt to consider other lines of analysis comes from Haave-Audet et al. (2022), who conclude from a meta-analysis that individual differences in resource acquisition may affect behavioural differences and muddy the relationship between reproduction and survival. They argue that "future studies examining the mechanisms maintaining behavioural variation in populations should test the link between behavioural expression and resource acquisition – both within and among individuals", as they found co-variation between resource

acquisition and other behavioural traits led to “state-dependent shifts in behaviour that simultaneously increase both survival and reproduction”, an approach built on the behavioural syndrome concept.

1.2.3 Ecological implications of individual behavioural variation

Individual variation in behaviour can have a number of ecological consequences, primarily when it represents individual specialisation. Where individuals are specialised on different resources, use different habitats and have different exposure to parasites and predators, incorporating this variation into population models will give a more accurate picture of the species’ ecology, and helps to place them in the context of evolutionary ecology, since variation is a necessary condition for selection (Bolnick *et al.*, 2003).

Beyond individual specialisation specifically, differences in movement patterns are the most obvious way in which these population-level effects might play out, influencing the distribution and structure of populations (and therefore breeding and demographic distributions), the likelihood of interaction with conspecifics and other organisms, and the flow of nutrients, propagules and pathogens around ecosystems (Shaw, 2020). The extent of this may be species-specific, and so an increased understanding of variation within a population may be invaluable for understanding its ecology in greater depth.

Populations with specialised individuals will be also more vulnerable to environmental change, given that the individual animals lack the flexibility to cope with changes in resource levels. Understanding a population’s degree of individual specialisation is therefore important in knowing how to conserve it, with specialising species at higher risk of lethal consequences of environmental change (Brooker *et al.*, 2016). Though most pronounced for species in which all individuals have the same narrow niche (species specialists), and this may also be true of species in which there is variation between individuals as to which resources they prefer to exploit (species generalists), especially at small population sizes. Conversely, conservation practices or other anthropogenic pressures that force a population to become more specialised overall – for example, by selecting against generalist

individuals or those occupying a specific portion of the species' niche but not others – may limit its long-term viability (Brooker *et al.*, 2016).

Recent work also suggests that differences in behavioural tendencies shape distribution of species over a larger scale (Rehage and Sih, 2004; Short and Petren, 2008; Atwell *et al.*, 2012; Kitchen and Chalcraft, 2020; Lichtenstein, 2020). The possibility that behavioural syndromes might bias sampling of wild animals towards those more tolerant of humans and handling (Vanden Broecke *et al.*, 2021) also deserves attention from researchers outside the field of individual behavioural differences.

1.3 Space use and movement ecology

1.3.1 Biologging

Tracking the movement of animals with miniaturised tags has become more feasible in the past couple of decades with improvements in technology and the decreasing cost of animal-borne devices (Rutz and Hays, 2009; Nathan *et al.*, 2022). Using these tags – biologging – can also provide information as to the animal's physiology and environment, and is especially valuable with species that are hard to observe during the behaviours of interest, because they avoid humans, are nocturnal, travel long distances or live underground or underwater.

Animal-borne devices offer greater volumes of more reliable information on the movement of individual animals than alternative methods of tracking, such as passive recording (e.g. direct or camera observation; recovery of marked animals). Relevant to this thesis are two of the most commonly used technologies, global positioning system (GPS) tracking and light-level geolocators (global location sensors: GLS). GPS devices use satellite triangulation to determine position across the Earth's surface, where GLS devices record daylight measurements which can be used to estimate position from day length and sunrise and sunset times. These device types record an animal's probable location at a given time, with varying degrees of error, and allow reconstruction of *space use* – "proportion of time per unit area spent […] in the neighbourhood of a point in space" (Matthiopoulos,

2003), which itself has relevance to much of an animal's behavioural domains and ecological interactions (Shaw, 2020).

Alongside recording an animal's position in space, devices that include tri-axial accelerometers, immersion loggers, and time-depth recorders (TDRs) can also provide concurrent information about its three-dimensional orientation or diving activity. Animal-borne cameras are also increasingly informing us about novel behaviours (e.g. Michel et al., 2022), though at present are restricted to larger animals. Archival devices must be retrieved, capping their lifespan as there is some chance of being lost. In general, there is a trade-off between device size and battery life, via battery size; this has a particular effect on tracking small animals, for whom large devices would represent a greater proportion of their bodyweight. Concern for the effect of biologgers on animals' behaviour is important for welfare, ethical implications and the validity of results; if carrying devices changes an animal's behaviour, there is a limit to what we can infer about naturalistic behaviour from them. Equally, there is concern that with improving technology that allows ever more variables to be recorded with ever smaller devices, research risks shifting focus away from testing specific hypotheses and towards gathering as much (potentially unused) data as possible (Boyd, Kato and Ropert-Coudert, 2004).

In the context of welfare concerns, it is therefore doubly important to ensure the data collected will be valid and used in the way justified by fitting devices in the first place. Recent work has shown that trackers may affect seabird behaviour more than originally assumed (Gillies *et al.*, 2020). One meta-analysis of biologger use found that externally attached (rather than implanted) devices had an overall negative effect on multiple behaviours, though these decreased with time (White *et al.*, 2013), while a second, later analysis further suggested that, while controlling for phylogenetic effects, biologgers had consistent, though small, negative impacts on traits such as survival, reproductive success and parental care (Bodey *et al.*, 2018) Furthermore, some animals experience compensatory mass loss when carrying devices, suggesting in particular that fitting them should be avoided around periods of regulated mass change (Portugal and White, 2022).

1.3.2 Individual variation and space use

Given the ubiquity of movement in animals' lives, it is an obvious place in which to study individual variation since it can give insight into many aspects of an animal's behaviour or life history (Shaw, 2020). Variation in foraging movements and locations might tell us about dietary specialisation and reaction to environmental conditions (e.g. Patrick et al., 2014), or suggest what cues animals use to locate food resources (e.g. Kane et al., 2020), while variation in migratory route might inform us about its ontogeny or function (e.g. Guilford et al., 2011), or the use of navigational cues required to follow it.

Animals may vary across all three main types of movement: daily foraging movements, dispersal and migration (Shaw, 2020). This could be a result of differing interactions with conspecifics or a cause of them and learning may also play a role, especially where differential experience of the environment has strong effects on an individual's ability to navigate around it. Broadly, variation in animal movement and space use has been categorised along three axes: tendential, temporal, and spatial (Shaw, 2020). Individuals vary in their tendency to move at all (particularly in relation to dispersal and migration), the timing or frequency of their movements, and the spatial details of those movements, such as distances travelled, range, path tortuosity and other characteristics.

Behavioural tendencies can be inferred from general patterns of movement rather than single locations. Repeatability can, in the right context, be used as a proxy for specialisation, and is broadly how foraging site fidelity is calculated. However, deriving meaningful information about individual variation in space use and movement behaviour requires data to fulfil a number of criteria (Hertel *et al.*, 2020). The temporal resolution, or fix interval, of the data needs to be enough to detect the focal behaviour, and the resolution of course also needs to be comparable across individuals. Measurements, i.e. periods of movement or foraging trips, need to be taken with enough repeats to avoid pseudo-replication and to capture repeatability over the right timescale, which for some species and some study questions (e.g. about learning and memory) might cover a significant proportion of the animal's entire lifespan. Finally, and particularly when estimating specialisation, a sufficient sample size is needed to ensure variation at the among-individual level can be separated from

background population-level variation. Essentially, the data need to capture sufficiently both the among-individual differences in the focal behaviour, and the degree to which it varies within a single individual alone. Taken together these can provide meaningful insights as to the effect of individual variation and what 'individual variation' represents in a particular context.

As well as allowing general characteristisation of an animal's movements, space use can give some of the most useful insights for studying IBV where an individual's tendency to occupy a given space (site occupancy), or to revisit given locations (site fidelity) can be estimated. Both approaches are taken in this thesis, and the latter is especially useful for studying IBV in foraging behaviours and particularly to relate it to learning and cognitive mechanisms, as is intended here. Below, I describe the contributions of foraging theory to understanding IBV in animal movement, particularly with respect to the focal taxon of this thesis (Procellariiform seabirds) and the general category in which they are conceptualised (*central place foragers*). Together with the above sections this discussion will set the current study in context and allow development of specific hypotheses for future chapters.

1.4 Foraging theory

1.4.1 Foraging theory and predictions about the role of memory

Animals must find food in often variable environments, while balancing other requirements like mating and offspring care (itself usually involving food finding), territorial defence, sleep, and avoidance of predators. How animals allocate time to these various tasks of course depends on their life history and the distribution of their prey resources, but foraging strategies that maximise food intake in balance with these other tasks will be most adaptive. Optimal foraging theory takes this view in understanding foraging behaviours as working towards intake rate maximisation, and has envisioned resources as distributed between three hierarchical levels (Stephens, 2008; Stephens and Dunlap, 2008). These range from individual prey items (1), which themselves are spread out among *patches* (2), which in any bout of travel through the environment a forager can choose to exploit or ignore, through to entire habitats (3) characterised by a particular mix of resources (Stephens and Dunlap,

2008). In large habitats where patches are out of the immediate perceptual range of the forager, the question of how to maximise food intake rate depends largely on how best to find these patches (Bartumeus and Catalan, 2009; Reynolds, 2012), gauge their quality (Valone and Brown, 1989; Valone, 2006), and how long to spend exploiting each one (Charnov, 1976).

Resource quality is rarely evenly distributed and most realistic environments are spatially heterogeneous and vary over time, whether seasonally or due to prey depletion. Strategies for exploiting resources most efficiently in changing environments therefore often hinge on search strategies, and how to balance sampling the environment for up-to-date information on patch locations and quality with patch exploitation (Kamil and Roitblat, 1985), though of course exploitation is not mutually exclusive with information gathering about the local patch itself. Once this information has been acquired, there is the additional question of whether retaining it is adaptive: if past experience of an environment is a useful guide to its present state, foragers might use memory to guide foraging bouts to most efficiently locate prey over time and space (Robira *et al.*, 2021). However, theoretical work on optimal foraging in variable environments over recent decades has produced a complicated picture of the adaptiveness of memory-guided search, offering many considerations on when memory-less search might instead be more efficient (and mechanistically less costly). In an environment where resource location and quality vary rapidly or entirely stochastically, past information is of no value and foragers do better with random search strategies (Stephens and Dunlap, 2008; Gautestad and Mysterud, 2013); similarly, if resources are only predictable through the retention of vast quantities of environmental information, the costs of learning and storage might be so great as to outweigh the benefits in terms of foraging efficiency (Dukas and Real, 1993; Bélisle and Cresswell, 1997; Esposito *et al.*, 2010; Bracis *et al.*, 2015). Overall, the “benefits of memory heavily depend on the needs of the forager” (Nauta *et al.*, 2020), in addition to the possibilities afforded by its life history and preferred resources. Recent work lends empirical support for there being energetic, and therefore fitness, costs to learning and memory, such as those involved in DNA methylation and other gene regulatory changes required for learning (reviewed in Fagan et al. (2013); and at the behavioural level, experiments with honeybees (*Apis mellifera*) have demonstrated

empirically the energetic costs of learning and memory and how the resulting cognitive impairment affects survival (Jaumann, Scudelari and Naug, 2013).

Analytical approaches to modelling search strategies have shown that random searches, especially when integrated to vary their characteristics over different spatial scales (Humphries *et al.*, 2012), can be highly efficient at locating prey and in certain conditions out-perform memory-informed searches (Gautestad and Mysterud, 2013). Lévy walks and Brownian motion-like random searches are theoretically efficient for locating resources in patchily and uniformly distributed resource environments respectively (Regular, Hedd and Montevecchi, 2013), and a forager switching between them on encountering some patch-related cue might make the most of both strategies. Indeed, something similar is observed empirically in animals initiating particular, tortuous, area-bound movement patterns on a fine scale after searching more linearly through larger spatial areas (area-restricted search, ARS). However, in many taxa theoretical and empirical work suggests that memory-informed ARS (i.e. patch location via memory, and local random search for prey) is indeed more efficient (Benhamou, 1994; Boyer and Walsh, 2010). However, this depends on the underlying spatial resource distribution (i.e., how patchy rather than predictable it is), since the sparsity of patches influences the characteristics of the ideal searching strategy. Very patchy or scant resources that are hard to find (and therefore encountered at low frequency through random search) might give advantage to those foragers able to use memory to re-locate them (Bracis *et al.*, 2015).

1.4.2 Theory on central place foragers

For particular groups of animals whose foraging follows particular temporal patterns and spatial constraints, memory seems especially likely to play a role in patch location and exploitation (Merkle, Fortin and Morales, 2014; Bracis *et al.*, 2015). Spatially constrained foragers include those with bounded home ranges (such as territorial terrestrial predators; Börger, Dalziel and Fryxell, 2008) and *central place foragers* (CPF), who must make repeated foraging trips out from a breeding location to provision and care for offspring (such as nesting birds with altricial young, and many marine predators

whose offspring are left on dry land, like seabirds and pinnipeds). Repetitive trips through what becomes a familiar environment raises an obvious opportunity for memory-informed movement, and as a lifestyle central place foraging therefore suggests (at least theoretically) a bias towards an advantage for memory. In longer-lived species, like many marine CPF species, learning and memory may have particular advantages, and indeed, assuming a certain amount of resource predictability, it is possible that these advantages might accrue with age, though little investigation of this possibility has yet been done.

Central place foragers face particular challenges with respect to travel time and the accessibility of various resource patches, as when feeding offspring for example they must return at regular intervals and therefore suffer costs for travelling to distant resource patches, or spending longer exploiting them (Kamil and Roitblat, 1985; Matthiopoulos, 2003). As a group CPFs have received particular attention within the field of optimal foraging theory aimed at understanding how travel time constraints shape foraging strategies (e.g. Orians and Pearson, 1979; Kacelnik, 1984). A number of CPF species have received disproportionately frequent attention compared to general taxa (and especially temperate and polar species), and a growing body of movement and diet data has enabled empirical testing of predictions from optimal foraging theory (e.g. Andersson, 1981; Kaspari, 1991; Elgin, Clark and Morrissey, 2020; though cf. Ford et al., 2015) and indeed implied a role for memory in locating resources across these taxa (Davoren, Montevecchi and Anderson, 2003; Iorio-Merlo *et al.*, 2022). In contrast, studies in certain wide-ranging taxa like albatross have suggested a greater importance of memory-less random search (e.g. Humphries et al., 2012). However, interrogation of the models describing random search strategies cautions that memory might be systematically under-reported by such studies, which ignore the influence of artefacts arising from movement data (Gautestad and Mysterud, 2013).

1.4.3 Empirical studies of individual variability in central place foragers

Overall, the best evidence for the role of memory in CPFs specifically is the common phenomenon of site fidelity ("area-restricted space use behaviour", Börger, Dalziel and Fryxell, 2008), and individual foraging site fidelity (IFSF) specifically, where individuals return to the same area over multiple foraging trips, sometimes over very long time periods. IFSF has been observed across a range of CPF taxa. Perhaps most notably it is seen among charadriiform, suliform and procellariiform seabirds, where it is often associated with particular pelagic foraging patches often out of site of the colony, suggesting they are anticipated in advance (Votier *et al.*, 2010, 2017; Kotzerka, Hatch and Garthe, 2011; Patrick *et al.*, 2014; Wakefield *et al.*, 2015; Sztukowski *et al.*, 2018; Borrmann *et al.*, 2019; Guiry *et al.*, 2022). Studies have also identified IFSF in chiropterans, including instances where foraging site choice was consistently divergent across individuals from the same roost site, but overlapping across roost sites (Rydell, 1989; Kapfer *et al.*, 2008; Rodhouse and Hyde, 2014; Mordue *et al.*, 2019); and pinnipeds, in which it has been observed especially in females, presumably due to the parental care tendencies of this taxon (Baylis *et al.*, 2012; Augé *et al.*, 2014; Oksanen *et al.*, 2015; Knox, Baylis and Arnould, 2018; Foo *et al.*, 2020; Iorio-Merlo *et al.*, 2022).

Though these studies measured IFSF over varying timescales, evidence predominantly from seabirds implies that under certain circumstances fidelity is maintained over years. More detail about the study of individual site fidelity specifically is found in (1.5.2), particularly how it has been used to investigate memory and learning in seabirds, and methodology. In general, with sufficiently intensive data (see Bonnet-Lebrun et al., 2018), discussion above) recording multiple foraging movements from the same individuals over time (typically, months or years) it is possible to investigate hypotheses about the learning of site fidelity, particularly when it is combined with other measures of foraging movements (e.g. trip characteristics and especially directionality, see discussion of Wakefield et al., 2015, in 1.5.2).

It is crucial that sufficient care is taken to disentangle memory (in terms of private or personal information, *sensu* Stephens and Dunlap, 2008) from other mechanisms in these cases, such as social enhancement or other sources of public information (Goyert, 2015), or perhaps consistent

environmental cues that allow repeatable perception of resource location without recourse to memory, such as when individuals respond consistently to environmental gradients (Patrick *et al.*, 2014). For instance, if individuals vary in their tendency to respond to certain cues (independent of memory), IFSF could emerge in a stable environment. In theory, this might be accounted for, by investigating behaviours that indicate anticipation of resource location and therefore reliance on memory – for instance directed movement towards a location when out of range of perceptual cues (Davoren, Montevecchi and Anderson, 2003). In practice, identifying the exact cues used, and the distances over which they are available, is mostly not yet possible.

1.5 Seabirds: previous work and expectations for Manx shearwaters

1.5.1 Ecology, phenology, life history and space use

Long-lived pelagic seabirds – those spending much of their lives foraging at sea – are of particular interest to studies of space use and IBV, and as a group are highly studied via biotelemetry, which has produced extensive data on their movement patterns. Since they forage across the open ocean, often locating prey and distant wintering grounds reliably from their first year of life, they are often used as models for animal navigation (Padget *et al.*, 2019, 2022; Wynn, Collet, *et al.*, 2020; Wynn, Padget, *et al.*, 2020; Wynn *et al.*, 2022) and foraging, as described below. Their longevity and natal philopatry also allow questions of age and experience to be investigated naturalistically in a way often more challenging for other taxa.

In addition, as central-place foragers, the area in which they can forage is thus limited by the location of the home area, and how individual animals use this space has the potential to tell us much about many aspects of their lives: prey sources and energetic requirements, social interactions and group attributes (such as the behaviour of young vs. old birds), learning and navigation, and individual preferences and tendencies. For example, Manx shearwaters (*Puffinus puffinus*) are known to show segregation by age at sea, with older birds consistently using different areas from immature birds (Fayet *et al.*, 2015); by analysing mass gain as a proxy for foraging success, the authors found that

this segregation was likely a result of differing foraging efficiency, suggesting a role of experience in determining the space use patterns of these animals. Similar inferences can be drawn by examining space use during dispersal: a study on white-chinned petrels (*Procellaria aequinoctialis*) showed that movement patterns were best explained by different factors at different life stages – wind in juveniles and attraction to productive foraging sites in adults – that again highlights the role of age in shaping behaviour patterns (Frankish *et al.*, 2020). This also draws attention to the variety of processes influencing the behaviour of these birds at sea, and the potential of spatial analyses to evaluate them.

The nature of their environment means seabirds often exploit temporally and spatially varying resources, which in some cases might be unpredictable (Weimerskirch, 2007), and in any case are distributed over very large areas. Seabirds may present a good model of learning in one respect since many species are abandoned by their parents before fledging, and inexperienced young birds must learn to forage and migrate alone (Guilford *et al.*, 2011; Frankish *et al.*, 2020). As Frankish *et al.* note, individual variability is interesting here for its implication of the role of learning during this period.

In terms of life history, most species raise few chicks, are monogamous, and have little sexual dimorphism or dichromatism (Schreiber and Burger, 2002). Nonetheless, sex differences are inevitable when one sex has to produce eggs, and it seems that in some species these are mostly mediated by behavioural differences between the sexes (e.g. the pre-laying exodus; Dean, 2012). Many species are migratory (whether facultative or obligate) and therefore season and climate are important for their annual movement cycle, as well as affecting prey distributions throughout the year; this is especially true of species living at high latitudes (closer to the poles), where seasonality is strongest.

The same attributes that make long-lived, pelagic seabirds interesting to study also make that study difficult: they spend much of their time away from the colonies in which they live, and some of that time underwater; their lifespans rival that of some researchers, making life-long studies difficult and expensive; and their breeding colonies are often difficult to access, in caves, on cliffs or in burrows.

In addition, most is known about high-latitude seabirds since this is often where research with the most funding is based (Ceia and Ramos, 2015), and the lack of knowledge about tropical species might limit our understanding about generalisations across the group. Nonetheless, advances in tracking technology mean that a lot of insight into the lives of these birds has been gained in the last couple of decades and increasingly we have the opportunity to study ever more intricate aspects of their behaviour.

1.5.2 Individual variation and specialisation in seabirds

Perhaps the best estimate of the degree of individual variation and specialisation in seabirds comes from a review by (Phillips *et al.*, 2017). Though not exhaustive, it reported widespread findings of individual repeatability, both in foraging site use ("individuals of most species tracked to date showed a very high degree of foraging site fidelity") and, indeed, that for other trip characteristics ("all studies that tested for individual consistency in foraging behaviour have found evidence"); though consistency was lacking in a number of other behaviour types where it was studied in various species, and the potential for publication bias among the (un)reported studies should not be ignored.

In this case, *individual specialisation* is defined as "the variation among individuals, in terms of distribution, behaviour, diet or other aspects of resource acquisition, that remains after accounting for the group effects" (Phillips *et al.*, 2017) and it is worth noting the substantial overlap with other terms such as some definitions of *individual differences* and *personality*. Additionally, in many individual studies, different 'specialisations' are usually considered independently (e.g. habitat v. diet) and foraging site fidelity (FSF) is often investigated separately (as in this project). The authors also note that the term is often applied to some concept of consistency, the time period for which is not generally agreed upon. Along with potential publication bias, this therefore likely inflates their estimate of the extent of individual specialisation, since there is no common threshold for what time period it must cover. The inclusion of predominantly higher-latitude species, and those heavy enough to carry tracking devices introduces additional bias.

However, the included studies suggest that these taxa display consistent individual variation across a range of behaviours, separate from that due to age or sex. Phillips *et al.* (2017), expanding from the work of Ceia and Ramos (2015), listed significant evidence of specialisation in distribution, movements, activity or diet in penguins (*Aptenodytes, Eudyptes, Eudyptula, Megadyptes spp.*), albatross (*Thalassarche, Phoebetria, Diomedea spp.*), petrels (*Procellaria, Pterodroma spp.*), shearwaters (*Puffinus, Ardenna, Calonectris spp.*), prions (*Pachyptila belcheri*), northern gannets (*Morus bassanus*), cormorants and shags (*Phalacrocorax spp.*), Atlantic puffins (*Fratercula arctica*), skuas (*Stercorarius spp.*), gulls (*Larus, Leucophaeus, Rissa spp.*) and guillemots (*Cepphus, Uria spp.*).

Phillips *et al.* noted several patterns suggested by this research: that site fidelity is generally lower in the breeding than non-breeding season (though reliability is compromised by the difference in resolution between tracking devices commonly used in these periods, i.e. GPS vs. GLS); and that when breeding success is controlled for, migration schedules appear consistent within individuals over time. Studies finding evidence for consistency in foraging behaviour all looked in particular at diving depth and bout duration, the proportion of daylight and darkness spent in flight, and other similar estimates of foraging activity at a fine scale, though this was not a universal finding.

By another measure, and specifically in terms of “inter-individual niche variation”, individual specialisation in foraging strategies has been found in at least 12% of the world’s seabird species (341; BirdLife International, 2014) and where it was looked for, it was found in 87% of cases, and 95% of species studied (Ceia and Ramos, 2015). Despite this apparently widespread occurrence of individual specialisation, elements of seabirds’ life histories mean the ecological implications are still not well understood, especially as they are long-lived, hard to observe, and are thought to often change habitats and foraging strategy (Ceia and Ramos, 2015). Coupled with the often patchy nature of their environment, this uncertainty suggests a complex picture of individual behaviour in seabirds. And though their similar life histories and ecologies make comparisons across the group informative, the polyphyletic grouping itself masks species differences by lumping together birds “living in and

making their living in the marine environment" (Schreiber and Burger, 2002), while simultaneously excluding other species that do just that, by convention.

Why might seabirds show individual variation?

Consistent inter-individual differences could be a consequence of individual-level strategies for coping with the patchily distributed resources that seabirds commonly exploit. Where patches are far apart and impossible to exploit simultaneously or within the same foraging trip, selection of a single resource or small groups of resources per trip is a more profitable strategy. Indeed, this would be expected if memory-guided search was adaptive (see 1.4.1); memory alone appears to be sufficient to drive segregation of individuals (Aarts *et al.*, 2021). In addition, specialisation on certain habitats might bring fitness benefits (Patrick and Weimerskirch, 2017; Van Den Bosch *et al.*, 2019) perhaps through increased efficiency of foraging trips, or through spatial partitioning that results from (and reduces) intraspecific competition. There is evidence for the effect of competitive ability on spatial consistency, for instance, where body size affects site fidelity (Van Donk *et al.*, 2020) or where juveniles are segregated from adults (Fayet *et al.*, 2015). Unless birds come across patches at random through extensive exploration on every trip, this implies some directionality on leaving the colony, in order to target known areas.

If resource patches need to be *known* and *targeted*, this would require that individuals learn the location or direction of resource patches, learn to identify the cues that indicate the presence of resources, or a combination of the two. Individual responses to environmental gradients, for instance, have been proposed to underlie individual specialisation (Patrick *et al.*, 2014). Consistent differences between individuals might arise from differential learning, either by chance through a random process of early exploration, or a result of different preferences unrelated to learning (for example, one of the three scenarios envisaged by optimal foraging theory, described by (Araújo, Bolnick and Layman, 2011). It is known from the study of migration that routes develop progressively with age over long

periods of learning and refinement in some seabird species (Guilford *et al.*, 2011; Campioni *et al.*, 2020), suggesting potential for learning to shape the spatial preferences of individual animals.

Whether learning about a patchy environment can produce individual variation also depends on the degree of predictability of the patch distribution, which itself can vary between habitats (Phillips *et al.*, 2017). In general, though many studies have reported individual variation in foraging behaviours in seabirds, there are also many that failed to find it, and Phillips *et al.* report that despite predictions about the predictability of some habitats over others (neritic vs. pelagic habitats, for example) there are positive and negative results on all sides. Though these factors might be our best guesses at what drives individual variation or specialisation, its empirical basis is far from established. However, a number of potentially confounding factors have been thrown up across studies that give extra context for viewing the relationship between specialisation and resource predictability: the timescale over which resources remain predictable and how stable local environmental features are, to aid location of resources.

Resource predictability is in part determined by how responsive resource patches are to environmental change, and indeed site consistency in individuals has been found to be vulnerable to changing environmental conditions (Michelot *et al.*, 2021), and to persist only over the short-medium term in some cases (little penguins, Camprasse et al., 2017). Rodríguez-Malagón and colleagues found that consistency in Australasian gannets (*Morus serrator*) decreased with increasing timescale between measurements, but also varied between habitat types (Rodríguez-Malagón *et al.*, 2020). Yet, in a comparison typifying the variation in the field, Grecian et al., 2019), working on the same genus (Northern gannets, *Morus bassanus*), found that individual consistency persisted despite high between-year variation in environmental variables.

Such variability in findings suggests that this relationship between predictability and consistency is highly dependent on context. Some species' niche and habitat characteristics may mean that environmental change affects resource availability very little, while for more ephemeral resources conditions may need to be tracked continuously; in such cases we might expect no specialisation to result, but instead that birds retain flexible behavioural strategies to exploit changing conditions

(Dehnhard *et al.*, 2020; Tarroux *et al.*, 2020). Understanding resource distributions for a particular species in detail might therefore be crucial for making predictions as to the degree of individual variation, consistency and specialisation, as predicted from optimal foraging theory (see 1.4.1). This dependence on environmental structure might not be just the difference between species: it might also affect subpopulation differences (e.g. Ceia et al., 2015; Kane et al., 2020).

Though species might differ in their place along this continuum, some degree of behavioural flexibility is likely always valuable; indeed, even when individual birds show habitat, site or resource preferences, they might show a lack of repeatability in more fine-scale behaviours that suggests they retain a degree of flexibility in how they interact with these sites or resources. Patrick *et al.* (2014) for instance, working with black-browed albatross, found low consistency in trip duration and distance travelled per trip, despite overall consistency in foraging patterns and response to environmental variables.

The stability of local features may be easier to estimate, as long as we have an idea of what cues a species attends to. Benthic habitats for instance are more likely to have static features, making it easier for animals to locate areas based on visual topographical information (Phillips *et al.*, 2017). Neritic habitats might be similarly recognisable by association with distinctive features of the adjacent coastline. For pelagic species such cues may be sparse, and cues associated with fronts and shelf breaks might be more reliable, indicating upwelling and therefore high productivity. Some birds are known to be able to track of patterns of surface ocean flow, whether via visual or olfactory information, to guide foraging behaviour (Kai *et al.*, 2009). It is likely that individuals are able to use multiple cues given the range of cue modalities available, and which cues are most useful to seabirds depends on spatial scale (Nevitt, 2000, 2008), so they may use different modalities in different contexts. This may also allow individuals to use different cue types to locate prey, especially if they have different prey preferences. For example, Patrick et al., 2014) found that individual northern gannets (*Morus bassanus*) initiated searching behaviour in relation to different environmental gradients, measured as sea surface temperature, chlorophyll *a* concentrations and copepod concentration (though here of course exact modality cannot be inferred directly).

In summary, consistency in site selection is likely to be advantageous where it pays to know and repeatedly exploit resource patches in a heterogeneous environment. But this works as long as those patches remain stable, and if they are vulnerable to environmental change, we should expect to see consistency only as long as conditions allow. Overall, we might predict that we will only see individual consistency a) where prey distribution is patchy but somewhat predictable, b) that the consistency seen depends on the timescale of prey predictability, and c) where there is some stable feature of the local environment that allows navigation to these areas.

Interaction with sex and breeding stage

As well as the interaction of individual effects on behaviour with age, which might shed light on cognitive processes underlying such differences, it is important to consider the degree to which other factors might show significant interactions. Many studies investigating these phenomena include sex in their analysis, and though some found significant effects of sex on, for instance, specialisation (e.g. Sztukowski et al., 2018), there seems to be little consistent effect across species (Phillips et al., 2017), suggesting that species-specific effects are important. This is perhaps expected, as the degree of dimorphism and behavioural segregation between the sexes varies between seabird species. Incorporating sex into analyses of space use might also provide more context for these sex differences.

The effect of sex can also depend on the breeding stage in which tracking occurs; Manx shearwaters, for instance, show sex-specific behaviour in the pre-laying period when females leave the colony to forage out at sea for an extended time called the ‘exodus’, and males remain on the colony (Dean, 2012). Breeding stage itself – whether the pre-laying period, incubation, or chick-rearing – also influences at-sea behaviour as birds experience different constraints with regard to diet requirements and proximity to or time spent at the colony. Studies of other groups have found individual-level consistency in some, but not all, breeding stages (e.g. Ceia et al., 2014), while some studies only focus on a single breeding stage, making wider generalisations difficult. For dual foraging species

especially, chick-rearing represents a unique constraint where parents alternate between provisioning the chick and self-feeding away from the colony (e.g. Tyson et al., 2017). There are also suggestions that parents might respond to chick-provisioning differently in Manx shearwaters, with males provisioning more in total and being less responsive to rates of chick-begging (Hamer *et al.*, 2006). This would presumably affect the energetic and dietary requirements and play out in variation in foraging behaviour.

In general we might imagine individual level variation to be expressed to a greater degree during periods when other constraints are felt less strongly, but ensuring comparisons are made when animals are at equivalent stages of the breeding sequence is necessary. In this study, differences in trip characteristics and site use are investigated between breeding stages before being analysed at the individual level, with the aim of parsing out these sources of variation.

Site fidelity

For central place foragers, like seabirds, not all areas of even the immediate environment are equally accessible, given the finite period of time available on a foraging trip (Matthiopoulos, 2003). In addition, marine prey resources are often patchy (spatial heterogeneity; (Skákala and Smyth, 2016; Trevail *et al.*, 2021) and may also vary over time (temporal predictability; Weimerskirch, 2007). Marine predators that forage from a central place (the *home colony*) are therefore confronted with a choice of where to forage on any given trip. Various cues might inform the naive individual about the productivity of a specific patch, whether direct perceptual cues (e.g. olfactory or visual; Nevitt, 2008; Bastos *et al.*, 2020; Darby *et al.*, 2022) or indirect indicators like the presence of con- or heterospecifics (public information *sensu* Stephens and Dunlap, 2008); see also (Ward and Zahavi, 1973; Thiebault *et al.*, 2014; Wakefield *et al.*, 2015; Evans, Votier and Dall, 2016; Jones *et al.*, 2018), but location of patches in the first place requires some degree of exploration unless they are in direct perceptual range of the colony (Weimerskirch *et al.*, 1993; Patrick, Pinaud and Weimerskirch, 2017). Experienced animals may, by contrast, remember the location of productive foraging areas or even

anticipate them based on more distant environmental cues (Pettex *et al.*, 2010), and are therefore able to target patches specifically during trips.

Many pelagic seabird species are very long-lived, and generally have extreme life histories characterised by high adult survival and low annual reproductive success (Ricklefs, 1990; Hamer, Schreiber and Burger, 2001; Weimerskirch, 2001). For philopatric species with high interannual fidelity to their breeding sites, these lifestyles constitute extensive opportunities to learn the location of foraging patches in a heterogeneous environment. In classic models of foraging distributions, individuals are assumed to be ecologically equivalent, with equal propensities to exploit the same resources (Fretwell and Lucas, 1970; Kennedy and Gray, 1993; Bolnick *et al.*, 2003), yet in more recent years analysis of tracking or diet samples in seabirds shows that individuals of many species show considerable variability (Phillips *et al.*, 2017).

Individuals may vary with respect to a number of intrinsic factors, such as age or morphology, which influence their foraging behaviour, whether through ability or preference (Fayet *et al.*, 2015; Votier *et al.*, 2017) sex-based variation is usually partitioned from that attributable to individuals and will be considered so henceforth). Morphological or physiological variation may contribute to between-individual differences via differing dietary preferences, competitive ability (particularly with regard to body size), or range capacity (such as through tolerance for higher energetic expenditure). While age might correlate with certain physical attributes, whether positively through muscular development or negatively with senescence, it is also the best natural correlate of experience, and analysing individual variation with respect to age allows us to test the effect of experience, and by proxy learning, on foraging behaviour. For instance, Votier *et al.* (2017), in their study of northern gannets (*Morus bassanus*) found breeding individuals (five years and older) to show higher levels of individual consistency than immatures (aged 2-3), which were more exploratory and lacked site and route fidelity; this they argue supports a canalisation of foraging behaviour over the individual's lifetime, a formulation of the exploration-refinement hypothesis (Guilford *et al.*, 2011), to be returned to later.

The literature of individual variation in seabirds describes similar phenomena in a plethora of terms, as discussed in (1.2), with the addition of the distinction between *individual consistency* (relating to

within-individual similarity, though meaningful only relative to population-level consistency), and *individual variability* (the existence of differences between individuals). Though applied in a variety of contexts, the widespread use of biologgers to study the movement ecology of these species has meant that individual consistency and variability are most often applied to space use. Here, we will focus on the phenomenon of foraging site fidelity (FSF) as an instance of individual consistency (and / or variability) that offers an opportunity to investigate the role of memory in foraging behaviour.

Observations of site fidelity in seabird species (discussed below) have prompted suggestion of a role for "local knowledge" in guiding foraging movements, with individuals remembering "where and when they were successful" (Irons, 1998). However, to determine the relative importance of memory in maintaining IFSF we need to investigate the contribution of other potential causal factors, such as intrinsic physical differences between individuals and other immutable characteristics like sex, as well as contingent factors like body condition. Indeed, insights from foraging theory reveal that memory-guided search is not always adaptive (see 1.4; Stephens and Dunlap, 2008) and indeed other mechanisms might allow for site fidelity in some instances, so care should be taken to differentiate where possible. Ideally, social factors would also be controlled for, such as the role of social enhancement in locating foraging sites, sometimes referred to as "public information" (see above). The role of such social information in guiding space use is little understood, especially around the colony (Ceia and Ramos, 2015) and in its influence on behavioural variation (Phillips *et al.* 2017), though practical limitations means this is often impossible.

For instance, intrinsic or morphological factors may influence individuals' preferred foraging strategies, including their degree of site fidelity. This may act via dietary preference to drive IFSF through dietary specialisation, or through sexual segregation where diet or physical differences are attributable to sex (e.g. Cleasby *et al.*, 2015). These possibilities might be accounted for with diet data or by analysing the sexes separately. However, for the present study where diet, sex and morphometric data are not uniformly available, the influence of morphology can be tested indirectly. Morphological differences like body size could drive differential site use if, for example, larger individuals were better able to balance the energetic trade-offs of commuting to more distant patches.

It is possible that larger birds may be better able to withstand the energetic costs of flying longer distances, though this relationship is complicated by the impact of body size on available flight speeds (Ellington, 1991) but generally seems to apply to species capable of sustained non-flapping flight (Hedenström and Møller, 1992), like procellariiforms.

Foraging patches across a heterogeneous environment might therefore vary in their "energetic accessibility" for individuals of different sizes (Matthiopoulos, 2003), leading to individuals showing differences in their foraging behaviours or site use as a result. Indeed, Shoji et al. (2016) showed that the depth to which Manx shearwaters dived scaled with body mass; bigger birds might for instance be able to exploit prey only found in specific locations at greater depths. If this was the case, we might expect birds that were repeatable in their use of foraging locations to be similarly consistent in their trip characteristics, such as the duration or distance covered on trips, or the maximum distance travelled. In the case that bigger birds were able to exploit a wider variety of foraging sites, for example, we would expect that they were more variable in trip characteristics and site use, therefore with low measures of both trip metric consistency and site fidelity over years. Overall, in this scenario we would therefore expect trip metric repeatability to correlate with site fidelity. Alternatively, if physical differences play little role and differential site use is a result of relying on private information – individual memory – we may not see such a relationship, as site use might depend more on individual choice than constraint. Investigating the interaction between consistency in foraging trip metrics and site fidelity therefore offers an opportunity to tease apart the contribution of physical and cognitive influences on foraging behaviour, in the absence of direct biometrics. The mechanisms underlying any observed site fidelity can then be investigated in relation to other non-physical factors (like age) or contextual information (such as environmental conditions). Combining the two approaches offers a comprehensive way to examine how birds interact with a patchy environment, as well as illustrating the potential extent and causes of individual consistency and variability.

As a case study, Wakefield and colleagues' analysis of IFSF in northern gannets (*Morus bassanus*) found them to be individually consistent over multiple breeding seasons in a number of aspects (Wakefield *et al.*, 2015). Individuals showed consistency in their departure direction on trips, and in

their larger scale foraging distributions, as well as in habitat use (in terms of sea surface temperature) and dietary specialisations, though these latter points were independent of IFSF. The authors tested multiple hypotheses to explain the persistence of individual foraging distributions over such multi-year timescales: (1) win-stay, lose-shift strategies; (2) habitat specialisation; (3) dietary specialisation; and (4) site familiarity. In the absence of any correlation between habitat or dietary specialisation and IFSF, they found no evidence for hypotheses (2) and (3), but their results provide an interesting exploration of the other two hypotheses, which I use here to inform predictions for the behaviour of Manx shearwaters.

Win-stay, lose-shift (WSLS) foraging describes the strategy whereby individuals revisit a known patch for as long as it remains productive, and switch when through exhaustion or over-competition it remains no longer profitable for the focal individual (Kamil, 1983; Davoren, Montevecchi and Anderson, 2003). Recent evidence suggests it is employed by black-browed albatross (*Thalassarche melanophris*), and indeed that it has some degree of adaptive value when evaluated in relation to chick mass (Bonnet-Lebrun, Collet and Phillips, 2021) unlike Wakefield *et al.* 2015 data collection for this study was only within one breeding season, so it is unclear whether WSLS drives multi-year IFSF in black-browed albatross.) A key prediction of the use of WSLS would be for decay of IFSF over time, as individuals would be expected to shift resource patches at a rate which matched that of the change in profitability of patches themselves. However, in gannets, Wakefield et al. did not find that IFSF decayed over time, but indeed remained at a similar magnitude between and within years, suggesting that it is not direct tracking of known resources that explains IFSF (or, alternatively, that prey patches shift spatially over much longer timescales than expected).

As an alternative, the authors therefore suggested a role for ‘site familiarity’ in maintaining individual fidelity to foraging sites. The term is associated in the literature with models of retention of breeding sites (Piper, 2011), particularly as an alternative consideration to the assumptions of ideal free and ideal despotic models. Even for central place foragers with their constraints on spatial accessibility, we should imagine that the dynamics of switching are different for foraging and breeding sites, as even in the simplest habitats (at least for larger vertebrate species, like seabirds and pinnipeds)

foraging opportunities are likely heterogeneous and therefore multiple patches will be available to any individual. However, the concept and investigations into its effect on switching between breeding sites may still be informative of its role in influencing foraging site fidelity. 'Site familiarity' refers simply to "accumulation of information about a single, unique space that an animal occupies or visits" (Piper, 2011). In the foraging context, experience of foraging at a particular site could be seen to confer an advantage to staying, whether through roles for local knowledge (e.g. of bathymetry, currents, or wind conditions, which may directly impact foraging success) or, perhaps more likely, through improving navigation efficiency in a heterogeneous environment where complex maps of multiple resource sites may be hard to learn and remember (Bradshaw *et al.*, 2004). This can be conceived as a kind of opportunity cost to switching, as familiarity and its benefits take time to acquire and cannot be immediately transferred to another patch (unlike generalised foraging ability).

Viewed this way, site familiarity gives the prediction that site fidelity should in fact *increase over time*, or be higher in older individuals, as they have accrued higher opportunity costs to switching patches given that their foraging ability at a given patch relative to others increases with continued exploitation. This also implies an element of competitive advantage to site familiarity, though it could apply to an individual foraging in the absence of any conspecifics. Furthermore, this hypothesised explanation is eminently testable in relation to the effect of age on site fidelity, as its predictions are directly at odds with those of competing hypotheses for the advantages of age. Other common explanations for variation in foraging behaviour with age appeal to improved generalised foraging ability as a mechanism for older individuals to out-compete juveniles at saturated patches (e.g. Fayet et al. 2015). With higher competitive ability, older individuals would therefore be expected to switch patches more frequently (to track patch productivity) if site familiarity played no role.

For IFSF in seabirds to be driven by the benefits of site familiarity, the species in question ought to have a sufficient "capacity to learn and remember features of an inhabited space" (Piper, 2011); for IFSF measured over longer timescales such as years, as in Wakefield *et al.* (2015), this would obviously rely on multi-year memory. Evidence from procellariforms suggests they are able to integrate spatial information over such timespans, with site fidelity observed over multiple years in

several species, such as Campbell albatross (*Thalassarche impavida*, Sztukowski et al., 2018) and black-browed albatross (*Thalassarche melanophris*, Patrick and Weimerskirch, 2017). It is also worth noting that the predictions of site familiarity-based IFSF would also be concordant with the exploration-refinement hypothesis laid out by Guilford et al. (2011) appealed to by Votier et al. (2017) to explain their observation of higher IFSF in breeding northern gannets; indeed, site familiarity could be a mechanism by which exploration-refinement behaviour is sustained (both within the individual and evolutionarily).

A final consideration is the possibility of information transfer between individuals, either at sea or at the colony, which might enable individuals to find successful foraging locations. Due to the constraints in the design of most tracking studies it is rarely possible to investigate this directly. It is unusual to track both adults from a breeding pair to account for information transfer at the nest, though where this has been investigated no evidence of within-pair information sharing has been found (black-legged kittiwakes, *Rissa tridactyla,* (Irons, 1998); Australasian gannets(Machovsky-Capuska *et al.*, 2014), and covering enough individuals to track all potential coordinated foraging at sea is impossible given the size of seabird colonies (before even considering information transfer between heterospecifics or conspecifics from other colonies). However, the effect of information transfer may be gleaned indirectly, by comparing the overlap of individuals' foraging distributions over a sufficiently long timespan, especially where sites targeted by different individuals would be equally accessible to others over the same time period, or by comparing departure directions. It has been hypothesised that birds use information implicit in conspecifics' arrival (Weimerskirch *et al.*, 2010) or departure directions (Racine *et al.*, 2012) to inform their own foraging movements, though results are mixed and appear to vary widely by species (Jones *et al.*, 2018; Urmy, 2021).

Public information likely plays a role in first locating areas for naive individuals, and so its influence cannot be discounted entirely, but population-level measures of individual site fidelity over longer timescales (months to years), such as high repeatability of site use among individuals, imply an independence of individuals at odds with a dominant role for social information transfer. In addition, highly consistent departure directions on trips – high directionality – may support the importance of

private over public information; when combined with site fidelity directionality implies anticipation of the location of foraging areas in advance of the presence of other foragers (though empirical examples of this relationship are inconclusive, see Wakefield *et al.* 2015). However, directionality on leaving the colony has also been observed in the absence of site fidelity where it has been suggested to form a 'trap line' strategy (Wanless, Harris and Morris, 1990; Wakefield *et al.*, 2015). Under this strategy birds may be faithful to first exploring a particular arc of habitat closer to the colony, before moving on if these areas prove unsuccessful. Measuring repeatability in departure direction, and how it relates to the site fidelity, is therefore another useful approach for interrogating the foraging strategies these animals may be using (see also Davoren, Montevecchi and Anderson, 2003; Pettex *et al.* 2010; Goyert, 2015). Given the potential for social cues to influence departure direction (Weimerskirch *et al.* 2010; cf. Carter *et al.*, 2016), individual strategy should only be considered in the cases of repeatable directions over longer periods of time where individuals can be shown to vary consistently from each other.

Summary

Overall, though an increasing number of studies describe evidence of consistent individual variability, whether diet or habitat specialisation, consistency in fine-scale foraging activity, or foraging site fidelity, findings vary widely between species and even within them (compare Bartumeus *et al.*, 2010; Courbin *et al.*, 2018). Reviews of variability have to date tended to take a broad definition of the phenomenon, and this is perhaps why results vary so widely between taxa and studies. In particular, little is understood of the mechanisms underlying variability, and the variety of approaches taken to investigating it (e.g. personality assays, environmental correlates, social information transfer) seems to have diffused confidence in understanding any one potential cause. In relation to individual specialisation in particular (and therefore measures of site fidelity and environmental covariates), Bonnet-Lebrun *et al.* (2018) recommend that, with limited resources for research, we should prioritise intensive rather than extensive sampling of individuals, as long as there is no *a priori* reason to expect that the population consists of highly specialist individuals.

This project aims to take specific manifestations of individual variability (differential foraging trip characteristics, and site fidelity) to investigate potential causes and consequences of between-individual variability (and within-individual consistency) in a species in which it has not yet been investigated. By using a combination of intensive and extensive datasets, I hope to make use of a large extant dataset to approach some of these remaining questions, with hypotheses based on alternative and interacting cognitive and life history-related explanations as developed above.

1.5.3 Manx shearwaters

Manx shearwaters (*Puffinus puffinus*) are highly pelagic, medium-sized seabirds breeding across the North Atlantic, with the majority of the global population found in the British Isles (~ 80-90%; Newton, Thompson and Mitchell, 2004). The UK sub-populations are therefore considered representative of the global population, though recent work suggests populations around the southern extent of their range (around the Macaronesian Islands – the Azores, Canaries and Madeira) are morphologically and genetically distinct and might be better considered a sub-species (Rodríguez *et al.*, 2020). Despite their trans-Atlantic migration, the species has a long breeding season, with adults present at the breeding colony between March and September. Ringing records from the UK colonies show that birds reach their 30s not infrequently; the oldest individual was recovered in 2008 50 years after being ringed as an adult (British Trust for Ornithology, 2022).

Tracking of individuals on foraging trips during incubation and chick-rearing has shown that birds from various colonies around the UK and Ireland use a large area of the Irish and Celtic Seas to forage (Guilford *et al.*, 2008; Dean *et al.*, 2012, 2015; Wischnewski *et al.*, 2019; Kane *et al.*, 2020), with a subset making longer trips further out into the North Atlantic (Dean *et al.* 2012). Analysis of chlorophyll concentrations across the region shows both spatial and temporal heterogeneity (Skákala and Smyth, 2016), which alongside heterogenous fishing activity, is known to affect the abundance and distribution of marine vertebrate communities (Shephard *et al.*, 2011, 2012). As a particularly long-lived species with an extensive, heterogeneous, foraging area available within reach of their breeding sites, Manx shearwaters offer a valuable model to investigate how individuals learn about the location

of foraging patches, and what informs how they use them. In addition, as noted by Kirk (2016), they make a suitable model for studying individual consistency in behaviour since they are long-lived and mostly return to the same burrow year on year, and so are easy to recapture and track repeatedly. On top of this, they have now been studied at the UK field sites, particularly Skomer and Copeland, for over a decade with regular GPS and GLS deployments, producing a large dataset pertaining to detailed at-sea behaviours. Over this time individuals had already been repeatedly tracked and provide an ideal starting point for investigating individual variation in behaviour.

Studying individual variation in space use in shearwaters

As discussed, examples of individual specialisation have been found in multiple species of shearwater (Phillips *et al.*, 2017). Bartumeus *et al.* (2010) identified site fidelity in Cory's (*Calonectris borealis*) and Balearic shearwaters (*Puffinus mauretanicus*), Manx's closest relative. Though the latter share certain aspects of Manx's foraging ecology, there is enough variation between the two species to caveat any generalisation between them; for instance, Manx are not thought to follow fishing vessels whereas it is commonly observed among Balearics. At the time of writing, only one study of individual behavioural variation has been undertaken in Manx shearwaters, and it looked in particular at that in breeding and migratory phenology, rather than more fine-scale movements during the breeding season. Kirk (2016) used GLS to investigate the "otherwise cryptic behaviour and ecology" of the species with data from 2007-2012, and investigated individual consistency and colony-level, annual and sex differences in the phenology of migration.

In terms of migration, findings were of "considerable inter-individual variation in migration route" in both the north- and southbound directions, though this did not account for a significant proportion of the variation in the southbound route: a nearest-neighbour distance analysis showed no significant difference in mean distance calculated in within-individual pairs and between-individual pairs on the southbound route; but in the northbound route, within-individual pairs were significantly more similar (diff = ~240km, $p < 0.001$). A repeatability analysis also showed that the degree of westerly movement

was consistent within individuals. Notably, there were no consistent sex differences in either route. For stopover sites, locations used by individuals were more similar to themselves than to those of other birds, though the proportion of time spent at these sites was not repeatable. However, the timing of breeding season events showed high repeatability: date of first night on the colony ($R = 0.343$, $p = 0.006$), date of first day spent in breeding burrow ($R = 0.224$, $p < 0.001$), date of first incubation stint ($R = 0.064$, $p = 0.02$), all showed some signs of within-individual consistency. However, there was no significant repeatability of last incubation stint, last night on the colony, or the number of incubation stints, suggesting timing at the beginning of the season is more important and birds are constrained by the development of their chick more than seasonal timing at the end of the breeding stage.

These results suggest that individual Manx shearwaters show somewhat consistent differences in the timing of significant events in their annual cycle, particularly those concerning arrival at the colony and the first events in breeding. Whether this consistency translates into consistency in other behaviours is unknown, and furthermore the phenomenon has not been investigated with regard to age among the set of known-age individuals.

A study of Manx shearwaters' foraging activity at two colonies on Ireland's west coast also found notable variation, and was able to relate these to environmental factors (Kane *et al.*, 2020). Colonies' foraging areas showed some overlap but were clearly segregated, and there was pronounced "spatio-temporal variation in foraging behaviour in general". Some of this was explained by the distribution of chlorophyll concentration, a proxy for productivity. This highlights the need to take into account the effect of colony differences, and also the potential of environmental covariates to explain portions of individuals' behaviour. It is also noted that differences in prey preference between colonies (Skomer birds prefer fish, while squid is preferred on Rum: Brooke, 1990; Dean, 2012) might go some way to explaining colony differences, especially where temporal activity patterns are dictated by those of prey. Overall, this caveats against using a single colony's behaviour as indicative of the entire population; the influence of colony-specific effects should always be taken into account. In Chapter 2, we therefore outline colony variation in the present dataset to provide such necessary context for the following analyses.

Initial exploration of GPS tracks of foraging trips of Manx shearwaters suggest some degree of variability in the directionality and site use exhibited by individuals. This highly pelagic species has a very large range on foraging trips, and previous studies of foraging trip characteristics around the UK colonies suggest variability between sub-populations in the distances and durations of foraging trips; this seems likely to be at least in part explained by utilisation of different resources at sea driven by proximity (Dean *et al.* 2012). In addition, birds vary the distances and durations travelled on trips across the two breeding stages of incubation and chick-rearing (Dean *et al.* 2012) and females are known to vary from males in at-sea foraging distribution during exodus (Dean, 2012). In Chapter 3, the extent to which individuals show foraging site fidelity (IFSF) will be investigated under the hypotheses for explaining IFSF laid out in the previous section.

Many of the factors proposed by various studies apply to Manx shearwaters as to other seabird species, with the caveat that little is known about intraspecific social information transfer away from the colony in this species (though there are reports of interspecific foraging associations, e.g. with cetaceans; Skov et al., 1995). From a resource distribution perspective, site fidelity should be possible since the study populations' main foraging areas, across the Irish and Celtic Seas are known to vary spatially (Skákala and Smyth, 2016) but show relative stability over time especially around the Irish and Celtic Sea Fronts (Simpson and Hunter, 1974; Dean *et al.*, 2012), with particular areas known for congregations of seabird species including Manx shearwaters (Kober *et al.*, 2012). Understanding whether, how and why this species might exhibit fidelity is therefore the next step.

1.6 Outline of research chapters

This thesis will comprise three data chapters to explore the extent, character and potential causes and consequences of individual variability in at-sea behaviour and foraging strategies of Manx shearwaters, as outlined above. Results that are supplementary or tangential to the main narrative are presented in the Appendices.

Chapter 2 and the first analysis of 3 both use simple trip “metrics” derived from biotelemetry data to give high-level descriptions of foraging behaviour across variables of interest. For brevity, and in the hope that it makes the two related analyses easier to understand, descriptions of methods are not repeated in Chapter 3 where they are shared with Chapter 2; much of the introduction of Chapter 2 is likewise relevant to both parts.

Chapter 2 describes in detail how these metrics are derived, and looks into how foraging behaviour can be seen to vary at this level between the two main breeding stages for the species, incubation and chick-rearing, as well as across the five study colonies around the British Isles. We also look at within-individual change over time, to investigate to what extent the observed behaviours are plastic at the individual level, making use of a small known-age subset at the Copeland colony. As discussed above in this chapter, this is done with the intention of demonstrating the use of these metrics to describe foraging behaviour, to extend a previous analysis that used the same rationale with additional data, and to quantify the background variation in these behaviours ahead of investigating it at the individual level in Chapter 3.

Chapter 3 then uses biotelemetry data from the Copeland colony to analyse variability at the individual level. The extent to which behavioural variability is attributable to individuals, above that observed as age-related variation in Chapter 2, is explored. (Unfortunately, we do not have sex data for enough individuals to control for this, the implications of which are discussed in Chapter 4.) As well as using the same metrics as described above to identify IBV, we identify foraging sites and quantify individual foraging site fidelity, and test a number of hypotheses as to the mechanisms of any identified fidelity (or, in its absence, discuss the implications relative to these hypotheses), using repeat data collected over multiple years from the same individuals. The approach of combining an analysis of IBV in simple metrics, informed too by the findings of Chapter 2, with analysis of how fidelity changes over time allows investigation of potential underlying mechanisms. A summary of the main findings and integrated discussion is presented in Chapter 4.

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Chapter 2: Variability in foraging trip characteristics with respect to breeding stage, age and colony

Introduction

Pelagic seabirds are able to make use of large areas to forage, yet are constrained by the location of their breeding site in where and how they do so (Matthiopoulos, 2003; Burke and Montevecchi, 2009). These constraints vary both temporally and spatially across the stages of their breeding season, which simultaneously limit the time and energy they can invest in foraging, and place different nutritional requirements on foraging trip outcomes (Dean *et al.*, 2012; Shoji *et al.*, 2015; Tyson *et al.*, 2017). Their local marine environments, while thought to be generally predictable (Weimerskirch, 2007), are heterogeneous in the resources they offer, which is known to influence both their foraging strategies and breeding success (Trevail *et al.*, 2019).

Seabirds are known to use a range of cues to locate prey or known landscape features that are themselves associated with prey (Nevitt, 2008; Kai *et al.*, 2009; Lieber, Langrock and Nimmo-Smith, 2021). Reliably locating resources across a large heterogenous area therefore suggests a clear benefit to learning to target and exploit more profitable areas where possible, either through learning locations of stably productive areas (Regular, Hedd and Montevecchi, 2013; Goyert, 2015), or by association of relevant cues in less predictable ones (Bastos *et al.*, 2020). Consistent foraging strategies are advantageous as they reduce commute and search time and therefore increase foraging efficiency in terms of energy expenditure (Phillips *et al.*, 2017). Long-lived species are, over the course of their lifetimes, exposed to vast amounts of information as to the location and profitability of different foraging resources, and, as learning and memory constraints allow, may integrate this into foraging decisions in any one foraging trip (Stephens, 2008; Stephens and Dunlap, 2008; Dunlap and Stephens, 2012; Bracis *et al.*, 2015; Robira *et al.*, 2021). Though shared life history and environmental factors influence all individuals, the large areas over which these birds forage means individuals may by chance gather different information about foraging opportunities, and therefore learn different

strategies for exploiting them (Guilford *et al.*, 2011; Ceia and Ramos, 2015; Phillips *et al.*, 2017; Votier *et al.*, 2017).

Individuals may vary in their use of foraging areas as a result of different experience, whether it affects generalised foraging ability and therefore competition between individuals for resources (Fayet *et al.*, 2015), or through access to memory of profitable foraging locations (Bracis et al., 2015; Aarts et al., 2021; see also exploration-refinement, Guilford *et al.*, 2011; Votier *et al.*, 2017). Equally, individuals breeding at different colonies will be exposed to different information, and have different experience of foraging opportunities, even if separated by short distances, given the complex local coastline and mainland geography surrounding many seabird breeding colonies, and heterogeneity of marine resources. Colony variation is therefore a potential source of behavioural variation in these taxa, though has so far been little studied.

Manx shearwaters (*Puffinus puffinus*) are highly pelagic Procellariiform seabirds breeding across the North Atlantic, with estimates of 90% of the global population found in the British Isles (Newton, Thompson and Mitchell, 2004). The Oxford Navigation Group has been using biologging devices to study Manx shearwaters at various UK colonies across the Irish Sea since 2004. An important tool in behaviour and ecology, with the development of lighter, cheaper and higher-storage devices, use of biologging has increased rapidly over the last decades (Bograd *et al.*, 2010), and for pelagic and migratory species like shearwaters has proven invaluable in understanding otherwise intractable behaviours (Yoda, 2019; Chung, Lee and Lee, 2021). Tracking campaigns have been carried out across the UK study colonies using global positioning system (GPS) and light-level geolocator (GLS) loggers at different times in the breeding season, covering the incubation and chick-rearing periods. Tracking data have shown these birds make use of a large area encompassing most of the Celtic Seas for foraging trips throughout the breeding and pre-breeding seasons (April – September) both to feed themselves and to provision their chicks (Guilford *et al.*, 2008; Padget *et al.*, 2019). Thanks to work at the UK and Irish colonies over the last 20 years, we now understand more of the species' extent, phenology and migratory routes and destinations (Guilford *et al.*, 2009; Freeman *et al.*, 2013;

Kirk, 2016), and more of the variation in foraging behaviour between colonies and breeding stages (Dean *et al.*, 2012, 2015).

Here, we collated data from over 600 GPS logger deployments on breeding Manx shearwaters conducted by the Oxford Navigation Group between 2008 and 2022, to further investigate the characteristics of foraging strategies in this species with regard to three main sources of variation. Extending work from previous studies we aim to understand the extent of variation in foraging behaviour between colonies, and to formally compare behaviour between the breeding stages for the first time. We also examine how foraging behaviour changes over time, both at the population level in the interest of understanding environmental factors, and within individuals, to look at the effect of experience. By characterising individual foraging trips in terms of simple metrics (an approach often used to analyse large biotelemetry datasets describing foraging trips, e.g. Davoren, Montevecchi and Anderson, 2003; Kirkwood and Arnould, 2011; Dean et al., 2012; Goyert, 2015; Wakefield et al., 2015; Harris et al., 2020), we summarise foraging strategies as variation in space use, itself an effective proxy for foraging behaviour (see Chapter 1). From each analysis we investigate sources of behavioural variation in light of ecological and cognitive hypotheses, detailed below. In outline, these cover how the differing requirements of incubation and chick-rearing influence space use and foraging behaviour, how colony geography and size impact birds' foraging opportunities, and how learning and senescence might result in age effects.

Firstly, we predict different distributions of trip lengths in the two main breeding stages, incubation and chick-rearing. Across a breeding season in which energetic and time constraints vary, birds might switch between foraging strategies as changing breeding requirements dictate, prioritising different areas or varying foraging effort. Previous studies suggest that within chick-rearing itself, adults alter trip length in response to chick condition, shortening trips when chicks are in poor condition despite a cost to their own (Wischnewski *et al.*, 2019). This trade-off between current and future reproduction could mediate the breeding stages' different priorities as the pattern of investment in self- and offspring-provisioning varies between them. Like other seabird species (e.g. Weimerskirch et al., 1994; Magalhães, Santos and Hamer, 2008; Wojczulanis-Jakubas, Araya-Salas and Jakubas, 2018),

in the chick-rearing period Manx shearwaters show a dual foraging strategy, whereby parents alternate between self-feeding and chick-provisioning (Shoji *et al.*, 2015; Tyson *et al.*, 2017; Gillies *et al.*, 2022). This contrasts with a simpler alternation in the incubation stage, where parents simply take turns to incubate the egg while the other forages to feed itself. Unconstrained to feed the chick frequently, birds on self-provisioning trips and during incubation may therefore have more flexibility to commute to areas providing them with higher value prey, or save effort overall by spending higher proportions of trips foraging away from the colony than commuting; in either scenario, we would expect trips of longer duration at these times. Indeed, Dean et al. (2012) found from analysis of GPS tracks from two UK colonies that birds spent more time per foraging trip during incubation than during chick-rearing, and behavioural classification also showed some variation in the distribution of time spent in different behavioural states between breeding stages, and in the locations used for foraging. Though this variation has so far been assumed to be influenced by the differing requirements of incubation and chick-rearing, how exactly these constraints contribute to different behavioural strategies is less well understood. Here we hope to confirm the previous study's finding for trip duration with a bigger dataset and a different modelling approach. In addition, by extending the analysis to look at distance metrics we hope to resolve which of the two scenarios described above – i.e. which foraging strategy – explains the difference in trip duration.

Dual foraging – seen as variation in space use between self-feeding and chick-provisioning -- has been interpreted as a response to parent-offspring conflict (Shoji *et al.*, 2015; Wischnewski *et al.*, 2019), or as a consequence of foraging for prey with different handling times (Ydenberg and Davies, 2010). The latter would more strongly predict different trip distances between incubation and chick-rearing, as Ydenberg and Davies show that any difference in "resource geometry" between optimal prey for parents and offspring would result in parents segregating their space use by whether they are foraging for themselves or their chicks. By contrast, if dual foraging has emerged under conflict between parent and offspring by mitigating the cost to parental condition of the high intensity of frequent chick-feeding, we would not necessarily expect that self-feeding trips needed to cover longer distances, just that they were longer in duration to reduce proportional commuting to foraging time

and thereby maximise energy gain. Despite the predictions of these theories, more recent observation of the dynamics of foraging parents at the colony also suggest that strategies are not as stereotyped as perhaps imagined, and indeed that parental coordination varies throughout the breeding season (Tyson *et al.*, 2017) and is not dependent on physical contact of parents (Gillies *et al.*, 2022), further characterisation of the variation during each breeding stage might clarify the role of various life history factors. As well as extending the approach of Dean *et al.* to use additional metrics that might elucidate the manner of variation between incubation and chick-rearing, we also look at how these metrics change throughout each breeding stage, to clarify how flexible the behaviours are and how much variability previously attributed to breeding stage differences may be explained by confounded factors such as seasonal progression (further detail in Methods).

Second, we make use of the multi-colony dataset to examine colony differences in foraging routines. Specific areas around the British Isles are already known for concentrations of foraging Manx shearwaters, such as the Irish Sea Front (ISF), a tidal-mixing front occurring throughout this species' breeding season (Simpson and Hunter, 1974). The section of the ISF roughly between the Isle of Man and Anglesey, a designated SPA, is reportedly the UK's third largest marine aggregation for Manx shearwaters (Kober *et al.*, 2012). Dean *et al.* (2012) showed that birds from both Copeland and Skomer visit the area to forage. We suggest a likely source of variation between colonies is, thus, how the local geography makes commuting to such productive areas more or less efficient—we predict that foraging strategies are influenced by the colony's location with respect to the wider heterogeneous resource distribution.

Comparing foraging behaviour between these two colonies, Dean *et al.* (2012) found no difference in trip duration between colonies in incubation or chick-rearing, but significantly greater distance covered and maximum distances reached from the colony on Skomer in both breeding stages. Using behavioural classification models, it was also found that Skomer birds spent a higher proportion of the day in directed flight than foraging, suggesting that the colony disparity in distance covered on trips results from a need to travel further to locate resources. This could be due to the increased distance from areas like the ISF compared to Copeland, or to Skomer's higher population size

(Newton, Thompson and Mitchell, 2004) inducing local competition, though some studies have suggested that shearwaters and other pelagic seabirds are unlikely to experience resource depletion at high population sizes (Gaston, Ydenberg and Smith, 2007). Other potential factors, such as geography and proximity to other colonies, could not be explored in this original study, but by including tracks from other colonies of varying sizes in this analysis, we hope to offer further insight into the mechanisms underlying colony variation (though this remains purely commentary in the absence of environmental data). Social factors like competition from conspecifics (Fayet *et al.*, 2015) will also influence where a bird is able to forage at a given time, while wind speed and direction may also make some destinations more or less energetically favourable to reach from the colony at a given time. Manx shearwaters are known to alter their flight routes to maximise energy harvesting from wind during dynamic soaring, doing so on outbound flights from the colony but not return flights (Kempton *et al.*, 2022), suggesting that wind conditions influence birds' choices of trip destinations. Birds' ability to consistently target productive areas is therefore likely somewhat constrained, and it is conceivable that these constraints vary in strength between colonies, due for instance to geography or population size. Here we are of course unable to disentangle the two by acknowledge the relevance of these factors outlined in recent research.

Throughout these analyses we control for interannual variation. Though uneven sample size across years make explicit testing of trends over time impossible in the present study, we present plots of the annual variability in each metric in Appendix 1B. Climate predictions for the UK region suggest increasing temperatures over the next decades, especially in the summer months (Lowe *et al.*, 2018) We might expect climate-related disturbance to marine ecosystems to manifest in less predictable prey distributions for predators like shearwaters, and though a growing literature posits behavioural changes with a warming climate (e.g. Ancona *et al.*, 2011; Carroll *et al.*, 2015), ecological differences make cross-species extrapolations difficult and expectations for foraging behaviour in particular has not been studied in depth. Nonetheless, in the case of less predictable resource patterns, we predict to see positive trends over years in trip duration, distance covered and range from the colony, as birds

compensate by spending longer during search behaviours, but no necessarily trend in mean speed across trips.

Finally, we predict that, in the absence of very high inter-annual variation, birds will be able to accumulate knowledge of the marine environment allowing them to target more productive areas more reliably as they age. Though for the reasons discussed above there is reason to doubt that individuals can target particular sites entirely at will, we expect that over many trips the effect will be visible in greater average values for metrics indicating range, as older individuals will be more likely to have by chance acquired reliable knowledge of productive patches further from the colony. Using a subset of known-age individuals at the Copeland colony we investigate the relationship directly, and then use within-individual change over time as a proxy for age-related behavioural change in the wider dataset. We would also expect more consistent behaviour among older individuals (i.e. lower within-individual variance), but the current dataset did not allow investigation of this with respect to trip metrics directly. Consistency in site use and its relationship with metric consistency is explored in Chapter 3 to shed more light on this phenomenon.

Methods

Study sites and logger deployment

Data presented here have been collated from 14 years of tracking campaigns conducted with different aims and technological requirements; as a result, details of device deployment vary slightly across study sites and years. GPS loggers were deployed at five colonies of breeding Manx shearwaters in the Irish Sea studied by the Oxford Navigation Group: Skomer and Skokholm Islands, Wales (51°44'N, 5°17'W; 51°42'N, 5°17'W); Lundy Island, England (51°11'N, 4°40'W); Lighthouse Island, Copeland archipelago, Northern Ireland (54°42'N, 5°31'W); and the Isle of Rum, Scotland (56°59'N, 6°17'W). Data were collected between 2008-2019 and 2021-2022 variously for the five colonies, during the incubation period (late April/May-June) on Skomer and Copeland, and during chick-rearing (July-August) for all colonies.

Birds are selected from the “study colonies” on these islands, which consist of a number of burrows within a small area of the overall breeding colony that are monitored each year during the breeding season. Selection of individuals for tracking in any year’s campaign was limited to those adults present at the colony during the relevant window (either, at least one parents’ stint after laying during incubation, or the equivalent following brood-guard after hatching during chick-rearing), whose breeding attempt was showing no signs of failure (i.e. regular and normal length nest attendance by both parents) and whose condition was assessed as within the acceptable bounds via body mass measurements (>390g). Of the suitable breeding pairs present, the birds selected for tracking were the incubating or provisioning parent of each pair visiting the colony on the night when personnel availability allowed logger deployment. Individuals were identified from ID rings fitted to the leg, and for those ringed as pulli on Copeland, were aged from the date ringed in the nest, or if caught on the surface prior to first migration, then aged only if identified conclusively as first years (e.g. by the presence of down). Ages are as calendar years from hatching.

Across all years, 571 deployments on 417 individuals recorded data used in this analysis. Loggers deployed were modified i-gotU GT120, TechnoSmArt Axytrek, or SnapperGPS models, configured to record at either 1, 5 or 10 minute intervals. Breeding birds were taken from burrows either while incubating or while feeding their chicks, weighed before deployment, and loggers attached to contour feathers on the back using Tesa marine cloth tape (Guilford *et al.* 2008). Total deployment mass varied between tracking campaigns, though with a maximum of 18g (3.5-5% of body mass). Deployment mass in the range of 4-5% of body mass is known to impact short-term behaviour in this species (Gillies *et al.*, 2020), and recorded foraging trip behaviour should therefore be interpreted accordingly.

Though protocols varied slightly over the study period and across colonies, birds were monitored for several days before deployment of GPS devices, and devices were attached and started recording fixes as close as possible to the bird’s anticipated departure from the colony. Natural variation in how long birds spent in the burrow means some deployments captured time on the colony before the first trip. During incubation however, the first recorded trip represents the bird’s first trip during its stint at sea. During chick-rearing birds only return for brief periods to feed their chicks, so devices were

deployed on whichever partner was caught; chick-rearing deployments may therefore capture varying sections through the cycle of chick-provisioning or self-feeding trips.

Data selection and trip metrics

Variation in basic metrics of spatial behaviour was investigated across the two breeding stages and in each of the five colonies. Incubation data was only available for Copeland and Skomer, but the others, Lundy, Rum and Skokholm, were included for comparison within the chick-rearing stage. Data processing and statistical analysis were done in R version 4.3.0 (R Core Team, 2023).

Trips were selected as follows. Each GPS "track", representing the data recorded from one deployment of a device from attachment to retrieval (therefore potentially recording one or multiple foraging trips), was (in/ex)terpolated to 5 minute intervals based on piecewise cubic hermitean interpolation polynomials (using 'pchip' function from R package 'pracma'), to standardise fix interval across the dataset. This method was used by Dean *et al.* (2012) as a more reliable method of inferring trip trajectories, and had been shown to give better estimates of speed than other methods of interpolation or if fixes were left at greater intervals.

Each track was then split into its component foraging "trips" defined as any period spent continuously at greater than 500m from the centre of the colony island for more than 80 fixes. Manx shearwaters visit the colony in darkness in order to avoid predation by gulls and other species, and before arrival and after departure will join "rafts" of conspecifics resting on the sea near the colony (Richards *et al.*, 2019). Trips that only included rafting were excluded, so remaining trips represent decisions to leave the colony (and either egg or chick) in order to forage. Furthermore, trips were screened for completeness, i.e. whether the recorded fixes constituted a full trip out and back from the colony. This was done to ensure that the recorded trip duration and total distance reflected as closely as possible that resulting from the foraging decisions of the bird, and there were no unrecorded sections of movement away from the colony between last recorded fix and device retrieval that may have led to underestimates of these metrics.

Where visual inspection of trip trajectories identified that the bird had returned at night to within 1km of the centre of the colony for multiple fixes, these were also designated as breakpoints between trips under the assumption that the most plausible behavioural explanation is colony visitation during this period (as an expected average across all these instances, in the absence of corroborative data). For the last trip in a deployment, the criterion for completeness was extended to within 2km of the centre of the colony; birds may readily travel this distance in the average inter-fix interval (5 minutes), and given the chance of the recording being ended on retrieval at the colony (as in chick-rearing protocol), or failure to continue recording when the device is underground for an extended period (as when the bird returns to incubate during incubation), this avoids trips being excluded unnecessarily just because of a failure to record a fix on the colony.

Five metrics were chosen to capture variation in spatial behaviour at a coarse level: (1) the duration of the trip, calculated as the time in hours elapsed between the first and last included fixes; (2) the total distance travelled over the course of the trip, calculated as the sum of the inter-fix distances in kilometres; (3) the maximum distance from the colony reached on the trip, calculated as the maximum distance of any fix to the centre of the home island in km; (4) the average distance from the colony across the trip, calculated as the median distance from the centre of the home island across all included fixes in km; and (5) average speed, or the mean speed across the trip as (2)/(1), as a measure of the intensity of trip activity. Distances were calculated as Haversine great circle distances, using the ‘distHaversine’ function from the R package ‘geosphere’ (default radius = 6378137m).

Breeding stage, colony and year

If the different local geographies of colonies mean birds have different commute distances to productive foraging areas, we would expect some degree of variation between their metric distributions (particularly duration and max/median distance); if, as suggested by Ashmole’s halo, population size also influences the average range of foraging trips, we would expect bigger colonies like Skomer and Rum to show a greater spread and higher mean median distance values. Given the

different temporal and prey choice requirements when foraging for themselves or for their chick, parents are expected to vary their behaviour between incubation and chick-rearing. If this is driven primarily by a dual foraging strategy resolving conflict over parental condition, as outlined in the Introduction, we therefore expect to see a similar spread of values for all metrics in both breeding stages (as the self-feeding trips of chick-rearing are analogous to general incubation trips), but lower mean values in duration and total distance metrics during chick-rearing due to the higher expected frequency of rapid, local trips to provision the chick at regular intervals while on provisioning stints (we would also therefore expect slightly higher mean speed values during chick-rearing). As regular provisioning is likely most crucial for young, more vulnerable chicks, we would also expect a change in trip length over the course of chick-rearing, but no such change during incubation as we have no *a priori* expectation for a change in foraging requirements during their period (more below). If resource geometry, rather than parental condition, was the prime driver of difference in space use between the breeding stages, we would be contrast expect all duration and distance metrics to be longer in incubation than in chick-rearing, and mean speed to be higher during chick-rearing.

The effect of breeding stage and colony on trip metrics was assessed using generalised Gamma-distributed linear mixed effects models constructed separately for each trip metric, with breeding stage and colony fitted as fixed effects. For all models, year and individual ID were included as a random effects to account for the differences in the dataset's structure between years and across individuals, in terms of sampling across the colonies and breeding stages. Though this cannot here be disentangled from inter-annual variation due to e.g. climatic effects, we present visualisation of metrics across years in Appendix 1B to investigate trends over time. Normality and homoscedascity of residuals assessed by QQ plots and visualisation of residuals against fitted values; duration was square-root-tranformed, the distance metrics log-transformed, and the speed metric left untransformed, to best fit model assumptions. For each metric, Akaike information criterion (AIC) scores were used to compare the main model against alternatives dropping each effect term in turn, using R package 'AICcmodavg' (Mazerolle, 2023); the best-fitting model is reported in the Results alongside F values for the fixed effects.

To follow up these tests and investigate potential explanatory factors of observed changes across the breeding season, change in trip metrics with respect to time was assessed using models with the same structure and transformations as above for each trip metric, with the addition of ordinal date in interaction with breeding stage. To simplify the models and for ease of interpretation, for this we used the Skomer data only as it provided the widest sample for both breeding stages. Model fit was then compared against the previous model structure using AIC comparisons.

Age

Alongside ecological and life history effects, variation in foraging behaviour is potentially explained by cognitive or physiological trends at the individual level. As birds age, they accumulate knowledge about foraging opportunities; to test whether memory was thus a significant source of variation in at-sea behaviour, we looked at the effect of age on foraging trip metrics using a subset of the Copeland dataset, for which age information is available (n = 47, 145 trips total). While physiological changes with age likely also influence foraging behaviours, both via muscle development and thereby foraging ability in younger animals, and deterioration through senescence in older animals, the present dataset did not cover a wide enough range of ages to look at the expected periods for these factors to take most effect, so they are not investigated directly here. For the known-age subset, the effect of age on each trip metric was estimated using a linear mixed effects model with an additional quadratic term to account for diminishing change in the effect of learning over time (and/or potential senescence effects where visible in the age range here, up to 35), and with breeding stage fitted as an additional fixed effect and year and individual ID as random effects. Each metric was transformed as above, normality and homoscedascity of residuals assessed by QQ plots and visualisation of residuals against fitted values. Models were compared to null models with age terms dropped using AIC scores. Then, to assess whether the observed effects of age were attributable to behavioural changes within individuals, or to the outcome of turnover within the sample, we used the wider repeat-tracked Copeland sample (n = 107, 430 trips total) and assigned the year of each observation as an ordinal number in its sequence relative to the first year the individual was observed (i.e., bird A tracked in

2011 and 2012 would be given relative years 1 and 2; bird B in 2011 and 2013 would be given 1 and 3). This preserved the relative difference in age across individuals, though without exact information we are missing whether the extent of within-individual change between years might itself change with age (i.e. given diminishing returns of learning). A linear mixed effects model with the same structure as previously was then used to assess the relationship between relative change in the relevant square-root-transformed trip metric, and compared against the equivalent null model with relative year dropped, using AIC.

Results

We found evidence for variation in trip metrics between colonies, with significant differences between distributions between Skomer and Copeland (detailed below). The limited sample size and year coverage of Rum, Skokholm and Lundy makes more conclusive insights about further differences difficult without additional data and no further significant differences in metrics were found; colony comparisons reported below are therefore restricted to Skomer and Copeland. The additional colonies are included nonetheless in Figure 1(a-e), showing trip metric distributions, for reference and to contextualise the variability of the two main colonies.

The same is shown for both breeding stages across Skomer and Copeland in Figure 2(a-e). A detailed breakdown of the trips across colonies, breeding stages, years and individuals is included in Appendix 1A, and a graphical summary of the variation in trip metrics across years can be found in 1B. Results from modelling the change in trip metrics with respect to age and change within individuals is presented in a final section.

To establish that the observed variation with breeding stage was due to life history and not a response to seasonal environmental change, we also tested the effect of ordinal date on trip duration in conjunction with breeding stage in separate models using the Skomer data only. For all metrics, models including ordinal date provided a marginally better fit and it explained a very small amount of the total variance of each model; with a significant interaction with breeding stage, we assert that this

is likely potentially driven by changes within the breeding stages themselves. A significant and larger proportion of the variance for each metric remained attributable to breeding stage, indicating a role of life history differences. Appendix 1C reports model comparisons and effects, and presents the change in each trip metric with date graphically for reference and the relationship with trip duration is explored in more detail in Results. Temporal changes in trip metrics all show roughly the same pattern, with a broad increase throughout incubation towards hatching and then decline through chick-rearing, which might imply a change in behaviour around hatching and brood guard; however, uneven coverage throughout the seasons, and lack of information on tracking effort makes this difficult to interpret. We conclude that it is predominantly the influence of different life history strategies that drives the major trends described below, though intra-annual seasonal variation cannot be excluded entirely. Without contextual environmental or diet data, we also cannot differentiate between behaviour changes that result from e.g. changing chick-provisioning requirements and those that might follow from environmental constraints (e.g. changing wind fields, prey distributions, temperature range, etc.). Since breeding stage and time of year are partly confounded in this sample, future research looking into life history traits might look to track birds in the overlap period where some are still incubating while others are rearing chicks where possible to examine this further (there is no overlap in the present sample as general protocol does not track during this period because of the sensibility of brood guard). As it is not the main focus of this study, further investigation of change within breeding seasons was restricted to trip duration, to answer questions of particular biological interest in that metric. Full exploration of the interaction between date and breeding stage are left to a study with better power to resolve the two. While an initial analysis of the influence of chick mass was carried out during this work, insufficient statistical power meant it was inconclusive; regardless, future work that was able to collect more consistent chick mass data before logger deployment may use this to examine whether change throughout breeding seasons could be explained by changing chick-provisioning needs.

Trip duration

Comparison of trip durations across colonies and breeding stages are shown in Figure 1(a) and 2(a). Plots shown in Appendix 1B suggest no obvious trend across years. Comparing fitted GLMMs using AIC, we found the best fit included all parameters described in Methods, with 58% of cumulative model weight. Breeding stage had a significant effect ($t = 12.7$, $p < 0.0001$); comparing Skomer and Copeland directly (Fig. 2(a)), for which data from both breeding stages was available, shows the same pattern for both colonies, with incubation trips showing higher variance in trip durations and higher mean values during incubation than chick-rearing, yet the difference is more pronounced for Skomer (Skomer, incubation = 192.6 hours (n = 107), chick-rearing = 70.7h (n = 103); Copeland, incubation = 106.9h (n = 22), chick-rearing = 48.4h (n = 126)). This is concordant with our expectations that, due to the temporal constraints of foraging to feed a chick needing frequent feeding, chick-rearing trips should be shorter on average; inclusion of self-provisioning trips in this period leads to the longer tails of the trip duration distributions.

These findings generally corroborate those reported by Dean et al. (2012) for the same comparisons: median duration for Skomer's incubation trips is comparable (8 days v 8.88 days here), though Copeland's incubation trips are found here to be on average shorter (7 days vs 3.45 days here). Chick-rearing trip durations were similar to previous findings for both colonies (Skomer: 1 and Copeland: 2 vs 1.83 and 0.91 here). Though colony comparisons for trip duration were previously non-significant, an expanded dataset here shows a significant difference between the length of trips on Skomer and Copeland ($t = -2.93$, $p = 0.003$). As reported above, the difference is much more pronounced during incubation, with Skomer trips showing far higher variance and a higher median average during incubation than Copeland trips.

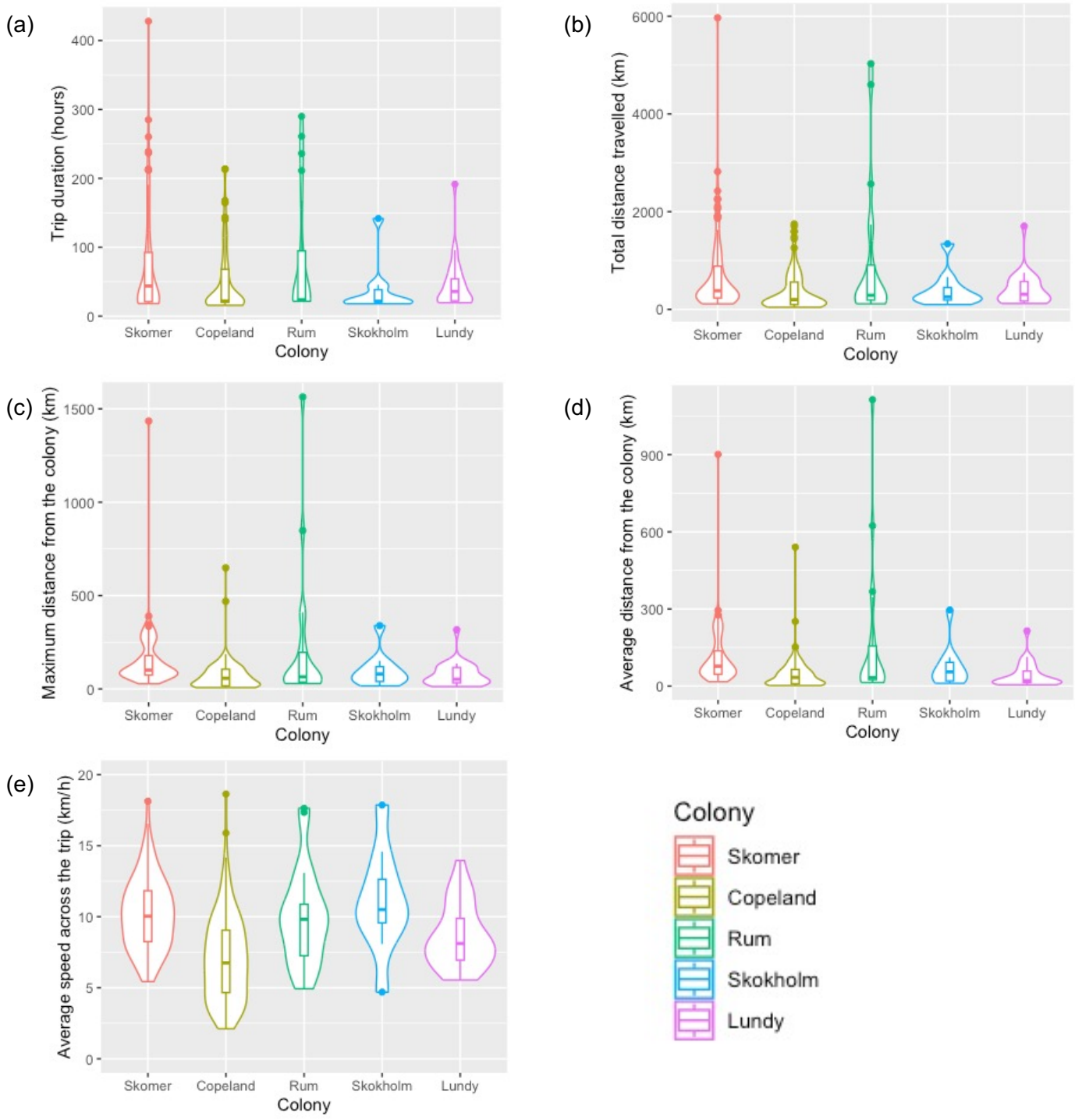


Figure 1. Variation in trip metrics in chick-rearing across the fives colonies with one trip sampled per individual: (a) trip duration; (b) total distance travelled per trip; (c) maximum distance from the colony reached per trip; (d) average (mean) distance from the colony reached per trip); (e) average (mean) speed across the trip. Data from Skomer is shown in red, from Copeland in yellow, from Rum in green, from Skokholm in blue and from Lundy in purple.

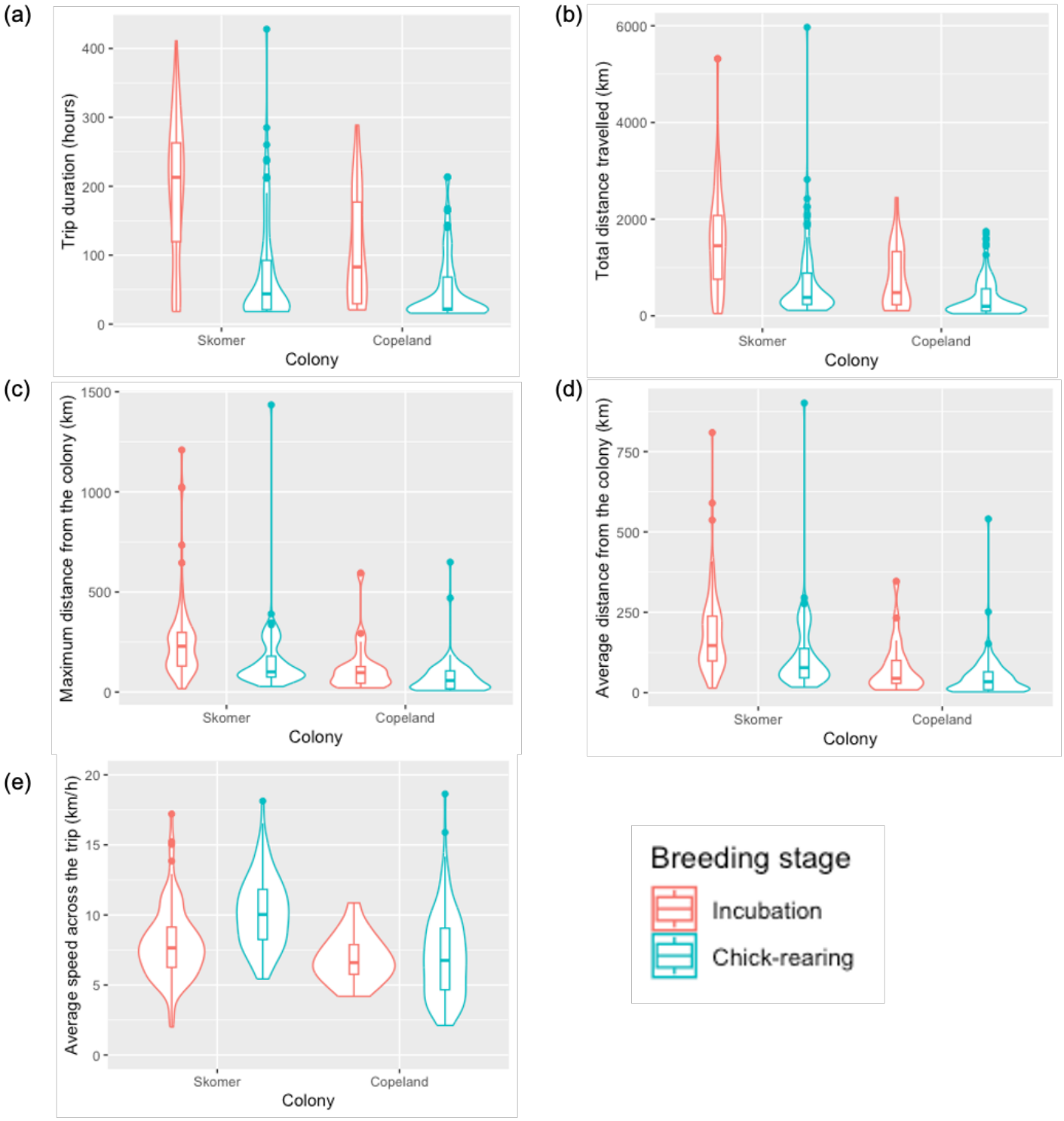


Figure 2. Variation in trip metrics across incubation and chick-rearing and between Skomer and Copeland, with one trip sampled per individual: (a) trip duration; (b) total distance travelled per trip; (c) maximum distance from the colony reached per trip; (d) average (mean) distance from the colony reached per trip); (e) average (mean) speed across the trip. Data represented separately for Skomer and Copeland, with incubation in red and chick-rearing in blue.

Unexpected was the frequency of short (< 48h) trips during incubation, which are not often observed during field monitoring and deployments. During this breeding stage parents alternate incubation duties, taking turns usually in generally relatively consistent stint lengths (Tyson *et al.*, 2017). If one parent is not relieved by its partner eventually it will leave the egg to feed itself (neglect), which has been shown in other Procellariform species to retard embryo development (Boersma and Wheelwright, 1979); optimising parental coordination therefore has adaptive value through its effect on breeding success. Occasionally the partner of an incubating parent has been observed to return to the nest before leaving again on the same night, swapping with its partner only on its return on a subsequent visit (personal observation).

We investigated whether this behaviour might explain the frequency of shorter trips during incubation, by asking whether successive trips decreased in length. As described in Methods, for incubation deployments the first recorded trip should represent the first foraging trip taken by the bird on that stint, as it was deployed on while incubating. Within each deployment's data (GPS track) each identified trip was given a "trip number" indicating its place in the deployment's sequence of trips. Using the Skomer dataset (with the better coverage of incubation), we compared the duration of trips during incubation by their place in this sequence, by fitting a linear mixed effects model with trip number as a fixed effect and year and individual ID as random effects; normality of residuals was confirmed by Shapiro-Wilks test (W = 0.99, p = 0.81). Results are shown in Figure 3.

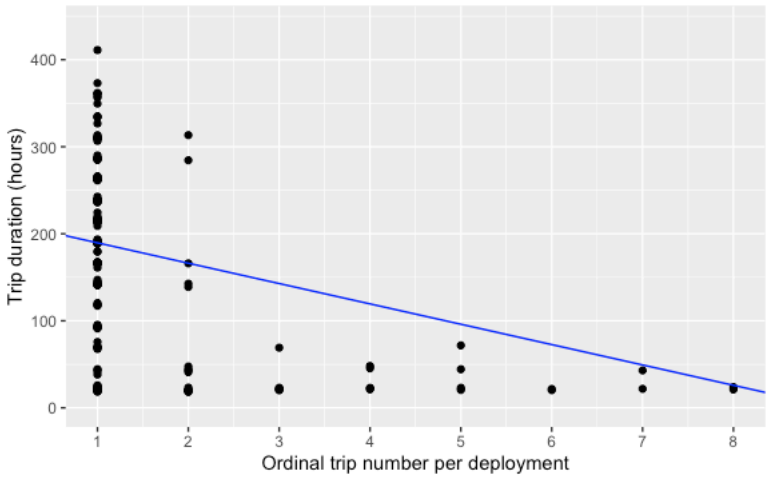


Fig. 3. Predicting trip duration by trip order within each deployment. Fitted line as by model coefficients.

Trip duration showed a significant negative relationship with trip number ($t = 4.12$, $p < 0.0001$), with duration decreasing by on average 23.4h per additional trip across the whole sample. However, comparison of the duration of those trips that would go on to be followed by others within the deployment with those for which the first trip constituted the whole track movement suggested the former are on average substantially shorter (model structure as above, with “whether followed” replacing trip number; 102h difference, $t = 4.64$, $p < 0.0001$). From this we cannot distinguish whether having gone on a shorter first trip predisposes birds to take additional ones before changeover, or whether this represents a more consistent strategy and therefore a decision prior to the first trip. If the latter, this would significantly alter our perception of the general character of self-feeding, and would be worth exploring further experimentally.

This suggests a number of possible explanations for the frequency of shorter trip durations during incubation. Birds neglecting eggs in the early stages of a deployment may visit the nest to check for the return of the partner after an initial foraging trip (of variable length), and leave for shorter trips when the other parent is found incubating. It would be interesting to investigate this further in future by using observations of partner identity on daily nest checks during tracking campaigns. Alternatively, this could represent an unusual and undescribed behaviour, whereby some birds choose to undertake multiple, shorter trips instead of leaving for multi-day trips, perhaps to take advantage of refuge at the colony at night if local foraging conditions are favourable. That total deployment length (summing all trips within a deployment) is normally distributed for incubation tracks on both Skomer (Kolmogorov-Smirnov test, $D = 0.05$, $p = 0.89$) and Copeland ($D = 0.10$, $p = 0.87$) somewhat supports this, as it suggests that overall birds are still choosing to spend roughly consistent periods away from the colony for self-feeding during incubation.

Finally, variable length foraging trips and numbers of trips per deployment could be explained by the point of progression of incubation that the pair had reached at the time of tracking. Pairs are known to become less coordinated throughout chick-rearing as the sensitivity of the chick to feeding frequency decreases (Tyson *et al.*, 2017). An opposite effect might be observed during incubation, where as hatching approaches parents return more frequently to the nest, in order to begin brood-

guard of the hatchling as soon as required. Though we found evidence for a significant interaction between ordinal trip date and breeding stage (see Appendix 1C), the effect size was so small as to limit much further interpretation. In conclusion, the frequency of short trips during incubation may just represent a foraging strategy in this species that until now has been undocumented, perhaps since standard protocols for retrieving devices during incubation has been based on the assumption that foraging trips during incubation are at least 2 days long.

Total distance

Figure 1(b) compares the total trip distances in chick-rearing across the five colonies and Figure 2(b) that across both breeding stages on Skomer and Copeland. Again, plots in Appendix 1B suggest obvious no trend with year. AIC comparisons between fitted models suggest that including all parameters formed the best fit, carrying 100% of cumulative model weight. Breeding stage had a significant effect ($t = 9.51$, $p < 0.0001$). Comparisons of distances covered on trips between Skomer and Copeland for both breeding stages are in line with previous results (Dean *et al.*, 2012). Birds also travelled greater distances during incubation than during chick-rearing at both colonies (Skomer, incubation = 1529.7km (n = 107), chick-rearing = 690.8 (n = 103); Copeland, incubation = 768.0km (n = 22), chick-rearing = 370.0km (n = 126)), and the difference between the two colonies overall was significant ($t = 5.23$, $p < 0.0001$).

Maximum distance from the colony

Figure 1(c) shows the variation in maximum distance from the home colony reached per trip in chick-rearing across the five colonies, also represented spatially in the map in Figure 4(a). Figure 2(c) shows that across both breeding stages on Skomer and Copeland. AIC model comparison again showed that the model with all included parameters gave the best fit with 100% of cumulative model weight. Breeding stage had a significant effect ($t = 6.33$, $p < 0.0001$), and, overall, trips from Skomer reached greater distances from their home colony than those from Copeland ($t = 6.33$, $p < 0.0001$); for both,

incubation trips reached greater distances from the colony than those during chick-rearing (Skomer, incubation = 249.8km (n = 107), chick-rearing = 152.9km (n = 103); Copeland, incubation = 121.6km (n = 22), chick-rearing = 70.9km (n = 126)). Comparisons between these colonies for both breeding stages are in line with previous results (Dean *et al.*, 2012). No trend with year is suggested (Appendix 1B).



Fig. 4. Spatial representations of the mean (a) maximum and (b) average distances reached from each colony across all foraging trips during chick-rearing. Skomer: red, Rum: yellow, Copeland: green, Lundy: blue, Skokholm: purple.

Average distance from the colony

Median average distance from the colony across the trip also varied between both colonies and breeding stages, and no trend with year is apparent (see Appendix 1B). Figure 1(d) shows the variation among colonies during chick-rearing, and the implied extent of foraging areas from each colony is represented spatially in Figure 4(b), giving a mean median distance reached from each colony across all trips. Comparing AIC scores gives 100% of model weight carried by the full-

parameter model. As above, testing the influence of breeding stage on the median distance sustained per trip gave the expected result, with breeding stage having a highly significant effect: comparisons between the two focal colonies of Skomer and Copeland (Fig. 2(d)) showed that, corroborating the findings of Dean *et al.* (2012), birds from Skomer stay out further from the colony than those from Copeland across trips on average ($t = 8.42$, $p < 0.0001$). Birds across both colonies do so significantly ($t = 5.35$, $p < 0.0001$) during incubation compared to chick-rearing (Skomer, incubation = 181.0km (n = 107), chick-rearing = 110.3km (n = 103); Copeland, incubation = 77.8km (n = 22), chick-rearing = 46.5km (n = 126)).

Average speed

As above, AIC model comparison upheld the full parameter model as carrying all cumulative model weight. Variation across colonies during chick-rearing is shown in Fig. 1(e). In particular, colony variation was perhaps greater than expected, with particularly trips from Copeland sustaining on average lower speeds across trips during chick-rearing than all other colonies; though conclusive inferences are again limited by the sample sizes of Rum, Lundy and Skokholm, the comparison between Skomer and Copeland for which most data is available is striking ($t = 7.03$, $p < 0.0001$). Across the two focal colonies (Fig. 2(e)), as expected, birds sustained faster average speeds in chick-rearing than in incubation (Skomer, incubation = 10.2km/h (n = 107), chick-rearing = 9.89km/h (n = 103); Copeland, incubation = 6.87km/h (n = 22), chick-rearing = 7.07 km/h (n = 126)), upheld by the overall result in the main model, with chick-rearing trips sustaining on average faster speeds than incubation trips ($t = 5.36$, $p < 0.0001$). This is in line with our expectations, and concordant with those for trip duration, suggesting that birds conduct trips at higher intensity during chick-rearing to return food to chicks when provisioning.

Effects of age or change within individuals

Assessing the relationship between age and trip metrics at the individual level (n = 47, across 145 observations), we found age to be positively correlated with a number of trip metrics. AIC comparisons between age and null models suggest that only for trip duration does age explain significantly more of the variation, making the model with the linear (and not quadratic) age term the best fit (59% of cumulative model weight), describing a very slight positive increase with age ($t = 2.25$, $p = 0.03$). The small effect and lack of effect among other metrics leaves us with little concrete conclusion as to how foraging behaviour changes with age from this sample. Instead, using the full dataset (n = 107, across 430 observations) to model change in trip metrics against the relative order in which trips were recorded over years instead of against age *per se*, we attempted to determine whether the observed effect of age on duration was most likely explained by within-individual changes over time or a between-individual effect given sample turnover, and extended this to include all five metrics to make use of the larger sample. AIC comparisons between models retaining relative year and the respective null models suggest a significant positive, though small, within-individual change over time in trip duration (99% of cumulative model weight; $t = 3.30$, $p = 0.0012$) and total distance travelled (80%; $t = 2.27$, $p = 0.024$); but for the other three metrics no evidence of a significant effect. The observed change in duration with age may therefore likely to be a result of behavioural change within individuals rather than turnover of individuals within the sample with certain behavioural patterns; with a bigger sample we also have reason to support a within-individual change over time in total distance travelled per trip. A known-age sample with a wider span of ages might resolve the difference in effects seen here, as we identified change over time in different metrics when using age, or relative year; as the known-age sample is skewed slightly older than the population average, it may be that the changes observed with the second method are concentrated in younger individuals, for instance (as would be expected if based on diminishing change with learning, see exploration-refinement hypothesis above).

Discussion

Using GPS data collected from five UK colonies of breeding Manx shearwaters, here we describe variation in five spatial metrics between colonies for chick-rearing trips and between the two breeding stages, incubation and chick-rearing, in the two colonies where data for both were available, Copeland and Skomer. We also describe the change in trip metrics over time, at both the population and individual level. These measures give an overview of spatial behaviour, and by proxy foraging routine, by summarising the duration of trips, the distance covered, the maximum distance reached from the colony and the average distance from the colony sustained over each trip, as well as average speed as an estimation of the intensity sustained over a trip. Overall, we found substantial variation between incubation and chick-rearing for all five metrics, with incubation trips on average longer in duration, covering longer distances in total, reaching further maximum and median distances from the colony, and sustaining lower mean speeds. In line with our predictions and results of previous studies, this confirms that the different demands of self-feeding and chick-provisioning induced by a central place forager life history, combined with the dual foraging strategy of this seabird during chick-rearing, result in substantial differences in space use at different times in the breeding season.

Shorter trips were predicted given the tighter constraints of central place foraging during chick-rearing, while the high variability still present in the chick-rearing metrics is a result of parents' dual foraging strategy. As parents alternate between chick-provisioning, requiring frequent short trips that usually result in foraging near to the colony, and self-feeding, which allows for longer trips, the distribution of trip durations during chick-rearing is expected to be different from that of incubation. For a given stint length, the provisioning parent makes many short trips while the partner is able to stay away from the colony for longer, therefore skewing the overall distribution towards shorter trips that stay closer to the colony, among some of longer duration contributed by self-feeding trips. The variability produced by the dual foraging strategy is most evident in mean speed, which for both colonies shows a higher spread of values during chick-rearing. Comparisons between the breeding stages here confirm that the restrictions of central place foraging, and the dynamics of a dual foraging strategy, have significant impacts on the variation of foraging trip behaviour between the breeding stages. Future work will be

able to elucidate whether these differences extend to selection of foraging areas, as is implied by the different maximum distances reached between incubation and chick-rearing at both studied colonies. Furthermore, we argue that these results support an explanation of the dual foraging strategy that combines both parent-offspring conflict resolution (in the sense that parents partition their time between self-feeding and chick-provisioning in order to mitigate the toll on parental condition induced by very frequent trips to feed the chick) and a more recently proposed explanation based on resource geometry (Ydenberg and Davies, 2010). Thus, when taking trips to self-feed, as during incubation and the longer chick-rearing trips, birds do not just spend longer times away from the colony but also travel further, covering greater distances in total and greater ranges from the colony, while travelling at lower speeds throughout. Under Ydenberg and Davies' hypothesis, this would result if prey that is preferred for self-feeding is distributed differently and has a different handling time than that preferred for chick-provisioning.

Further variation is observed throughout the breeding season that cannot be explained by the differences in breeding stage requirements alone, as ordinal date explains a significant additional portion of the overall behavioural variance, though with a very small effect, and also interacts with breeding stage. This could be explained by a number of factors, including seasonal variation in resource distributions, but we suggest the tentative patterns shown in Appendix 1C suggest it is at least in part due to changes in behaviour during the breeding stages themselves; hatching may require extra supervision from parents, for instance and thereby different parental coordination patterns, or altered self-feeding requirements, perhaps in females post laying. Further study that could make use of diet and sex data would be crucial to unravel these changes. Nonetheless, breeding stage differences remain the primary explanatory factor in these analyses, confirming the influence of life history factors on space use in this species. Chick mass should be a priority for investigating changes within chick-rearing, and further data collection would be necessary to answer this question. For chick-rearing in particular, as we hypothesise here that foraging behaviours have evolved in response to constraints on provisioning chicks and its conflict with self-feeding, we might expect a change in metrics with chick mass, which may explain the variation with date within each breeding

stage. Future investigations might take this further by measuring chick mass for multiple days before tracker deployment on the parent and using the change in chick mass up to the day before departure as a proxy for chick condition that might plausibly guide parental foraging behaviour. It should also be noted stage and date are partly confounded, having no overlap period; future projects may aim to track birds in this overlap period to truly separate these effects and better understand the influence of life history on foraging behaviour, as independent of potential seasonal effects.

During incubation specifically, we also describe a higher prevalence than expected of unusually short foraging trips, and suggest that behaviour during this period may not be as stereotyped as previously thought, with a substantial distribution of trips carried out in less than 48 hours. The following chapter investigates the extent of individual variation in these metrics, which could partially explain this finding, but the observation that short trips tend to be followed by many other short trips before changeover with the partner highlights the possibility that this is a parental coordination strategy, and has implications for the nature of interactions at the nest, with birds meeting at night without changing over incubation duties more often than previously thought. This is in line with recent field observations that meeting in the nest is not always followed by changeovers, and may relate to the converse findings of (Gillies *et al.*, 2022) that physical reunion in the burrow is not necessary to induce changeover during chick-rearing; the mechanisms underlying parental coordination remain poorly understood. To understand these findings fully, further work making use of nest attendance data is needed, both to investigate whether frequent short trips during incubation do indeed involve more frequent contact between breeding partners without changeovers. Previous work has suggested that it is entrainment of coordination timing during incubation that allows coordinated visits to the nest during chick-rearing (Gillies *et al.*, 2022); in a similar fashion, it is possible that entrainment earlier during the incubation period allows parents to go on longer trips later in the breeding stage, when coordination is established and egg neglect perhaps less likely as a result. Since parental coordination is known to decrease throughout the chick-rearing period (Tyson *et al.*, 2017), this overall suggests it reaches a peak around hatching, which would follow if parents are motivated to avoid neglect in the sensitive brood-guard period following hatching. Alternatively, it could be an attempt to take advantage

of refuge at the colony when local foraging opportunities are abundant. The potential for device impact cannot be ignored, as loggers are known to disrupt natural behaviours (e.g. White et al., 2013; for further discussion see Chapter 1), though previous studies have suggested that this tends in the opposite direction in this species (Gillies *et al.*, 2020).

Across both breeding stages and Skomer, Copeland and Rum, we observed substantial variation in trip metrics, highlighting the vast range this species uses regularly to forage. In particular, we also observed numerous trips over many years visiting the Atlantic via the north of the Irish Sea, as has been observed before in Manx shearwaters (Dean et al., 2012; though excluded from analysis), though its significance has been rarely commented on. Reaching these areas is unlikely by accident given the geography of the Irish Sea as mainly used by birds from these colonies to forage, and the question arises as to how knowledge of the productivity of such distant areas is acquired. That repeated use of such foraging areas represents a strong case for the role of memory in guiding foraging movements in this species is explored further via analysis of individual behavioural variability in Chapter 3.

With uneven sampling across years, we were unable to look in detail at potential interannual variation, and cannot comment on climatic influences, especially considering the lack of a consistent trend across the period as a whole (Appendix 1B) that one might expect if interannual change was a result of a monotonically changing climate. However, many potential yearly influences may be independent (i.e. the strength and direction of any effect may be specific to a given year), and here no trend would be expected (e.g. in the case of weather phenomena changing ephemeral prey distributions); from this dataset the possibility that environmental factors (e.g. from annual climatic variation and its indirect effects on prey distributions) do influence foraging behaviour in this species cannot therefore be ruled out and would merit further investigation, especially in the context of a changing climate to which seabirds are thought to be particularly vulnerable (Grémillet and Boulinier, 2009).

Patterns of variation across colonies observed here generally corroborate the findings of previous work that established colony differences in simple trip characteristics (Dean *et al.*, 2012), while extending these comparisons to an additional two metrics (4, 5) and three more colonies. We found

significant differences between Skomer and Copeland in both breeding stages, with Skomer birds travelling further, covering greater ranges, and over longer periods, than those from Copeland. Duration, total distance and maximum distance were also compared between Skomer and Copeland by (Dean *et al.*, 2012), with similar findings that in general Skomer's trips are longer in duration and total distance covered, and reach greater maximum distances from the colony during incubation. However, that study found no difference in chick-rearing trip durations between the two colonies, while here we find evidence that Skomer trips are significantly longer in duration, as well as total distance, in line with comparisons across both breeding stages for other metrics. While median values are comparable for Skomer between this analysis and that by Dean *et al.*, this expanded dataset suggests Copeland trips are shorter on average than previously observed, and the lack of a consistent trend over years suggests this is a result of greater sampling of the Copeland population rather than a temporal change. Further work will be needed to interrogate the causes underlying this variation, but the patterns shown here would support a role for colony size in determining colony level foraging characteristics (see below).

We also found substantial variation between the colonies in chick-rearing trips, though the details of this varied between the metrics. The low sample size on Skokholm limited the statistical power of comparisons with this colony, and for this discussion will be excluded, though worth noting that the existing sample does fall roughly within the variation of other colonies. In general, Skomer, Copeland Rum showed the highest values for the first four metrics, most of which were outliers compared to the general distributions, and likely represent long-range foraging trips into the Atlantic. Generalisations across specific colony pairings are complicated by contrasting patterns across the metrics, but overall, Skomer and Rum showed the greatest range of values across the metrics of distance and duration compared to other colonies, and Skomer the highest mean values, implying that the area covered by birds foraging from these colonies is the largest. These islands have the largest populations of the colonies studied here (an estimated 350,000 breeding pairs on Skomer and 90,000 on Skokholm:Perrins et al., 2019; 119,000 breeding pairs on Rum: Murray et al., 2003; 3,500 on Lundy: Booker and Price, 2014; and 4,500 on the Copelands, of which perhaps 2000-4000 are on Lighthouse

Island:Newton, Thompson and Mitchell, 2004). That the size of seabird colonies might predict the range required for foraging through depletion of local resources has been suggested under the hypothesis known as Ashmole's halo (Furness and Monaghan, 1987).

Using data from four seabird genera, Gaston, Ydenberg and Smith (2007) found evidence to support resource depletion around large colonies, though suggested this is likely undetectable for small colonies and for highly pelagic species like Procellariforms. Without analysis of prey distributions around the colonies we cannot conclude whether the observed patterns conform to Ashmole's hypothesis, but the clear difference between Skomer and other colonies here (both in chick-rearing and incubation) invites investigation along these lines. Particularly interesting in this regard is the lower average speed across chick-rearing trips from Copeland compared to other colonies, and particularly to the higher values from Skomer and Skokholm. This suggests birds here must work harder to forage for their chicks than those at other colonies, in that more energetic expenditure is required to maintain higher speeds; however, in shear-soaring Procellariform species the relationship between flight speed and energy expenditure is far from a linear, and in the absence of data on the wind fields surrounding these colonies we cannot rule out other influences. However, studying chick growth rates and parental mass change across trips in more detail in future may allow investigation of whether this does constitute different levels of foraging effort, and whether it has an impact on breeding success. Future studies could also focus on collecting GPS data from foraging birds on Skokholm, as despite its low sample size, it is interesting that Skokholm also exhibited high values for average speed; these islands are so close that if there were to be an effect of Ashmole's halo from Skomer it would likely also extend to Skokholm, linking the two colonies as a metapopulation with respect to available foraging resources.

We also found variation in foraging behaviour with age. In particular, older birds appear to spend longer periods of time on foraging trips away from the colony. Comparing this to changes in behaviour over time across the wider dataset suggests this is a result of within-individual behavioural change rather than a change in the composition of the sample. From this latter analysis we also found that individuals generally increased the total distance covered during trips over years. In the absence of a

significant relationship with mean speed or range from the colony, this is interesting; one potential explanation is that older birds spend longer searching within a similar range. Perhaps, with more extensive knowledge of local foraging patches gained through experience, they are more flexibly able to switch between multiple productive foraging sites within a single trip (thereby taking longer and travelling further via higher tortuosity, with reaching further from the colony); perhaps in older pairs, more established shift coordination allows for longer self-feeding trips that do not necessarily need to be further away. Finally, we would caveat that in addition to the smaller sample size for the age analysis, it is also worth noting without further data collection – particularly to collect repeat data from individuals of different ages over comparable timespans – it is also impossible to account for the fact that younger birds, having been around at the colony for less time over the study period, are less likely to have been tracked multiple times by chance. Any behaviours that might normally be unlikely to be observed during tracking, for instance because they are correlated with altered behaviour at the nest that affects capture probability, may therefore be observed in our dataset more frequently in the older cohorts, purely by chance. We may see as outlying behaviour restricted to older individuals; this might equally be what would be expected if senescing individuals showed anomalous behaviours, though we note that, given the highest recorded age for the species was far in excess of the oldest in our sample, this dataset does not offer the potential to truly investigate how senescence might influence foraging behaviours. For this reason we are also unable to investigate foraging behaviour may change at the upper end of the age distribution in line with expectations of terminal investment, as is observed in other seabird species (Catry et al., 2006; Velando, Drummond and Torres, 2006; Froy et al., 2013).

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Chapter 3: Individual foraging site fidelity and its potential causes

Introduction

Observed to date to varying degrees across seabird species, individual foraging site fidelity (IFSF) describes the repeatability of individuals to return to discrete foraging patches over time (see Chapter 1 (*1.5)* for a review of its occurrence across this taxon, and proposed mechanisms). Site fidelity has generally been interpreted as evidence of spatial learning and memory (Irons, 1998; Giuggioli and Bartumeus, 2012; Wakefield *et al.*, 2015; Collet and Weimerskirch, 2020), especially when observed across years. In particular, when defined and quantified in relation to both within-individual consistency and contemporaneous between-individual variability (see *1.4*), site fidelity must represent a decision by an individual to select one out of multiple possible foraging choices that are simultaneously exploited by conspecifics. As such it represents reliance on individual memory, and empirical evidence of IFSF in a particular species or taxon may therefore support the adaptive advantage of memory-based foraging in its ecological context (Stephens and Dunlap, 2008; Dunlap and Stephens, 2012).

Foraging theory and recent work in modelling the behaviour of foraging animals suggests that memory-based search is not always adaptive, as random walks and similar stochastic search processes can be as effective in locating resources (depending on their distribution; Stephens and Dunlap, 2008; Gautestad and Mysterud, 2013), and, in avoiding the costs of information acquisition and retention known to be incurred by memory-based foraging animals (Jaumann, Scudelari and Naug, 2013), may overall be more energy-efficient (Dukas and Real, 1993; Bélisle and Cresswell, 1997; Esposito *et al.*, 2010; Bracis *et al.*, 2015). Despite this, theoretical predictions suggest IFSF will occur when resource distributions are irregularly or sparsely distributed such that past experience is a better guide than random search alone (Benhamou, 1994; Boyer and Walsh, 2010; Merkle, Fortin and Morales, 2014; Bracis *et al.*, 2015), especially in cases where foraging animals face temporal or spatial constraints (such as central place foragers (CPF) or those with bounded home ranges; Börger,

Dalziel and Fryxell, 2008; Merkle, Fortin and Morales, 2014). Theoretical work suggests that differences in access to such information (so-called private information, Stephens and Dunlap, 2008) are alone enough to drive differential space use between individuals in populations of central place foragers (Aarts *et al.*, 2021). Indeed, there is growing evidence of IFSF over multi-year timescales in multiple CPF taxa (see *1.4*), notably seabirds (Votier *et al.*, 2010, 2017; Kotzerka, Hatch and Garthe, 2011; Patrick *et al.*, 2014; Wakefield *et al.*, 2015; Patrick and Weimerskirch, 2017; Sztukowski *et al.*, 2018; Borrmann *et al.*, 2019; Guiry *et al.*, 2022), in addition to mammalian CPFs (in pinnipeds, Baylis *et al.*, 2012; Augé *et al.*, 2014; Oksanen *et al.*, 2015; Knox, Baylis and Arnould, 2018; Foo *et al.*, 2020; Iorio-Merlo *et al.*, 2022; and chiropterans, Rydell, 1989; Kapfer *et al.*, 2008; Rodhouse and Hyde, 2014; Mordue *et al.*, 2019). However, results are far from consistent across species or studies (cf. Bartumeus *et al.*, 2010; Courbin *et al.*, 2018), which in light of the theoretical work discussed above (Bracis *et al.* 2015) suggests that even between closely related species ecological differences might result in different degrees of reliance on memory while foraging.

Pelagic seabird species make good models of the importance of memory in foraging behaviours since they are often long-lived (Schreiber and Burger, 2002), and forage repeatedly from a central place during their breeding seasons, making many trips over frequently very large areas over a relatively short time period (Dean *et al.*, 2012). As their prey are patchily distributed but thought to be generally temporally predictably so (Weimerskirch, 2007), they have the opportunity over their long lifespans to employ spatial memory on foraging trips, perhaps extensively, and have indeed often been studied in light of this. Various procellariforms (e.g. *Thalassarche* spp., Patrick and Weimerskirch, 2017; Bonnet-Lebrun *et al.*, 2018) sphenisciforms (e.g. *Eudyptula minor*, Camprasse *et al.*, 2017; *Pygoscelis adeliae*, Michelot *et al.*, 2021) suliforms (e.g. *Morus spp.*, Grecian *et al.*, 2019; Rodríguez-Malagón *et al.*, 2020), and charadriforms (e.g. *Larus argentatus*, Van Donk *et al.*, 2020; *Rissa tridactyla*, Irons, 1998; Harris, 2020) have been shown to exhibit some degree of IFSF, but to date no estimation has been made of the extent of IFSF during the breeding season in Manx shearwaters (Procellariiformes: Procellariidae: *Puffinus puffinus*). To our knowledge, this has been investigated in only one of their congenerics *sensu stricto*, and that in a behavioural context not relevant for Manx shearwaters, *viz.*

fisheries interactions *(Puffinus mauretanicus*, Bartumeus *et al.*, 2010. Bartumeus and colleagues also found IFSF in *Calonectris borealis*; see Heidrich, Amengual and Wink, 1998; Salvagni and Carlos, 2021 for osteological and mtDNA evidence for grouping *Calonectris* within the paraphyletic *sensu lato Puffinus* clade). This species arguably makes an especially interesting case study given its extremely "slow" life history (Ricklefs and Wikelski, 2002) even among seabird taxa, with individuals not infrequently observed in their late 20s and 30s and some even up to 50 years old (British Trust for Ornithology, 2022), in addition to the availability of age data for certain study populations. Study of individual consistency in over-wintering site use in this species shows some degree of site fidelity over years after migration to the Patagonian Shelf (Kirk, 2016) but beyond anecdotal evidence of consistent behaviour in certain frequently studied individuals, little is known of site fidelity during the breeding season.

As discussed in Chapter 1, patterns of site use represent general foraging strategies, and may be influenced many factors, with consistent variation from a number of sources, as demonstrated in Chapter 2 and elsewhere. That attributable to the individual level represents just one particular instance of individual behavioural variability (IBV), which has attracted interest from those seeking both proximate and ultimate explanations of animal behaviour (see Chapter 1 for discussion), and, in the context of population level variability, those looking to better understand a species' general ecology (Bolnick *et al.*, 2003; Violle *et al.*, 2012). Spatial metrics derived from biotelemetry data can capture the broad characteristics of foraging strategies and provide a straightforward and easily interpretable way to describe variability between individuals (e.g. Weimerskirch *et al.*, 1994; Kirkwood *et al.*, 2006; Kirkwood and Arnould, 2011; Harris *et al.*, 2020) and in wider contexts (Davoren, Montevecchi and Anderson, 2003; Dean *et al.*, 2012; Goyert, 2015; Wakefield *et al.*, 2015). IBV has been conceptualised under many terms and research frameworks (reviewed in Chapter 1, see Ricklefs and Wikelski, 2002; Bolnick *et al.*, 2003; Sih *et al.*, 2004; Réale *et al.*, 2007; Dingemanse *et al.*, 2010; Beekman and Jordan, 2017; Carneiro *et al.*, 2017; Kaiser and Müller, 2021). Of interest here is the sense that relies on there being, simultaneously, persistent between-individual variability and within-individual consistency in the behaviour in question; that is, we are interested in cases

where the behaviour of an individual animal is both different from that of others and similar to itself over repeat measures collected over meaningful timescales (here, over multiple foraging trips both within and between years). How individual animals vary in foraging trip characteristics – the general duration of their trips, how far they travel, the range they cover and their average speed (a proxy for intensity) – gives us an insight into how any differences in space use might relate to general differences between individuals. In particular, we argue that it also allows us to disentangle the influence of cognitive processes on space use from that of other sources of phenotypic variation, as well as environmental effects, and to comment on the likely roles of private vs. public information (Stephens and Dunlap, 2008).

In this chapter, we therefore aim to first quantify the extent individual variability in foraging behaviour as represented by simple trip metrics (distance covered, range, speed and duration of foraging trips, as used in Chapter 2), and then to estimate the degree of individual foraging site fidelity among Manx shearwaters from the Copeland study colony (County Down, Northern Ireland). Together these allow us to test two alternative explanatory hypotheses for observed site fidelity, by investigating its relationship with trip metrics and its maintenance (or lack thereof) between years. The analysis is restricted to Copeland as this provides the most repeat foraging tracks for the greatest number of individuals; as demonstrated in Chapter 2, Copeland birds appear to represent the typical variation between UK colonies in trip characteristics, though this is caveated by the small colony differences, to be discussed below. The following predictions are developed from the discussion in Chapter 1 (*1.5*).

Consistency in site use at the individual level can result from a number of contrasting scenarios, each implying different roles for memory. In seabirds, typically individual site fidelity has been hypothesised to result from resource-tracking strategies, which over large heterogeneous areas may lead to different resource use between individuals (Wakefield *et al.*, 2015; Bonnet-Lebrun, Collet and Phillips, 2021); heritable phenotypic differences, whether morphological or behavioural (i.e. personality/temperament; see Chapter 1 for further discussion) ; or canalisation of behaviour following

an exploratory juvenile period (Guilford *et al.*, 2011; Votier *et al.*, 2017). Under each hypothesis we would expect any observed site fidelity to show different characteristics with respect to the timescale over which it is measured, and variation in trip metrics (those used in Chapter 2, described in terms of individual variability), respectively (as outlined in Chapter 1). These co-variates are therefore used here to interrogate each hypothesis in turn.

Individuals may vary in their use of foraging areas as a result of different experience, whether it affects generalised foraging ability and therefore competition between individuals for resources (Fayet *et al.*, 2015), or through access to memory of profitable foraging locations (Bracis *et al.*, 2015; Aarts *et al.*, 2021; see also exploration-refinement, Guilford *et al.*, 2011; Votier *et al.*, 2017). Equally, physical differences between individuals may affect their competitive ability or commuting costs, such that individuals vary in the areas they were able to access and exploit (Matthiopoulos, 2003), or they may respond to environmental cues differently or in accordance with non-learned behavioural tendencies (Patrick and Weimerskirch, 2014; Harris *et al.*, 2020). Here we use estimates of variability in foraging strategy (i.e. trip metrics) to examine the latter hypotheses; in brief, if variability in site use correlates with consistent differences in trip characteristics like duration and distance covered, for instance, we cannot discount the possibility that individuals had unequal access to different foraging areas based on phenotypic differences (whether morphological or behavioural); highly consistent site use in the absence of consistency in other characteristics would imply a stronger role for memory, given it would indicate no other obvious constraint on movement.

To quantify IBV we therefore use a randomisation approach that integrates both components of IBV, comparing trip metrics directly within and between individuals. If birds segregate their foraging activity based on variation in access to different environments, whether due to competition or energetic constraints, we expect to see some degree of consistent between-individual variation in trip metrics, particularly in those indicating range from the colony. In the case that space use was guided by mainly environmental factors, such as varying climatic conditions or ephemeral prey distributions, we might expect higher IBV within rather than between years, since most within-year comparisons here are

essentially over the course of days or weeks. Finally, if site use is either random with respect to the variables discussed above, or is heavily informed by social (i.e. public, *sensu* Stephens and Dunlap, 2008) information and therefore has little between-individual variability, we expect to find little evidence of IBV with these measures.

Then, to quantify individual foraging site fidelity, we use a method for estimating site use similarity adapted from that used in previous studies of IFSF in seabirds, the randomisation approach to calculating "similarity indices" described by Patrick and Weimerskirch (2017) and Harris *et al.* (2020). This is used to give a measure of both within-individual consistency and between-individual variability in site visitation specifically, both within and between years. Though it has greater spatial sensitivity than other methods such as overlap of utilisation distributions (Wakefield *et al.*, 2015), this approach by contrast does not allow to compare the probabilities of encountering individuals in given areas directly (i.e. it has no explicit temporal dimension). However, given that tracks from different individuals in this sample were recorded over a wide timeframe and in many cases there are few repeats per individual, both of which limit the applicability of a UD approach, we believe here that the similarity index method is the most appropriate.

If shearwaters employ win-stay, lose-shift (WSLS) strategies, tracking and returning to resource patches as long as they remain productive, we expect to see a decay of IFSF over time, with within-individual comparisons becoming less similar over longer time periods ("decay hypothesis"). For this we would also expect higher mean IFSF across the population when measured over shorter timescales; under WSLS alone, we would also expect no relationship between IFSF and individual age. Alternatively, if IFSF is driven by site familiarity (Piper, 2011), we would expect to see maintenance of IFSF over time. Under the structurally similar exploration-refinement hypothesis (Guilford *et al.*, 2011), a model for the ontogeny of individual consistency in which initially explorative younger animals canalise their behaviour as they age, we might expect within-individual similarity to increase with age; Votier *et al.* (2017) for instance argued that this was responsible for the difference in observed IFSF in their study of northern gannets (*Morus bassanus*). Of course, all these factors

are not necessarily mutually exclusive, and a combination of WSLS and site familiarity might produce an intermediate situation, whereby the rate of decay of IFSF over time was predicted by individual age. Results from Chapter 2 tentatively support the idea that Manx shearwaters alter their behaviour at sea as they age, taking characteristically longer trips, in both distance and duration, as they get older. For this Chapter's work, data inclusion criteria meant that too few known-age individuals are available to fully investigate the age hypothesis here; between-year comparisons are instead relied on to investigate multi-year memory. Indeed, the typical span of ages of the known-age sample is likely too narrow to properly investigate the influence of exploratory learning; the findings of Votier *et al.* (2017), that immature gannets show more exploratory foraging behaviour than breeding individuals, would suggest such an effect would be easier to identify in a younger cohort, and this would fit within the general expectations of an exploration-refinement hypothesis (Guilford *et al.*, 2011). Unfortunately, the extended, multi-year migration of juvenile Manx shearwaters makes this period a difficult one to investigate, though perhaps as biologging technology improves this will one day become possible. For similar reasons we were unable to look into senescence effects, as discussed in Chapter 2. Future work that was able to make use of datasets with wider age coverage would be valuable in extending our understanding of these phenomena.

By assuming at least partial temporal stability of foraging sites, tests for IFSF are therefore also an indirect investigation of the nature of this species' favoured prey patches, and would complement investigations of the spatial and temporal heterogeneity of these marine resources using direct environmental observations. Previous studies have tended to find lower spatial fidelity in seabirds during the breeding than non-breeding season, though it is suggested that this might be due at least in part to differing spatial accuracy of the tracking devices used (Phillips *et al.*, 2017). Lower spatial resolution, as is common for longer-lived devices suitable for migration tracking, may lead to over-estimates of site fidelity, for instance. An explicit investigation of breeding-season site fidelity in a taxon for which over-wintering site fidelity has been estimated might therefore be useful in providing an additional datapoint for these comparisons across taxa.

Methods

Data processing and statistical analysis were done in R version 4.3.0 (R Core Team, 2023). Methods are described separately for calculation of trip metric variability (1), which follows those of Chapter 2, and site use (2), given different data filtering requirements. For reference alongside the below descriptions of individual variability, maps of tracks for all individuals for which multiple trips have been recorded can be found in Appendix 2A.

(1) Trip metrics

Data collection, processing and trip selection

GPS data were collected via tagging of chick-rearing parents in July-August, as described in Chapter 2 above, at the Lighthouse Island colony of the Copeland Archipelago in County Down, Northern Ireland (54°42'N, 5°31'W). Data processing, trip identification and trip selection were carried out as described above in Chapter 2. In total, included in this analysis are 39 birds tracked on Copeland between years 2008-2011 and 2013-2022, for a total of 225 foraging trips.

Calculating individual variability – randomised comparisons

The following non-parametric approach was used in preference to other more common methods such as calculating repeatability, which expresses individual differences in trip metrics as the variance across the population attributable to differences between group averages (here, groups of multiple observations from a single individual) as a proportion of that and residual variance (Stoffel, Nakagawa and Schielzeth, 2017). While standardisation across the field is useful for comparing results of different studies where possible, the repeatability method was not used here as individuals are represented unevenly and, given breeding season constraints on movement discussed in Chapter 2, we expect regardless to see significant overlap between them that would make remaining differences difficult to detect. A randomisation method was therefore also constructed to avoid these limitations

and to better make use of the full dataset; however, the structure of the dataset meant it was not possible to account for year variation. Given sample size constraints, only chick-rearing data were included, and the following process applied. The standard deviation (SD) of each metric was calculated for each individual by randomly sampling two trips from that individual's total set, taking the SD, and repeating over 1000 iterations and taking a mean of all re-sampled SDs. This was with the aim of correcting for different sample sizes between individuals. A mean of this value was this taken across all individuals to give the test mean SD. This was then compared to the mean of a randomly generated null distribution of standard deviations, through 1000 draws from the population sample with replacement with the same sampling structure as above, by taking the difference between the null mean SD and test mean SD along with the associated p value, calculated from the test mean's position relative to the null distribution.

(2) Site use

Data selection

All available GPS data from deployments at the Copeland colony (Lighthouse Island, Copeland archipelago, County Down, Northern Ireland, 54°42'N, 5°31'W), from the Oxford Navigation Group's dataset were used in this second analysis, covering the periods 2008-2011 and 2013-2022 and 150 individuals in total. As detailed in the Methods of Chapter 2, for each track the data were first inter/extrapolated to 5 minute intervals to standardise fix interval across the dataset. It is assumed that this will not affect identification of foraging locations, if anything making the process more conservative by artificially straightening trajectories leading to under-identification of the foraging state, but in so doing standardising this across all tracks from different individuals and tracking periods. As in Chapter 2, tracks were split into discrete foraging trips based on contiguous sections > 0.5km away from the colony for 80 or more fixes. However, for this analysis, the inclusion criteria for final trips in a deployment were relaxed: all were included no matter the position of the last fix in the sequence, such that some included trips were technically incomplete and did not include all of the bird's foraging trip before returning to the colony. Since locations visited are here the focus rather than overall metrics, this was not seen to influence the derived dataset, and indeed allowed for a

bigger sample to be included in the analysis (lost portions of the trip are almost always in the portion of returning to the colony, judging by retrieval time and date, though inevitably it is impossible to know if some foraging locations have been missed, and this should be considered a limitation of this analysis). In total this gave 567 discrete foraging trips from 150 individuals. All fixes between 10pm and 4am local time were excluded, leaving only fixes representing a rough approximation of the maximum possible period of daylight and civil twilight at colony latitude throughout the tracking period May-August, which could conceivably be used by these birds to forage as predominantly visual predators.

Finally, data were split by breeding stage (trip filtering left incubation trips between May-June, chick-rearing July-August). Since Chapter 2, alongside previous studies (Dean *et al.*, 2012), shows clear evidence of different behavioural tendencies in incubation and chick-rearing, the following analysis was done separately by breeding stage to examine the effects of potential life history constraints on site use; for the between-year comparisons, however, this was only possible for chick-rearing given a limited sample size in incubation (though SI measures to the individuals for which data were available are presented in the Appendix 2B for reference). However, as the dual foraging strategy of Manx shearwater parents during chick-rearing (Tyson *et al.*, 2017) allows them to undertake, at intervals, longer trips of a comparable length to those in incubation, there is no reason in principle why birds could not visit the same sites in both breeding stages, and so a third application of the method (for between- and within-year comparisons respectively) used the full dataset including both breeding stages together, to investigate overall consistency. This also allowed us to make use of the larger combined dataset.

Identification of foraging locations

Foraging locations were identified by combining the results of two mixture models (MMs) applied to the processed GPS data, using function ‘normalmixEM’ from the R package ‘mixtools’ (Young *et al.*, 2022). Models were applied to each trip’s data, separately for turning angle and speed (both

calculated from the previous fix to the focal fix), each model with two components; posterior probabilities were then used to assign each fix to either of the components of each model and then to a behavioural state given their assigned model components. Birds were assumed to occupy one of three behavioural states: “commuting”, represented by higher speeds and lower turning angles; “foraging”, represented by higher speeds and higher turning angles; or “resting”, by lower speeds and either turning angle component. Trials on a subset of trips showed that this gave consistent state identifications and assigned them at behaviourally plausible positions as expected from general understanding of the colonies’ foraging patterns, and as cross-referenced with previous studies using this methodology (Dean *et al.*, 2012). Though using the wider, multi-colony dataset (as in Chapter 2) to train the model might offer greater confidence, it is known that even small local variation in environmental factors (e.g. wind fields) and can cause the parameter thresholds to vary between colonies and years (Harris *et al.*, 2020); MMs were therefore tested just on the Copeland colony and applied separately to each track.

Once states had been assigned to all fixes across the trip, “foraging locations” were recorded by identifying periods of the trip in which two or more consecutive fixes were assigned to foraging states, and taking the mean latitude and longitude coordinates of each of these identified sequences. Manx shearwaters are often observed resting on the water surface following diving bouts, so this combination of assigned states was applied as a conservative method for capturing the majority of foraging behaviours. For the two methods of assessing similarity in space use as outlined below, trips were included if at least one foraging location had been identified using this process. This left a total of 530 trips across 145 individuals. Figure 1 shows identified foraging locations against interpolated GPS positions for an example trip.

Fig. 1. Foraging locations (in blue) identified using the double mixture model described above, against a trip trajectory (red) for which GPS positions have been interpolated to five-minute intervals, for an example trip from bird ET00957 (chick-rearing, 2019). Copeland is located near the point of the first fix in the centre of the map; the map includes the north-eastern extent of the island of Ireland, the Isle of Man, south-western mainland Scotland and the southern Inner Hebrides.



Similarity indices and comparisons between individuals

Using foraging locations identified per trip per individual as above, similarity indices (SI) were then calculated between pairs of tracks as described in Harris *et al.* (2020), which follows Patrick and Weimerskirch (2017), based on the nearest-neighbour distance method of Freeman *et al.* (2011) and Guilford *et al.* (2011) with alterations as below. Indices were calculated for those individuals represented in at least two different years in the dataset, but birds tracked only in one year were retained in the comparison dataset to represent the full tracking population from each year. For each individual, each site is used in turn as the focal site, and randomly paired with one site used by the same individual on a different foraging trip (within-individual paired site), and the distance between them calculated as the Great Circle distance (using 'distHaversine' function from R package 'geosphere', with default radius). A comparison distribution for this pairing was then constructed by taking a random site used by every other individual (i.e. one per bird) in that year (the comparison year for between-year pairings, and then same year as the focal track for within-year pairings), and calculating the distances between them and the focal site using the same method (between-individual

paired sites). The similarity index for this set of pairings was then the proportion of between-individual sites that were closer to the focal site than the within-individual site, and then converted to its inverse such that values closer to 1 represented high fidelity (within-individual pairings were closer than between-individual pairings) and closer to 0 low fidelity (between-individual pairings were closer than within-individual pairings). This SI method was done as separate analyses for between-year pairings, to investigate longer-term site fidelity, and within-year pairings, to look at short-term fidelity and its change over time. For the latter, we chose each comparison within-individual paired site from a different foraging trip from the same individual in the focal year. Indices were then calculated by repeated sampling of focal sites from each individual via a randomisation method over 1000 iterations, therefore giving 1000 estimates of site fidelity per individual for each analysis. In order to express this as a single estimate per bird, we then modelled similarity index against individual ID in a binomial generalised linear model (GLM) with the time difference between pairings as an additional fixed effect for the between-year comparisons and year as a factor for the within-year comparisons, and extracted the coefficient estimates for each individual ID from the model. These then formed general estimates of SI, or "similarity estimates", across all the individuals' respective trips, and were used to investigate associations with time and trip metrics as below.

To test the decay hypothesis, i.e. whether site fidelity is a result of tracking resource patches and changes over time, we compared SI results for between- and within-year comparisons, expecting higher values for the latter if birds used a WSLS strategy. Finally, we used the re-sampled SD measures of consistency for four trip metrics relating to the length and range of trips, to examine whether site fidelity was associated with consistency in general trip characteristics. We compared the between-year similarity estimate per individual (chick-rearing dataset for which SD estimates available, three outliers removed, n = 36) with its square-root-transformed SD estimate for each duration or distance metric (trip duration, total distance covered, maximum distance from the colony and median distance from the colony) using linear models. Normality of residuals was confirmed using Shapiro-Wilks tests and homoscedascity by visualisation of residuals against fitted values. Higher SD values indicate greater within-individual variability, lower values consistency.

Results

Trip metric variability

Assessing IBV in foraging trip metrics using randomisations to assess individual consistency over years suggested birds showed significantly greater similarity to themselves than to the population average in behaviour over different trips. Results are presented as boxplots to show within-individual variability against the population context in Figure 2.

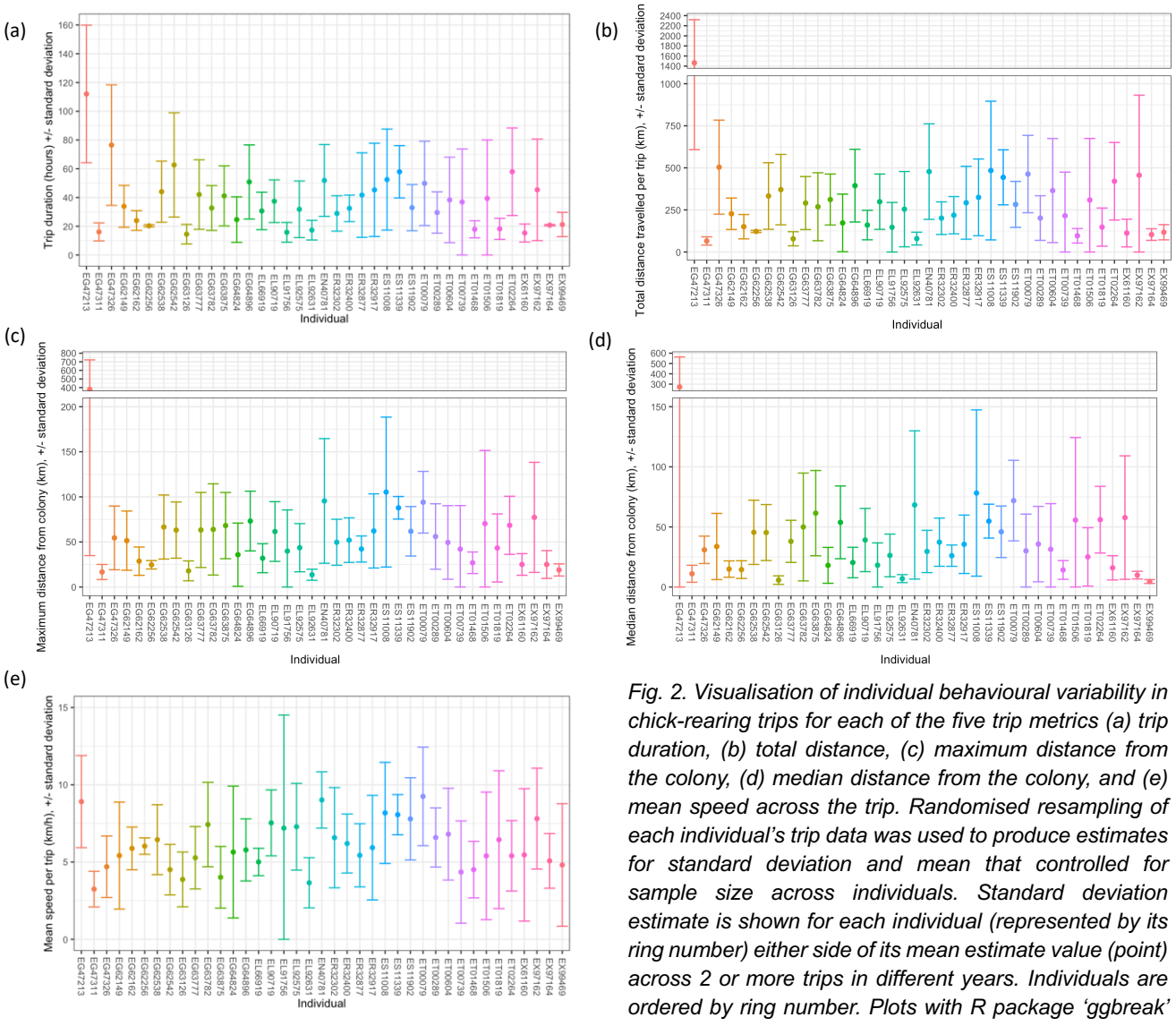


Fig. 2. Visualisation of individual behavioural variability in chick-rearing trips for each of the five trip metrics (a) trip duration, (b) total distance, (c) maximum distance from the colony, (d) median distance from the colony, and (e) mean speed across the trip. Randomised resampling of each individual's trip data was used to produce estimates for standard deviation and mean that controlled for sample size across individuals. Standard deviation estimate is shown for each individual (represented by its ring number) either side of its mean estimate value (point) across 2 or more trips in different years. Individuals are ordered by ring number. Plots with R package 'ggbreak' (Xu et al. *2021)*

For trip duration, within-individual comparisons showed a lower mean standard deviation than that expected by chance (diff = 3.64h, p = 0). Total distance travelled per trip showed the same pattern (diff = 46.5km, p = 0), as did maximum distance from the colony (diff = 6.37km, p = 0) and median distance from the colony (diff = 5.17km, p = 0.001), while for mean speed across the trip differences there was no significant difference (diff = -0.20km/h, p = 1). As this method compares within-individual differences against between-individual differences, this thus represents evidence of significant IBV, with individuals likely on average to take trips more similar to themselves, across time, in terms of their length, range and duration, than to conspecifics at the same colony.

Site fidelity

Measures of IFSF are first presented as similarity indices (SI), for ease of interpretation and for comparison with other studies, by individual for between-year (BY) and within-year (WY) comparisons in plots (a) and (b) of Figure 3 respectively. Overall, similarity indices indicated a high degree of within-individual consistency between and within years; across individuals, they were in the range 0.75-1, higher on average than those reported for similar studies (Patrick and Weimerskirch, 2017; Harris *et al.*, 2020). Overall, those for the combined dataset including both breeding stages were higher than for chick-rearing alone, and BY comparisons (combined, mean = 0.855, range = 0.801-0.976, n = 44; chick-rearing, mean = 0.831, range = 0.775-0.973, n = 40) gave slightly higher SI values than WY comparisons (combined, mean = 0.837, range = 0.784-0.929, n = 106; chick-rearing, mean = 0.813, range = 0.754-0.894, n = 97).

As WY comparisons were in effect comparisons between instances of foraging site use over the timescale of days or weeks, this suggests that observed site fidelity is not a result of tracking ephemeral prey resources as would be predicted if Manx shearwaters followed a WSLS strategy. Likewise, for BY comparisons, GLMs modelling SI by individual and the time difference between comparisons suggested temporal proximity had no effect on the consistency of individuals' site use (combined dataset: estimate = -0.005 per year, p = 0.58; chick-rearing only: estimate = 0.005, p = 0.60). For WY comparisons, year modelled as a categorical variable suggested some inter-annual

variation, though with no obvious trend over years (see Appendix 2C). In light of the similar lack of obvious trend in trip metrics observed in Chapter 2, we interpret this as in part likely the result of different within-individual sample sizes between years, though are unable to untangle this here from potential inter-annual environmental variation. Regardless, in the absence of a temporal effect in BY comparisons, and as year variation explained only a small portion of overall variance in WY comparisons, we did not investigate the source of this variability further.

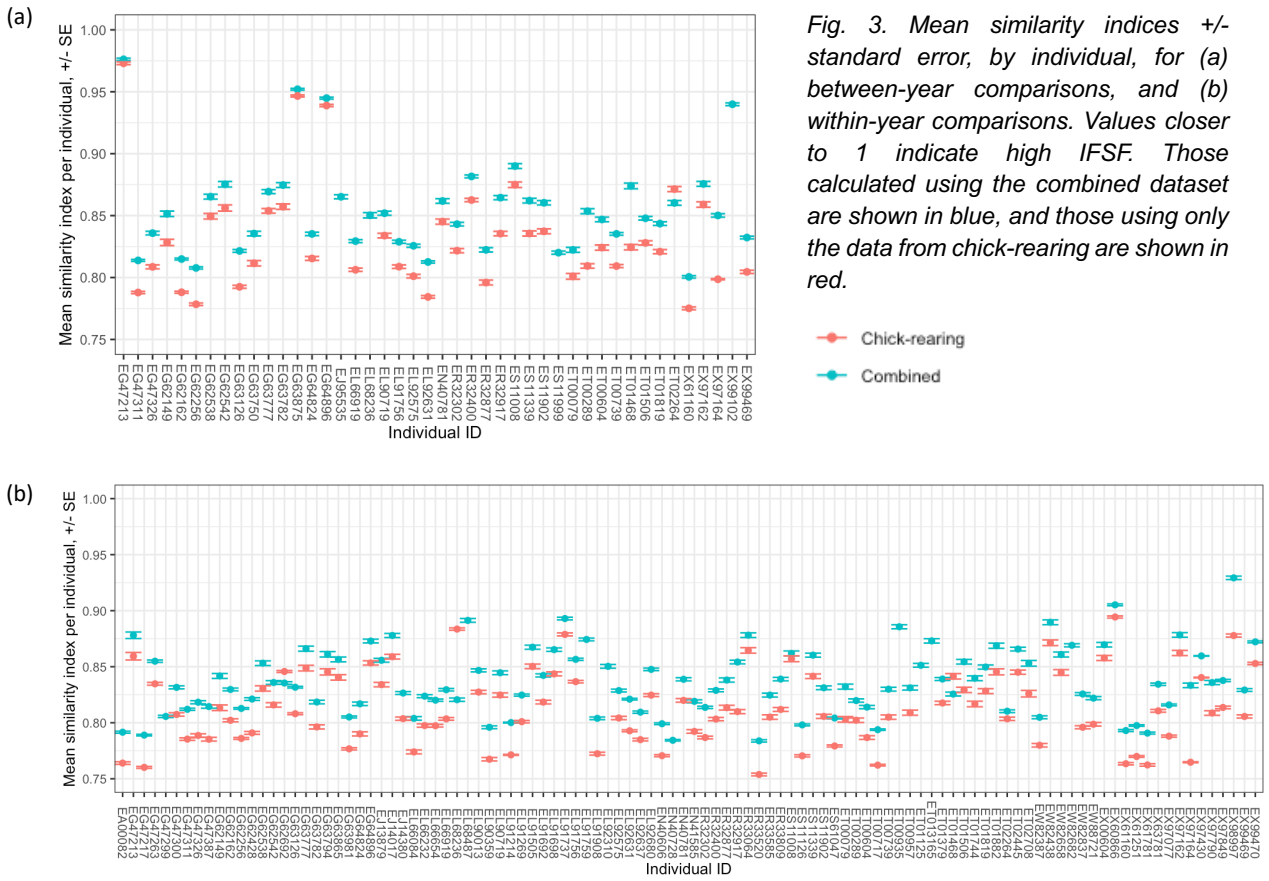


Fig. 3. Mean similarity indices +/- standard error, by individual, for (a) between-year comparisons, and (b) within-year comparisons. Values closer to 1 indicate high IFSF. Those calculated using the combined dataset are shown in blue, and those using only the data from chick-rearing are shown in red.

Finally, comparing variability in trip metrics to estimates of site fidelity, we found significant positive correlations between variability in trip duration ($t = 4.28$, $p = 0.0001$), total distance ($t = 4.80$, $p < 0.0001$), maximum distance ($t = 6.10$, $p < 0.0001$), and median distance ($t = 6.25$, $p < 0.0001$). These results are presented in Figure 4.

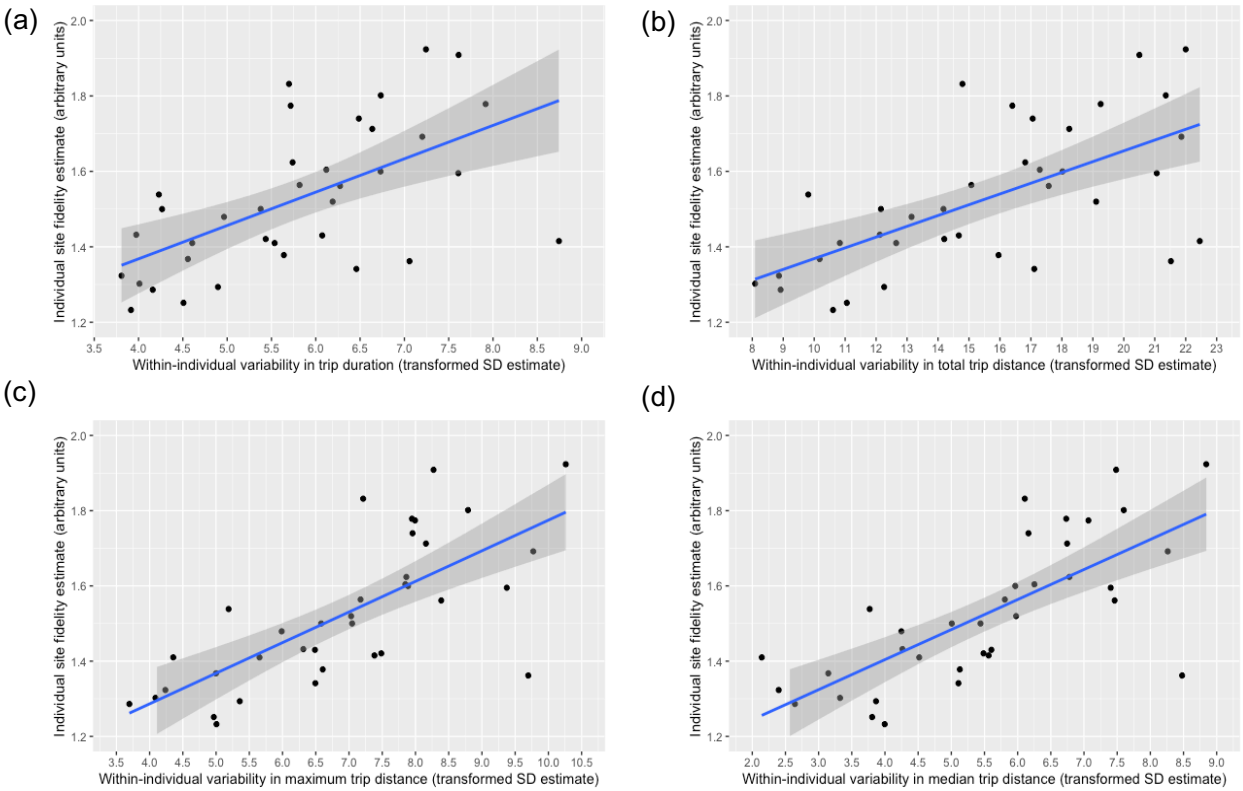


Fig. 4. Within-individual variability in trip metrics, (a) trip duration (hours), (b) total distance covered per trip (km), (c) maximum distance from the colony per trip (km), and (d) median distance from the colony per trip (km), against individual site fidelity estimate (chick-rearing only, n = 36). Variability as the square-root-transformed standard deviation in metrics as standardised to control for variation in sample size between individuals; lower values indicate higher individual consistency. Points are per individual, with smoothed lines to visualise linear model results.

Discussion

Using GPS data recorded from 145 individuals at the Copeland colony between the years 2008-2022, here we have assessed the degree of individual behavioural variability in coarse trip characteristics, and individual foraging site fidelity (IFSF) in Manx shearwaters and assessed the strength of several hypotheses to explain these findings. Describing trip behaviour in five simple trip metrics: trip duration, total distance travelled, maximum distance reached from the colony, median distance from the colony, and mean speed, we found evidence of significant, though modest, between-year individual behavioural variability. Looking at chick-rearing only with a randomisation approach we found that, across all metrics but mean speed, individuals' behaviour on trips was significantly less variable than would be expected by chance (compared to the population average), but the effect sizes were small.

Variability itself varies between individuals, as can be seen in Figure 1, and it is possible that these results are driven by high consistency (low SD estimate) of particular individuals, or potentially a result of unequal sample distribution between individuals, despite controlling for this as far as possible, or interannual variation, which we were unable to account for. Nonetheless, these results suggest that, in this subset, birds vary in their foraging routines to a small extent with respect to space use, concordant either with either memory effects or morphological differences between them. However, given that this analysis covered only chick-rearing, any potential differences in parental roles in dual foraging may be at play here, and without sex data for instance we cannot fully rule out such effects.

Following a method developed for use with seabird behavioural data in previous studies (Wakefield *et al.*, 2015; Patrick and Weimerskirch, 2017; Harris *et al.*, 2020), we then described IFSF separately for chick-rearing and for the combined dataset across both breeding stages for each individual, comparing site use between and within years. Overall, we found high levels of individual foraging site fidelity, both within and between years, indicating that individuals choose to exploit patches in a manner consistently more similar to themselves than might be expected by chance, relative to the general population. That between-year measures were slightly higher on average than within-year measures suggests that this is not simply a case of tracking ephemeral resources, over short timescales, for as long as they remain productive, with no recourse to memory (as would be predicted under a win-stay, lose-shift strategy; Wakefield *et al.*, 2015; Bonnet-Lebrun, Collet and Phillips, 2021). This is also supported by the finding that the time between pairings in the between-year randomisation had no significant effect, refuting the decay hypothesis. Rather, the picture presented by the data is of consistent differences in individual site use over long timescales, and that at the population-level this is found to a roughly consistent level over time. The maintenance of population-level within-year individual site fidelity over time, despite changes within individuals over the same period, is consistent with the interpretation that this is not simply a case of resource tracking, or indeed a dominant role for social influence on site use (Ward and Zahavi, 1973; Weimerskirch et al., 2010; Wakefield et al., 2015; Evans, Votier and Dall, 2016), which would predict lower between-individual variability, at least in the local area. Indeed, in Chapter 2 we saw that individuals from Copeland forage across a large range

(mean maximum distance from the colony per trip over years, incubation = 122km, chick-rearing = 71km), and in the method outlined here individuals were identified as foraging frequently at the distal points on trips; these observations both suggest it is unlikely that social influence plays a significant role in individuals' location of prey resources, given the diminishing probability of encountering conspecifics at greater distances from the colony (and indeed implied in high similarity index values, given the between-individual component). A lack of social information transfer at the colony or away from it, as this suggests, may add further to the debate around the role of information transfer in the emergence and maintenance of coloniality in this taxon (Evans, Votier and Dall, 2016).

Without sufficient age data, we have been unable to demonstrate conclusively how, as a correlate of experience and therefore learning, it may interact with foraging site selection and use. Equally, we cannot comment on any potential change in generalised foraging ability with age, and whether observed site fidelity may result from competition between individuals for access to foraging locations, as found for instance by Fayet *et al.* (2015). However, the finding in Chapter 2 that the duration of foraging trips increases with age, and that duration and total distance travelled per trip both increase over time at the within-individual level (Chapter 2), would suggest this is not the case, as any benefit of competing for resources would presumably be found in the lower costs of exploiting those closer to the colony. Though we found significant IBV in duration- and distance-related trip metrics during chick-rearing, which alone would be compatible with the idea that fidelity was a result of physical differences between individuals, effect size was small, and we argue that other results here make this an unappealing explanation (though, further research using biometrics to examine this effect would be most useful). Firstly, we suggest it is unlikely that physical differences alone could explain such high measures of site fidelity as found here, higher than those reported in similar species (see below). Secondly, we also found that high levels of individual site fidelity (i.e. uniqueness in use of foraging sites) was associated with lower within-individual consistency (higher variability) in trip duration, total distance covered, and the maximum and median distances reached across foraging trips, which suggests that birds using more distinct foraging locations do so by varying their behaviour across trips, rather than being limited in some way to be able to reach only those areas.

Similarly, though site familiarity may contribute to the benefits accrued by individuals in returning to the same places to forage (Piper, 2011) we found no evidence directly to point to its role here, given the lack of an effect of time difference in explaining between-year randomisation comparisons; that is, measures of IFSF between years here showed no significant relationship with the time difference between measurements. Regardless, we argue that such high levels of IFSF strongly imply a role for individual memory in guiding the foraging movements of this species, especially as it is observed over multi-year timescales (with SI values in the range 0.77-0.92 for comparisons 11 years apart, for instance). Previous work has established that individual memory – i.e. private information – is sufficient to drive such space use patterns in central place foragers (Aarts *et al.*, 2021). Without measuring consistency in directionality, that is, the consistency with which individuals orient towards foraging sites from the colony (Davoren, Montevecchi and Anderson, 2003; Pettex *et al.*, 2010; Goyert, 2015), which we were unable to do in this study, we cannot completely disentangle individual memory from inter-individual differences in sensitivity or reactivity to environmental parameters, which has been suggested as a different mechanism underlying behavioural differences between individuals (Patrick *et al.*, 2014). This would see individuals' differential site use as a result of different reaction norms to environmental cues while searching for prey, for instance. If reaction norms are conceptualised as product of learning, this is not incompatible with the interpretation presented here, though would present differently to an effect of purely spatial memory. However, if reaction norms are thought of as innate tendencies, we consider this a highly unlikely explanation, given the sheer degree of between-individual variability in reaction norms that would be needed to produce results as observed here. Such an interpretation is seemingly implied by personality-focussed literature, for instance, personality being normally defined as inter-individual behavioural differences that are consistent over time, negating a role for learning. Nonetheless, estimates of individual consistency in directionality could be assessed in future to disentangle the influence of spatial memory from local cue-based reaction norms; pre-emptive orientation towards the same foraging sites over multi-year timescales (independently of conspecifics) would be unequivocal evidence of memory-guided foraging, and so for a role of private information (Stephens and Dunlap, 2008).

Measures of site fidelity (as similarity indices) were also less variable and generally higher than those found in previous studies using the same method. Here in Manx shearwaters we found a range of 0.75-1, whereas that reported in kittiwakes (*Rissa tridactyla*) by (Harris *et al.*, 2020) found a range of 0.29-0.85 during incubation and 0.33-0.93 during chick-rearing; (Patrick and Weimerskirch, 2017) reported a range of 0.18-0.96 (original measures were reported without inversion, so have been inverted here for easier comparison) in black-browed albatross (*Thalassarche melanophris*). Similarity indices are influenced both by the self-similarity of individuals and the between-individual variability in a given period of measurement. We believe that it is likely a major difference in the latter that explains the differences between these species, that is, that Manx shearwaters likely show more between-individual variation in site use than kittiwakes and that this is to a large part responsible for the higher site fidelity found here. Shearwaters face lower energetic flight costs than kittiwakes thanks to their proficiency at shear-soaring (Kempton *et al.*, 2022) which likely allows individuals to travel across a greater area to forage (compare the median distance from the colony in Manx shearwaters here, 78km in incubation and 47km in chick-rearing, to the 44km reported as the maximum distance from the colony of any recorded foraging black-legged kittiwake, in the study by Ainley *et al.*, 2003). With individuals foraging over a wider area, there is therefore more scope for individuals to forage further away from each other, meaning between-individual variability is higher. Though flight costs in shearwaters and albatross are more comparable, it is notable that the range of SI measures in albatross were much more variable than in either kittiwakes or Manx shearwaters, and that Patrick and Weimerskirch identified a greater level of habitat fidelity than site fidelity. Without a measure of habitat fidelity in the present study it is hard to compare these results conclusively, but it is possible that the smaller variance across individuals' SI measures in Manx shearwaters could be due to a different role of habitat fidelity (a different preference for habitat variables, or less heterogeneity in habitat in the areas Manx shearwaters cover, for instance). Nonetheless, it is notable that the two species with lower flight costs (both soaring procellariforms) both showed higher SI at the top of the reported ranges, which would support the idea that this is at least partially driven by higher between-individual variability in species with greater foraging ranges.

We also see in general higher levels of site fidelity over the combined dataset than in chick-rearing alone, and argue that, as outlined in Chapter 2, this is a result of different patterns of constraint on movement faced by incubating and chick-rearing parents. Though the method used here is sensitive to sample size, that the between-year comparisons had a smaller sample but higher mean SI than within-year comparisons suggests the limit of this effect is reached well before that which would affect this contrast. That individuals are indeed more consistent in site use when considered over all their foraging trips than just within chick-rearing would require that they were each more idiosyncratic during incubation than chick-rearing (keeping more to "their" foraging areas between or within years). Given the lower time constraints encountered by foraging parents during incubation (as trips are for self-feeding and not chick-provisioning, and each parent's stint is longer, see Chapter 2), this is plausible, as each individual would have access to a greater area over which to forage, therefore allowing for greater differences to emerge between individuals. For the longer self-provisioning trips during chick-rearing, these areas would still be accessible, and so consistency would higher when considered the two were considered together. Unfortunately, we are unable to investigate this more thoroughly given the low sample size of incubation trips.

One limitation of the approach taken here is the inability to look in detail at changes in between-year site fidelity in relation to age; with a bigger sample of known-age individuals, we might construct a similar randomisation using only retrospective comparisons, and therefore be able to look at whether site fidelity increased within the same individual over time. However, that the time difference between pairings did not show any effect on site similarity suggests this may not be the case, though, as discussed above, we may expect to find this effect in younger individuals than the generally available datasets pertain to. Future studies that were able to simultaneously track a greater number of individuals for more repeat tracks might be able to make use of a different measure of site occupancy that outlined by Wakefield *et al.* (2015), which describes the extent of overlap between utilisation distributions. This would also allow a population-level measure of overlap between tracks, and has the advantage of accounting for the temporal dimension of site use. They might also then be able to

look to employ auto-correlation correction to look at utilisation distribution overlap, as this is established to give a more reliable estimate of similarity of site occupancy across individuals and different paired comparisons (Winner *et al.*, 2018). In particular, achieving a greater coverage of incubation tracks over multiple years would allow any future analysis of these questions to look in more detail at any potential breeding stage differences in site use, which would also complement the findings presented in Chapter 2 of this thesis and elsewhere (Dean *et al.*, 2012) of substantial differences in trip behaviour between the breeding stages. This may have broader implications if, as speculated above for example, incubation trips were found to show higher between-individual variability in foraging site use, as well as covering a greater area in general. If the population was reliant on a smaller area within which to forage during chick-rearing, this may make it more vulnerable to anthropogenic disturbance in this area, for instance, perhaps leading to implications for future conservation of this species in the Irish Sea (where the majority of chick-rearing trips across all colonies studied here are focussed, see Chapter 2).

Further ecological questions might also be answered by adapting the similarity index (SI) method used here and elsewhere to comparing space use between colonies themselves, by calculating SI values at the colony level. In light of the colony differences in trip characteristics identified in Chapter 2, this might prove a useful tool for interrogating how these relate to site use specifically. In addition, having a measure of consistency in site use at the colony level might shed some light on the causes of colony variation; if, as discussed in Chapter 2, population density plays a role in directing individuals' foraging movements, we might expect to see larger colonies showing lower similarity index values (as individuals must be more dispersed to cover a larger Ashmole's halo), and smaller colonies larger values, especially when comparing colonies whose local commuting range overlapped in theory. Similarly, repeating the method used here (i.e. applying the similarity index calculations to each individual) to other colonies, and then comparing average values between them, might allow us to look into the influence of local geography; where complex local topography restricted the available options for foraging (as, out of the colonies described in Chapter 2, would apply most keenly to Rum) we might therefore expect lower SI values on average, as between-individual differences would be

more constrained. This might also contextualise the range of SI values found here, particularly in light of the interspecific differences outlined above, and confirm how indicative of the general population the Copeland colony may be.

A final consideration should be the reliability of the method used here for locating foraging behaviour itself. Many methodological approaches to identifying search and dive behaviour have been used in similar studies, involving various degrees of complexity and accuracy, and indeed Dean *et al.*'s (2012) study of Manx shearwaters used an alternative (hidden Markov models). Bennison *et al.* (2018), reviewing seven such methods, found varying Type I and II error rates suggesting selection of the best method is highly context dependent. The method used is most closely analogous to what the authors describe as speed-tortuosity thresholds (differing in that our chosen method relied on an unsupervised algorithm approach to identifying thresholds), ranked roughly middling for false positive and negative rates. Future studies into IFSF in Manx shearwaters may profit by testing different behavioural identification methods that might test the robustness of these approaches, especially by ground-truthing them against other biologger data such as that from TDRs, immersion loggers or accelerometers. Bennison and colleagues' study also highlighted that, across models applied to behavioural data from Northern gannets (*Morus bassanus*), search behaviour was frequently identified in the absence of dives, which the authors argue reveals that "significant effort is spent in unsuccessful search behaviour, consistent with low prey encounter rates associated with foraging on spatially and temporally patchy prey resources". In the context of the present study it would be highly interesting to see whether these results replicate for Manx shearwaters; whether the high rates of site fidelity observed here represent fidelity to search sites or to foraging would be important to develop a deeper understanding of the character of IFSF itself.

In conclusion, here we present the first estimates of individual foraging site fidelity in Manx shearwaters, demonstrating a high level of site fidelity at the individual level, and that this is consistent over multi-year timescales. We argue that this is unlikely to be a result of simple resource tracking strategies, social influence, or physical constraints. However, we are unable to comment conclusively

on the influence of age on site fidelity, and therefore the pattern of learning involved, and suggest future work aim to study the phenomenon in young individuals specifically (Votier *et al.*, 2017). However, given the persistence of high between-year IFSF, we conclude that this demonstrates a role for memory-guided foraging in this taxon. This study also provides the first estimate of breeding-season site fidelity in this species. In contrast to previous observations in other seabirds (Phillips *et al.*, 2017), here we have found high levels of individual spatial consistency in the breeding season, and comparable to and on a finer scale than those reported for the over-wintering period in a previous analysis (Kirk, 2016), implying that the trend identified by Phillips and colleagues is not universal and indeed may not be a result of different levels of spatial resolution, as first suggested.

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Chapter 4: Conclusions

Foraging behaviour is often a focal point of study in behavioural ecology, with relevance to all aspects of life history, and with the development of lighter, cheaper and higher-resolution biotelemetry technology can be increasingly studied in previously obscure environments and taxa. Foraging and space use are intimately related aspects of animal behaviour, and while the latter can be investigated directly through tracking approaches, it can also act as a proxy for studying foraging itself. In this thesis, global positioning system (GPS) data are used to examine foraging behaviour and space use of free-ranging Manx shearwaters (*Puffinus puffinus*) at five colonies around the UK studied by the Oxford Navigation Group since 2004. Manx shearwaters are medium-sized, long-lived pelagic Procellariiform seabirds breeding across the North Atlantic and predominantly in the British Isles (Brooke, 1990). Raising a maximum of one chick per year, parents at the UK colonies studied here forage across the Irish Sea and north-eastern Atlantic, taking alternating foraging trips during incubation and adopting a dual foraging strategy during chick-rearing (Shoji *et al.*, 2015; Tyson *et al.*, 2017; Gillies *et al.*, 2022). Here we aimed to add to the findings of a previous study in this species (Dean *et al.*, 2012), which examined colony and breeding stage differences in foraging behaviour in this species, using an expanded dataset; and to extend this to look at other sources of variation in behaviour at one colony in particular—that resulting from individual differences and effects of age.

Individual differences in behaviour have been characterised under a variety of frameworks, reviewed in Chapter 1. Consistent differences in individuals' behaviour across time and space have been studied under the framework of animal "personality" or "temperament" (e.g. Réale et al., 2007), and the related concept of behavioural syndromes, which describes correlated suites of behavioural tendencies along different axes (Sih *et al.*, 2004). When applied as more than a descriptive (or philosophical, see Kaiser and Müller, 2021) framework animal personality research has come under increasing criticism (Beekman and Jordan, 2017), though the behavioural assays often used by personality researchers still find value in related research paradigms like that proposed by Ricklefs and Wikelski (2002), which look for a mechanistic link between consistent behavioural differences

and physiological or endocrinal mechanisms that might support an adaptive explanation for how they evolve and persist. Previous studies in Procellariiform seabirds show that in some cases consistent behavioural tendencies at the nest, identified for instance through novel object assays (and commonly conceptualised as lying along a “bold-shy” continuum), are correlated with at-sea behaviour (Patrick and Weimerskirch, 2014; Patrick, Pinaud and Weimerskirch, 2017; Harris *et al.*, 2020), suggesting the possibility of selection favouring contrasting life history strategies within one population (potential mechanisms are discussed in Chapter 1). In preparation for this thesis personality assays were developed for Manx shearwaters and tested in a pilot study, with the aim of measuring behavioural correlates of at-sea variability in behaviour (such as boldness, see Harris *et al.* 2020) in order to link any observed between-individual variation to broader behavioural tendencies, in line with the literature on behavioural syndromes, or the so-called physiology/life history nexus (Ricklefs and Wikelski, 2002; Sih *et al.*, 2004, 2012). However, this species proved particularly difficult to assay, being fossorial and nocturnal, and we were unable to develop a reliable method to use in this way. Here we have therefore presented an investigation of behavioural variability in Manx shearwaters with regard to a different aspect of individual variability – individual foraging site fidelity (IFSF) – for which there is a rich theoretical and empirical literature focussing primarily on central place foragers (CPF; reviewed in Chapter 1).

Alongside the various approaches to describing animals’ foraging movements, whether informed by optimal foraging theory (Stephens and Krebs, 1986; Mitchell and Powell, 2004) or more statistical predictions (Gautestad and Mysterud, 2013), the widespread occurrence of IFSF (Votier *et al.*, 2010, 2017; Kotzerka, Hatch and Garthe, 2011; Patrick *et al.*, 2014; Wakefield *et al.*, 2015; Sztukowski *et al.*, 2018; Borrmann *et al.*, 2019; Guiry *et al.*, 2022) points to an important role for cognitive processes like learning and memory in guiding foraging movements. Coupled with ecological, geographical and physiological constraints, memory-guided foraging may lead individual animals to tend towards different foraging patterns, a deeper understanding of which is important not only as a scientific endeavour but also in informing their conservation. In this work we therefore sought to establish to what degree Manx shearwaters show individual variation in behaviour—defined as a combination of

within-individual consistency and between-individual variability—in terms of simple trip metrics derived from biotelemetry data, and in foraging site use; to compare this against results from similar taxa; to examine potential correlates, such as individual age; and to place this variation within the overall context of behavioural variability in this species, that resulting mainly from life history constraints during the breeding season.

Firstly, consistent with previous studies (Dean *et al.*, 2012), we found significant variation in foraging trip behaviour between the main breeding stages, incubation and chick-rearing (see Chapter 2). Using five metrics (total trip duration, total distance covered, maximum distance reached from the colony, median distance reached, and mean speed across the trip) we found that birds take longer trips, in terms of temporal duration and distance covered, during incubation than chick-rearing, and that incubation trips are more variable in general. Birds also reach further distances from the colony on average during incubation, though sustain higher speeds during chick-rearing trips. However, we also identified a higher frequency of short trips during incubation than had previously been described in this species, which is supported by recent field observations, and may represent a different foraging strategy, and pair coordination mechanism, than previously thought (Gillies *et al.*, 2022). There were also significant differences between the colonies, though effect size was generally small, and comparisons beyond Skomer and Copeland are limited by the varying sample size on the other colonies (Rum, Lundy and Skokholm). Skomer birds, however, travel significantly further on trips than birds from Copeland, spending longer, covering greater distances and reaching further from their home colony.

We argue that breeding stage differences are consistent with expectations from the species' life history, being likely a result of the differing temporal constraints on CPF parents during self- and offspring-provisioning, despite Manx shearwaters' dual foraging strategy during chick-rearing; more frequent, shorter trips during chick-rearing contribute to the lower distances covered and higher mean speed during this breeding stage. We also suggest that this is likely not just a consequence of resolving parent-offspring conflict over parental condition, but also an inevitable emergence from prey

distributions that differ in preferability for chicks and adults (Ydenberg and Davies, 2010). Without environmental or diet data, reasons for colony differences remain speculative, but we suggest two likely influences. Individuals from larger colonies (i.e. Skomer and Rum) tend to cover the greatest distances, perhaps as a result of competitive exclusion from the areas closer to the colony by conspecifics (Furness and Monaghan, 1987; Gaston, Ydenberg and Smith, 2007); and those from colonies closer to known tidal mixing zones (primarily Copeland) are perhaps able to travel less far to exploit prey. However, future studies with a greater coverage of all colonies might repeat this analysis to see whether the patterns observed here are robust to sample size; a main caveat to the present study would be that without an *a priori* expectation for the degree of between-individual variability in foraging behaviour in a given population, it is difficult to establish how much coverage of the population is necessary to truly characterise each. Given that this species has an extraordinarily large area within commutable distance, with birds observed travelling hundreds of kilometres out into the Atlantic not infrequently, the scope for individuals to target different areas is vast.

How they might do this was the subject of the rest of the chapter, and, further, of Chapter 3. We first examined how trip metrics change with age, or, for those individuals for which exact age data was not available, how individuals altered over time. We found trip duration increased significantly with age, and that duration and total distance also showed significant positive within-individual change over time, though no effect in the other metrics. Birds therefore appear to spend longer away from the colony, occupying areas on average further away, as they age. In Chapter 3, we then first used the same metrics to describe the extent of IBV in this population, and described how using a randomisation approach to assess individual-level consistency in trip metrics found modest evidence of between-individual variability trip characteristics within or between years (significant consistency, but with a very small effect size), though individuals appear to themselves vary in how consistent they are, at least as observed in this sample. We recommend future work might make use of a more "intensive" dataset that was able to follow the foraging behaviour of a smaller subset of individuals over more repeats (Bonnet-Lebrun *et al.*, 2018) to further investigate the variability described here. The inability to look at the relationship between sex and foraging behaviour is also a substantial

limitation. Foraging behaviour in post-laying females is likely to differ from males given different nutritional requirements, and though little is known of sexual variation in prey choice in this species, females have been observed to visit different areas from males during the pre-laying exodus period (Dean, 2012), presumably for this reason. They are also known to differ from males in rates of chick-provisioning (Hamer *et al.*, 2006), which, in light of the fact that chick condition has been linked to space use and foraging strategy in this species (Wischnewski *et al.*, 2019), highlights the possibility of sexual differences in foraging behaviour and site use. Inclusion of sex data in any future analysis should therefore be a priority, especially in any attempt to reproduce the age effects observed here, as we equally have little understanding of sexual differences in longevity that might bias the older sample one way or the other.

Establishing the extent of IBV in foraging behaviour using coarse trip metrics, we were then able to use these findings to inform our analysis of the degree of IFSF in Manx shearwaters, giving the first estimate of breeding-season site fidelity in this species. Building on the work of Wakefield et al. (2015) and others, we then tested various hypotheses as to how and why IFSF might be maintained. We predicted that if exploration in the early breeding years was important for individuals to learn the locations of productive foraging areas, we would see an increase in site fidelity over time. Alternatively, if individuals are just tracking resource patches that change over time, we might see a decay in site fidelity with increasing time between measurements (i.e., that site fidelity depended on the temporal scale at which it was examined; “decay hypothesis”). Given only few individuals in this dataset were tracked over multiple successive trips within the same year, we were unable to look into very fine timescales (days or weeks) directly but were able to compare the levels of IFSF within and between years as a broader approximation. As foraging trips recorded during a single breeding stage for the same bird would come from a single logger deployment (and were therefore in quick succession), within-year IFSF estimates were regardless an approximation of IFSF at roughly this timescale, and comparing them to between-year estimates allowed us to test the decay hypothesis. We found evidence of very high IFSF, as measured by the similarity index method developed by Patrick and Weimerskirch (2017) and Harris *et al.* (2020), and that estimates were in fact slightly lower

for within-year than between-year comparisons, suggesting IFSF is not the result of birds tracking ephemeral prey patches and moving on when they become unproductive ("win-stay, lose-shift", WSLS), but are learnt and re-visited over much longer timescales. We conclude that these results suggest a role for spatial memory, and are in addition unlikely to be a result of social influence in prey location, or of individuals' suffering different physical constraints in accessing parts of the available foraging range, as more site faithful birds were in fact less consistent in their trip metrics across trips.

We therefore conclude that, as predicted from observations of individual birds' GPS tracks, Manx shearwaters exhibit high individual foraging site fidelity, which cannot be explained by the location of resources alone, and is likely a product both of the extensive opportunity for learning in such a long-lived species, and the vast area over which this population forages. The latter probably explains high between-individual variability in this species, predicted by their low flight costs and therefore large commutable distances, something also supported by comparisons with the other species studied using this method (see Chapter 3). Future studies should aim for higher coverage of known-age individuals, ideally tracked with high resolution GPS loggers for multiple foraging trips per year and especially during the incubation period where ethically permissible, to further investigate this phenomenon, especially with respect to age effects. In light of the fact that the viability of animal populations with extreme "slow" life histories, like Manx shearwaters, is highly dependent on adult survival and subadult recruitment (Becker and Bradley, 2007), the finding that individuals exploit highly variable foraging locations may certainly raise conservation implications (Bolnick *et al.*, 2003; Brooker *et al.*, 2016).

Indeed, previous reviews suggest this order's life history characteristics makes them particularly vulnerable to environmental change (Rodríguez *et al.*, 2019). Species with high longevity in particular, where individuals may have learnt to repeatedly exploit a restricted set of the total available foraging area, may be more dependent on the continued availability of these larger areas, particularly during the breeding season. Different age classes might, for example, suffer different probabilities of mortality though bycatch or other anthropogenic hazards like offshore wind farms (Votier *et al.*, 2010, 2017),

particularly those that emerge rapidly in these animals' familiar areas, leaving little opportunity for learning in response. As discussed in Chapter 3, an extension of the similarity index method to compare site use across colonies would be valuable in interrogating various ecological and environmental hypotheses. One application of this with relevance to conservation could be to analyse differences in colony site use across the Manx shearwaters' latitudinal range. In light of climate projections suggesting increasing surface temperatures across the UK region in the coming decades, especially in the summer months (Lowe *et al.*, 2018), we may have reason to suspect that colonies that more consistently used more northerly regions to forage may suffer less disturbance from a changing climate, given that the analyses presented here suggests that individuals are consistent over long periods in the areas they choose to exploit, and may therefore not adapt quickly. Indeed, a recent review of multiple projections suggests that the Irish Sea region may warm faster than the Outer Shelf (encompassing the area of the NE Atlantic accessible to Manx shearwaters from the UK colonies studied here), which again would suggest that more northerly colonies with easier access to this region may be less affected (Tinker *et al.*, 2020). While here this may apply to Copeland and Rum, there are numerous small Manx shearwater colonies across the Hebrides for which this may also apply (Newton, Thompson and Mitchell, 2004). As little work has currently looked into the effect of climate on this species, an approach that used the site similarity index method to examine differences along the species' latitudinal gradient would enable us to better understand the species' future vulnerabilities, and inform conservation efforts accordingly.

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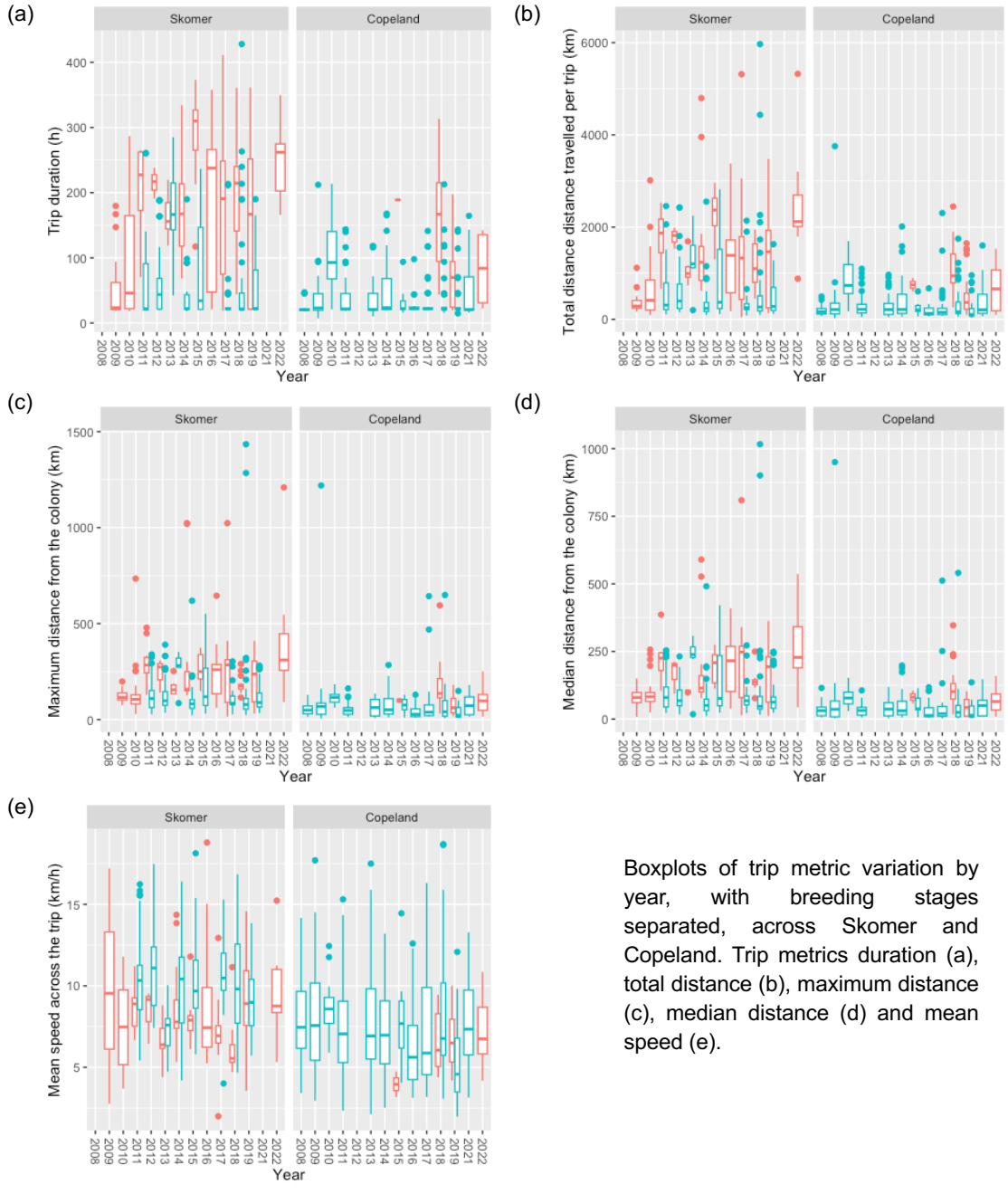
Finally, thanks to little Scotty, whose remarkable adventures out into the Atlantic drew my attention to the scope of individual variation in shearwaters in the first place.

Appendix 1

A - Breakdown of included trips by colony, breeding stage and year

			Year												
Colony	Breeding stage	No.	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2021	2022
Skomer	Incubation	trips	0	22	26	10	3	6	13	9	17	12	20	23	0	11
		individuals	0	9	15	10	3	6	13	9	11	11	17	14	0	11
	Chick-rearing	trips	0	0	0	45	53	7	41	36	0	29	43	39	0	0
		individuals	0	0	0	18	18	6	11	17	0	17	19	16	0	0
Copeland	Incubation	trips	0	0	0	0	0	0	0	2	0	0	17	21	0	6
		individuals	0	0	0	0	0	0	0	2	0	0	14	13	0	5
	Chick-rearing	trips	16	55	27	60	0	41	54	7	22	42	38	46	17	0
		individuals	6	20	20	22	0	11	19	2	20	21	21	21	8	0
Rum	Chick-rearing	trips	0	0	18	93	0	0	0	0	0	0	0	0	0	0
		individuals	0	0	8	14	0	0	0	0	0	0	0	0	0	0
Skokholm	Chick-rearing	trips	0	0	0	0	0	0	0	0	14	0	0	0	0	0
		individuals	0	0	0	0	0	0	0	0	10	0	0	0	0	0
Lundy	Chick-rearing	trips	0	16	25	27	14	0	0	0	0	0	0	0	0	0
		individuals	0	10	11	14	8	0	0	0	0	0	0	0	0	0

B – Representation of trip metric variation by year



Boxplots of trip metric variation by year, with breeding stages separated, across Skomer and Copeland. Trip metrics duration (a), total distance (b), maximum distance (c), median distance (d) and mean speed (e).

C – Breeding stage and ordinal date

AIC model comparisons suggested the full parameter models, for all trip metrics for Skomer,

including an interaction term between ordinal date and breeding stage, gave the best fit (86-100% of cumulative model weight across all metrics). Model results are reported briefly for reference in (i-v) below and variation is presented graphically for each breeding stage beneath.

(i) Trip duration: significant effect of ordinal date ($t = 8.84$, $p < 0.0001$), but very small effect (estimate = 0.001); interaction with breeding stage ($t = 11.4$, $p < 0.0001$) investigated by plotting data, see below. Confounding of two variables, small effect size and interaction, as well as observation that significant variance still attributable to breeding stage (estimate = 0.32, $t = 10.5$, $p < 0.0001$), suggest life history effects play dominant role. Changes within breeding stages are explored further for trip duration in main text.

(ii) Total distance: ordinal date had a significant effect ($t = 12.3$, $p < 0.0001$), but very small effect (estimate < 0.001); interaction with breeding stage ($t = 22.3$, $p < 0.0001$) visualised by plotting data (below). Again significant variance still attributable to breeding stage (estimate = 0.16, $t = 21.0$, $p < 0.0001$).

(iii) Maximum distance: significant effect of date ($t = 20.9$, $p < 0.0001$), and interaction ($t = 23.6$, $p < 0.0001$), but breeding stage still explains a significant proportion of variance with biggest effect size (estimate = 0.29, $t = 24.6$, $p < 0.0001$).

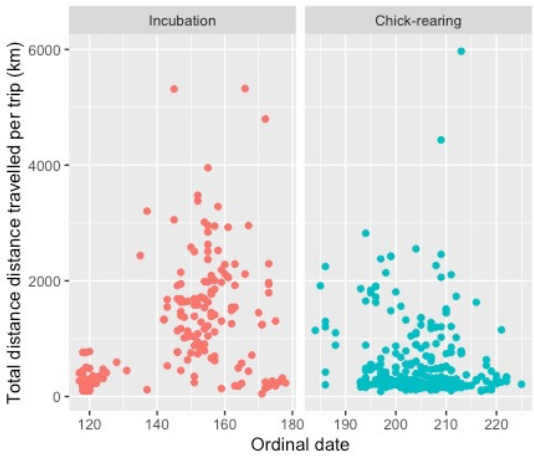
(iv) Median distance: significant effect of date ($t = 18.7$, $p < 0.0001$), and interaction ($t = 21.1$, $p < 0.0001$), but breeding stage still explains a significant proportion of variance with biggest effect size (estimate = 0.37, $t = 22.3$, $p < 0.0001$).

(v) Mean speed: significant effect of date ($t = 2.70$, $p = 0.007$), and interaction ($t = 4.06$, $p < 0.0001$), but breeding stage still explains a significant proportion of variance with biggest effect size (estimate = 0.084, $t = 4.84$, $p < 0.0001$).

(a)


Incubation
Chick-rearing
Trip duration (h)
0
100
200
300
400
120
140
160
180
190
200
210
220
Ordinal date

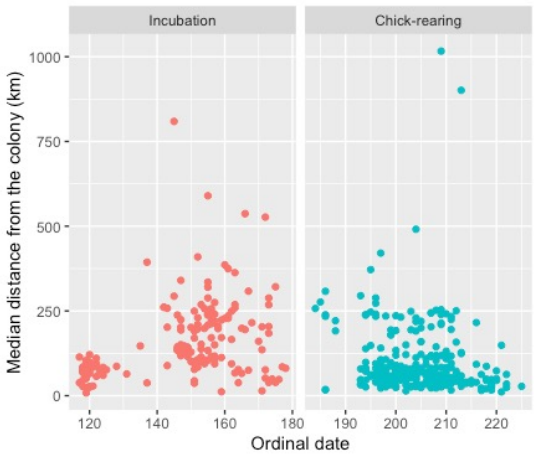
(b)


Incubation
Chick-rearing
Total distance distance travelled per trip (km)
0
2000
4000
6000
120
140
160
180
190
200
210
220
Ordinal date

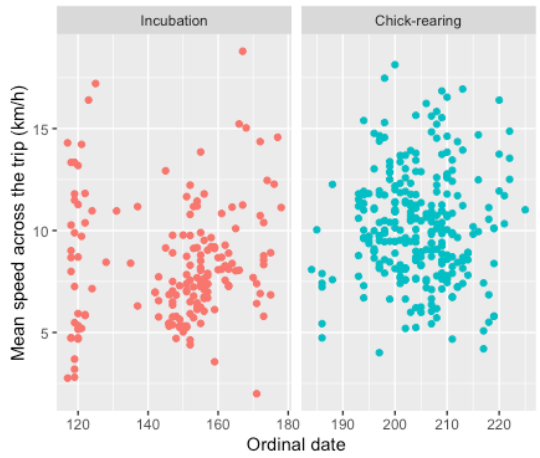
(c)


Incubation
Chick-rearing
Maximum distance from the colony (km)
0
500
1000
1500
120
140
160
180
190
200
210
220
Ordinal date

(d)


Incubation
Chick-rearing
Median distance from the colony (km)
0
250
500
750
1000
120
140
160
180
190
200
210
220
Ordinal date

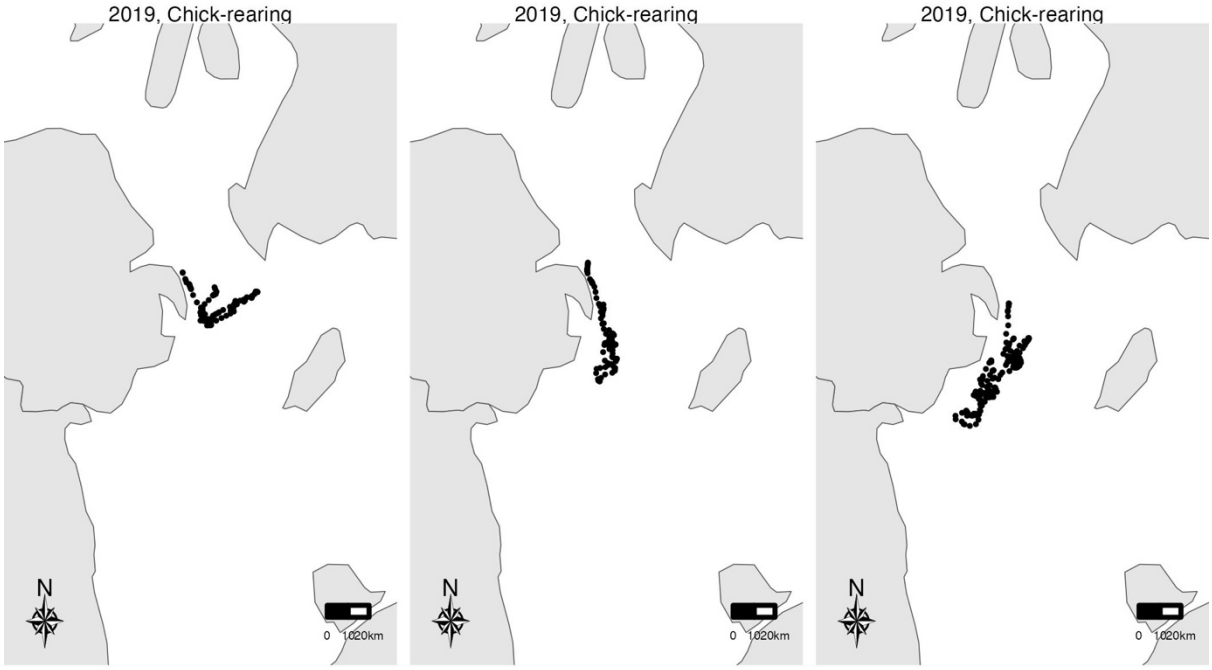
(e)


Incubation
Chick-rearing
Mean speed across the trip (km/h)
5
10
15
120
140
160
180
190
200
210
220
Ordinal date

Appendix 2

A – Trip maps for repeat-tracked individuals

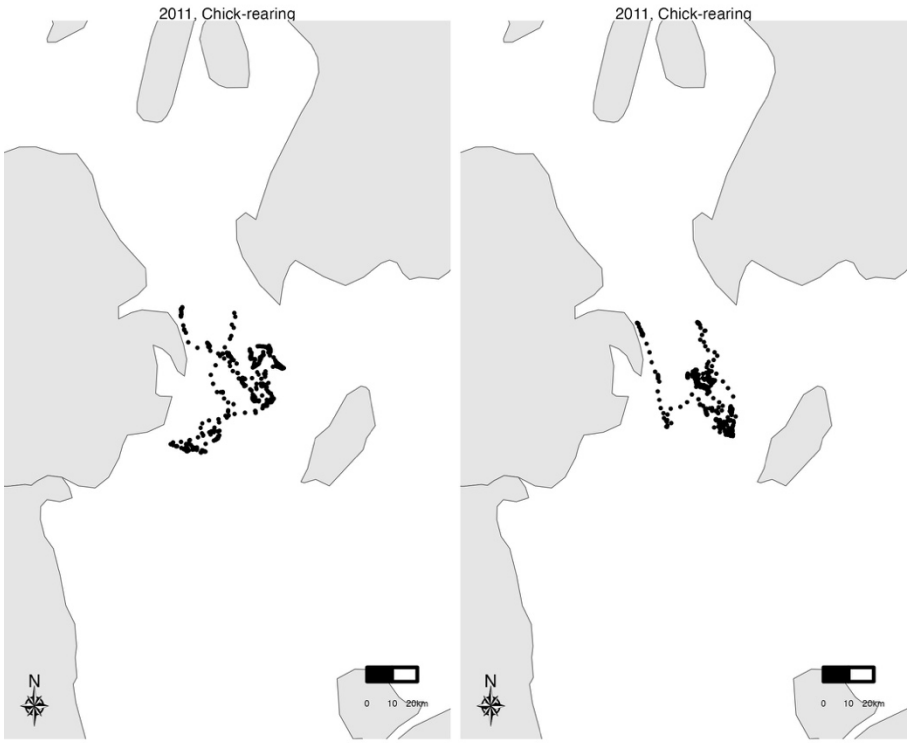
EA00082



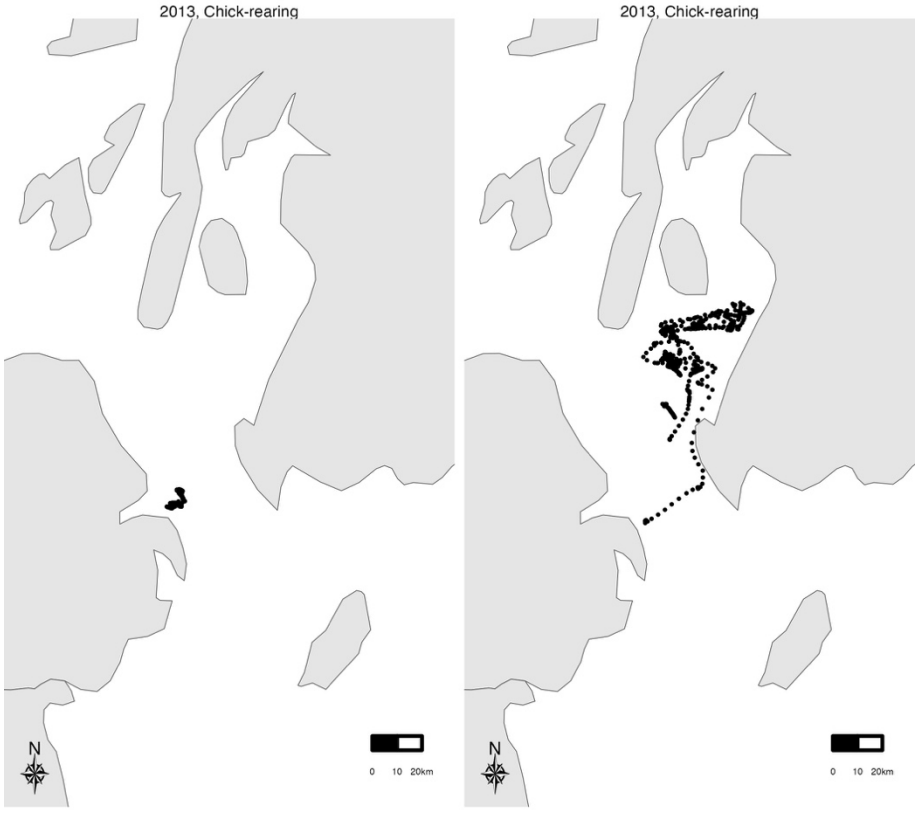
EG47213



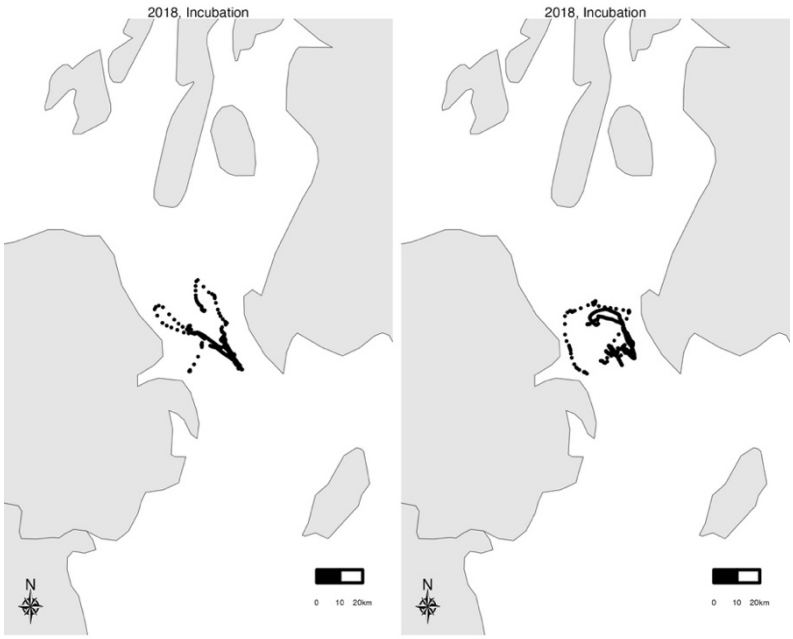
EG47217



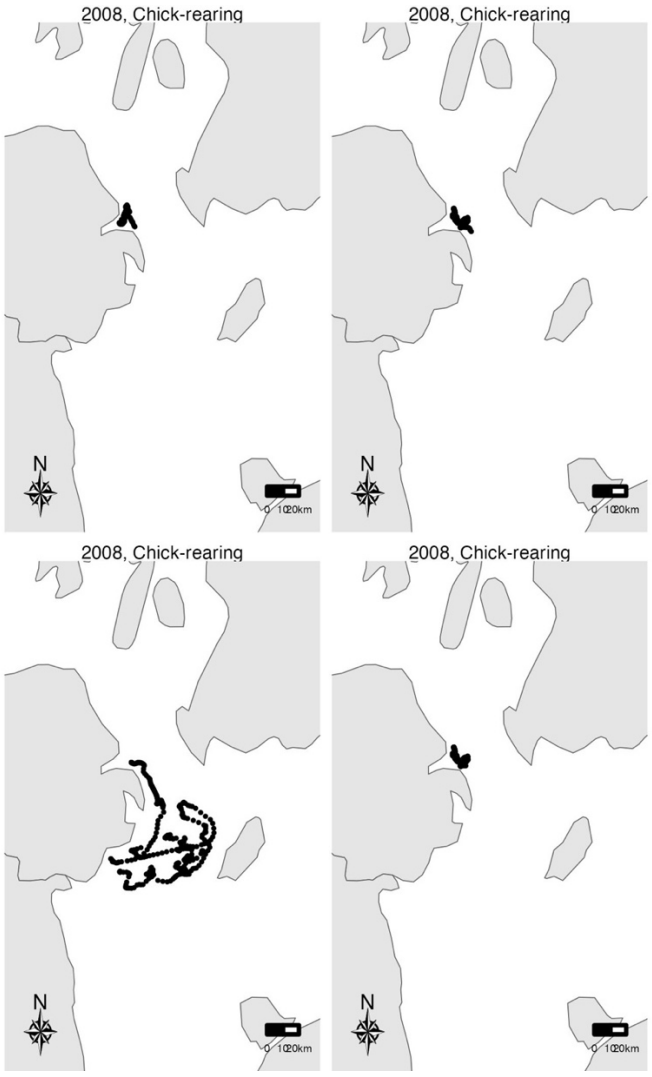
EG47263



EG47299



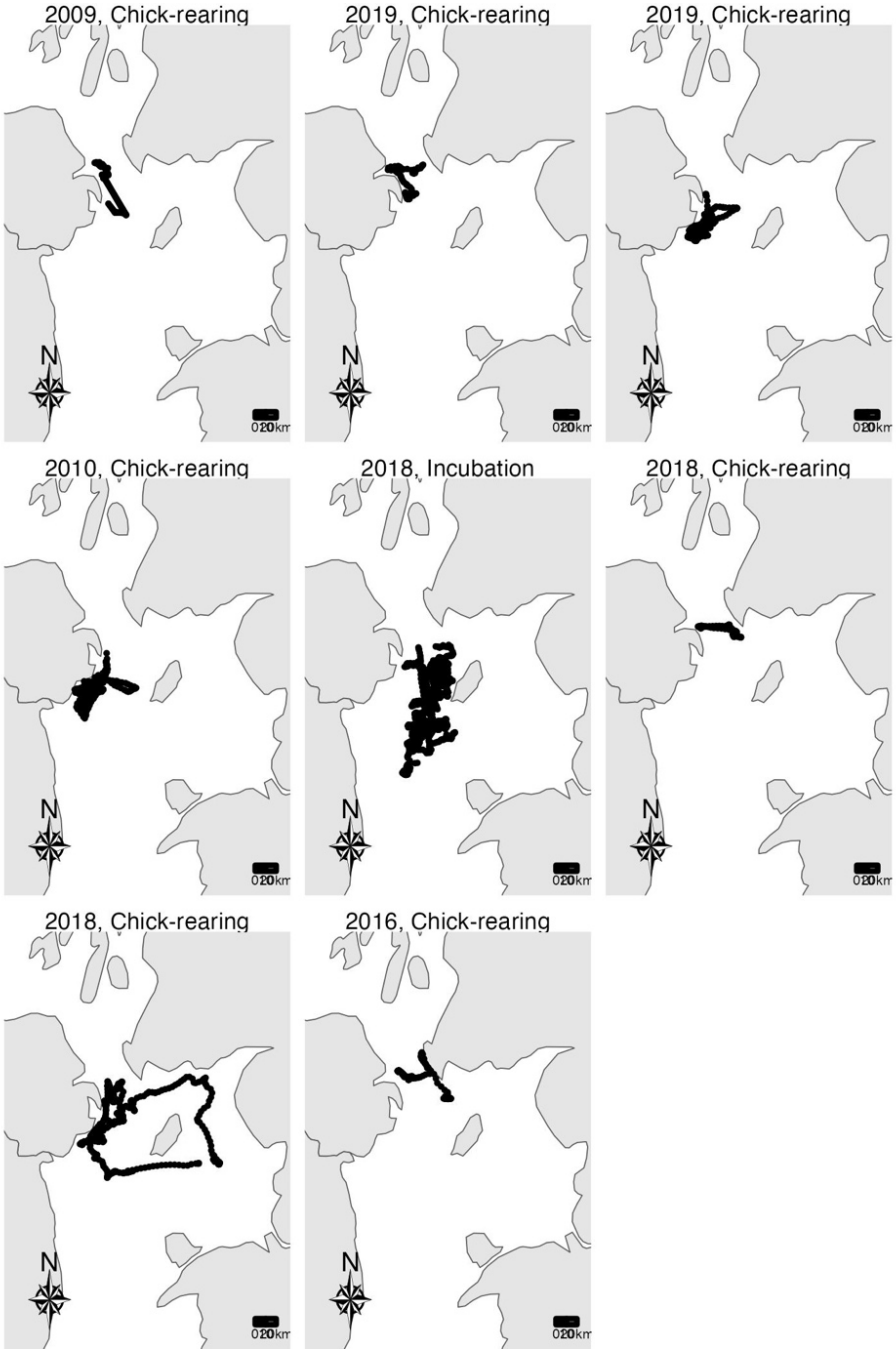
EG47300



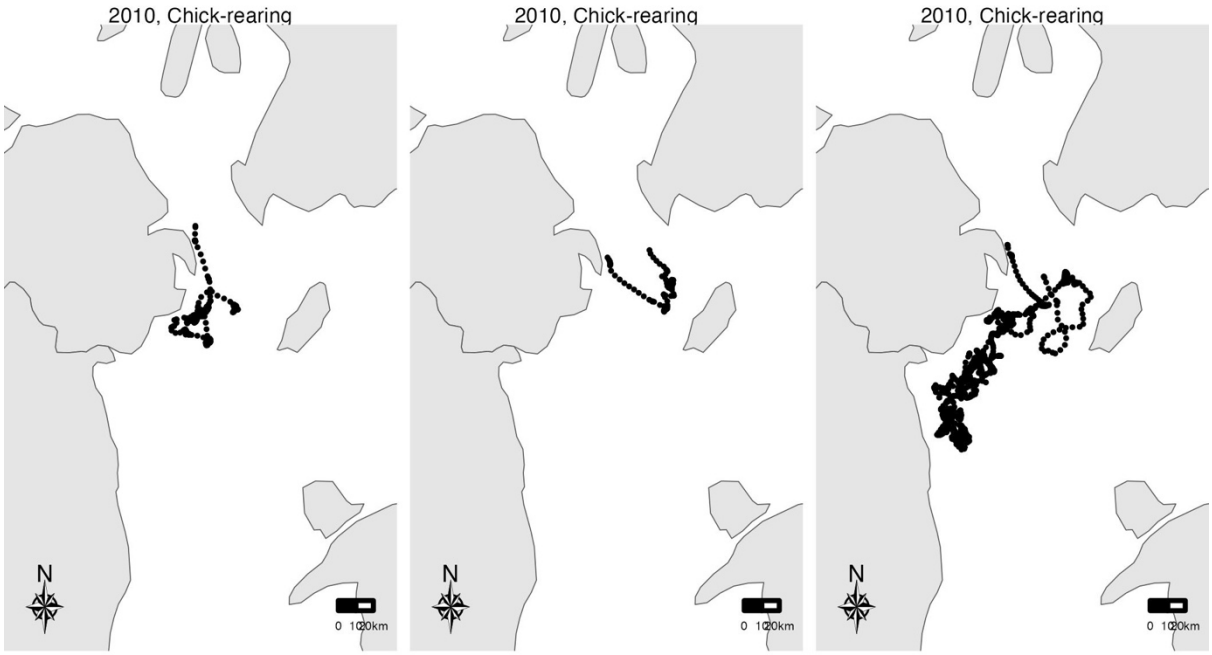
EG47311


2016, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
N
0 1020km

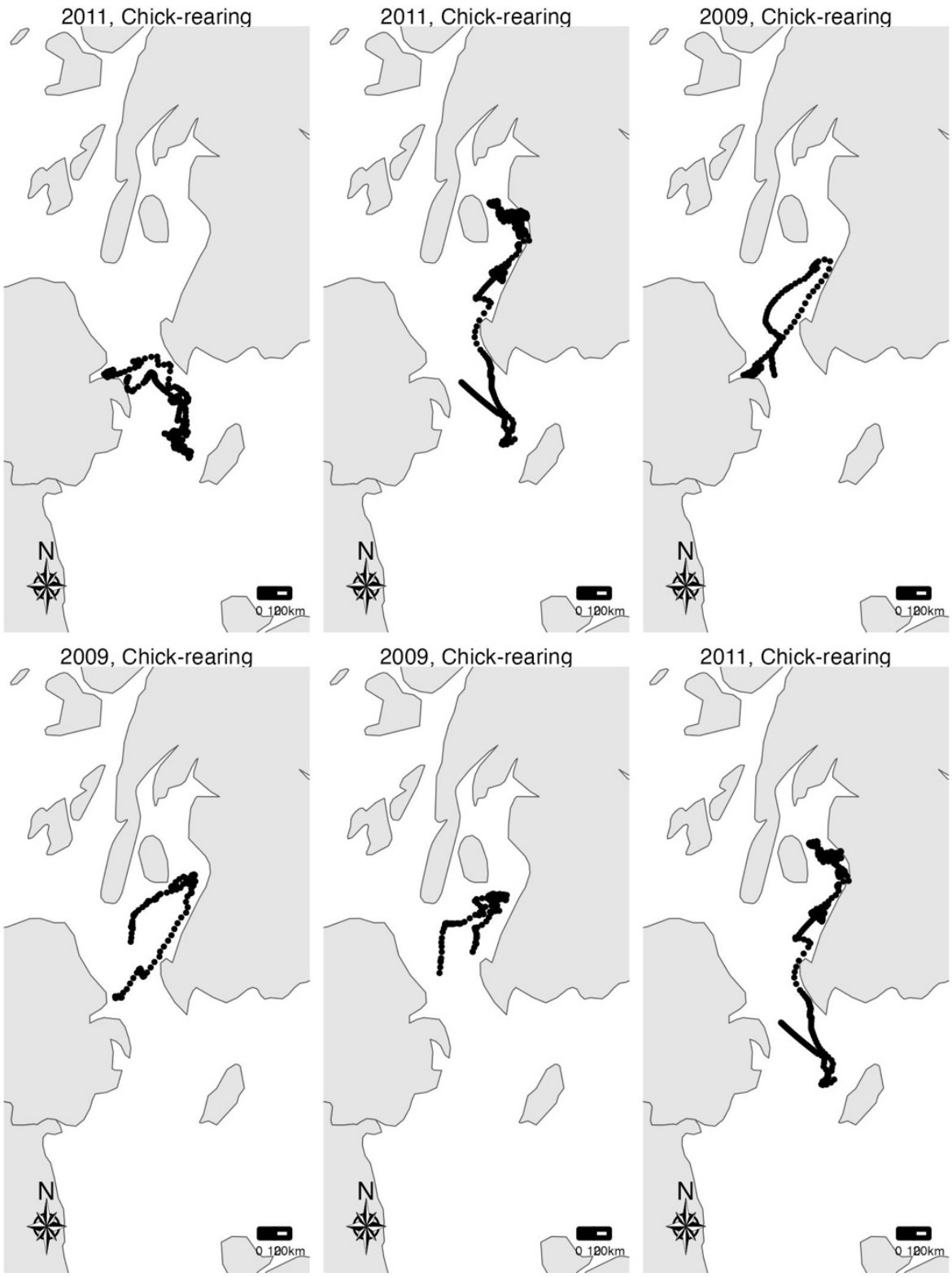
EG47326


2009, Chick-rearing
2019, Chick-rearing
2019, Chick-rearing
2010, Chick-rearing
2018, Incubation
2018, Chick-rearing
2018, Chick-rearing
2016, Chick-rearing
N
0 20 km

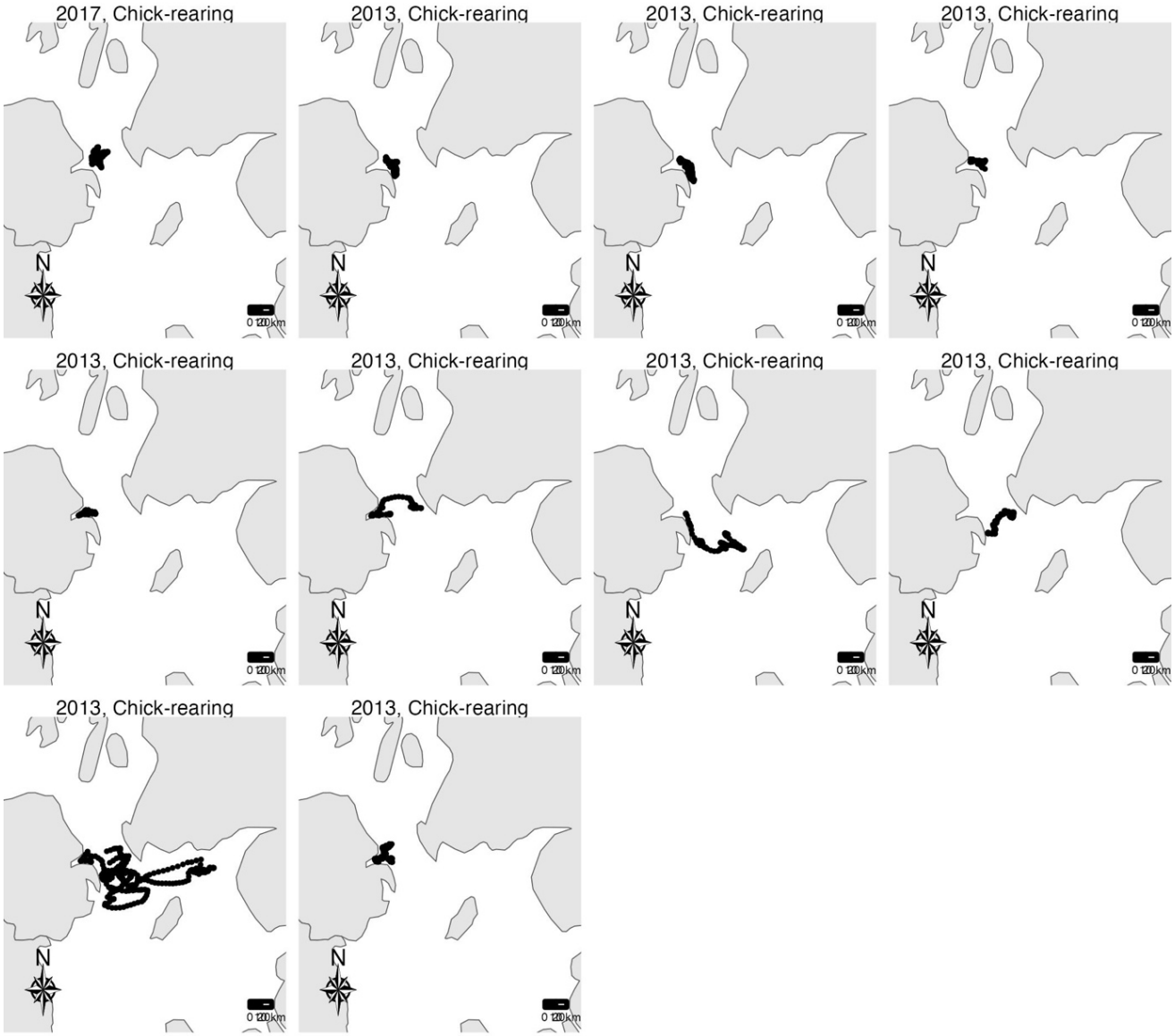
EG47387


2010, Chick-rearing
N
0 100km
2010, Chick-rearing
N
0 100km
2010, Chick-rearing
N
0 100km

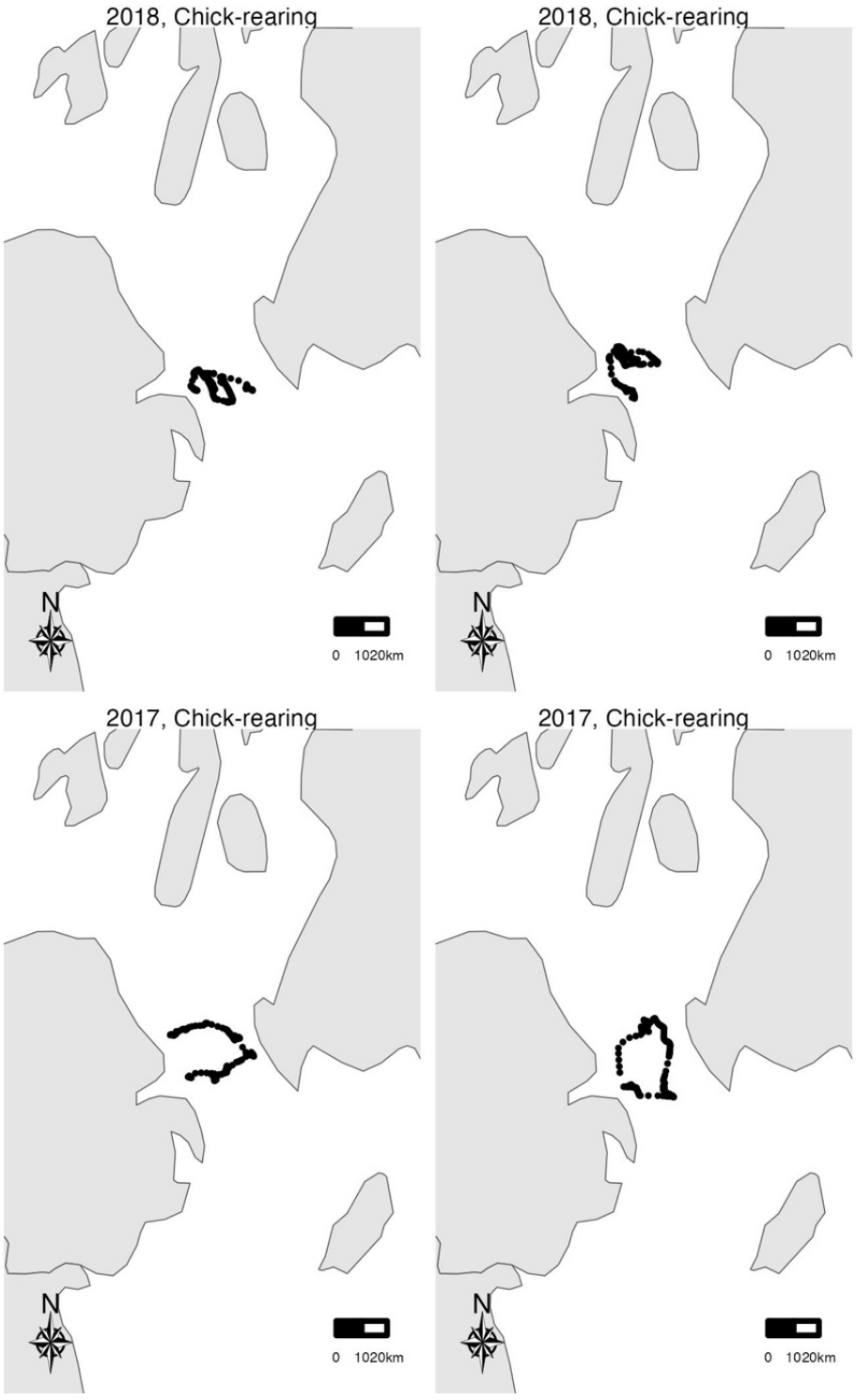
EG62149


2011, Chick-rearing
2011, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2011, Chick-rearing
N
0 120km

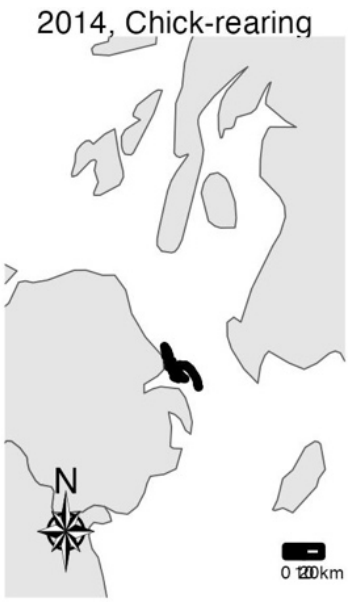
EG62162

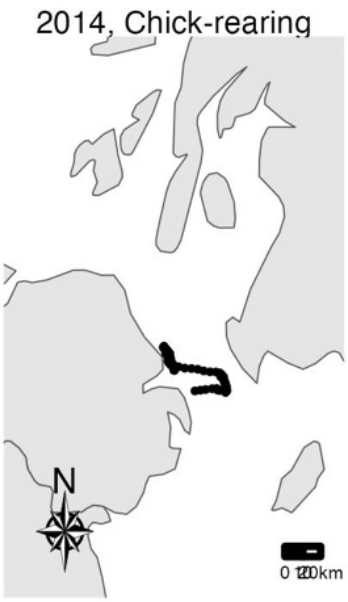

2017, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
N
0 120 km

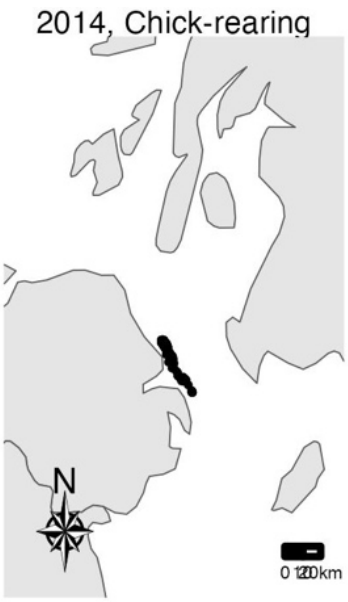
EG62256


2018, Chick-rearing
N
0 1020km
2018, Chick-rearing
N
0 1020km
2017, Chick-rearing
N
0 1020km
2017, Chick-rearing
N
0 1020km

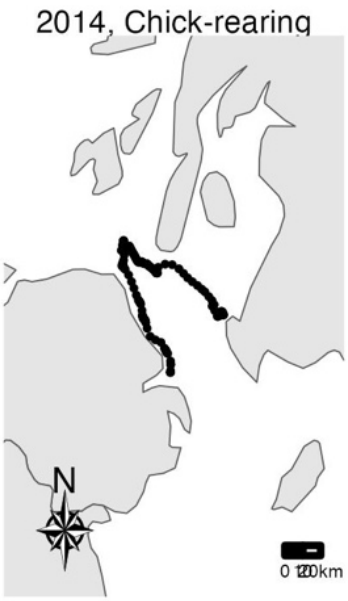
EG62428

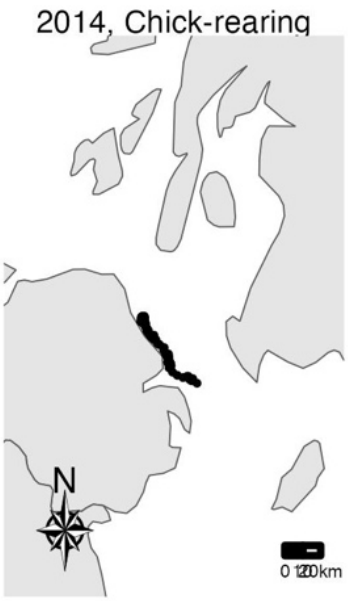

2014, Chick-rearing
N
0 120km

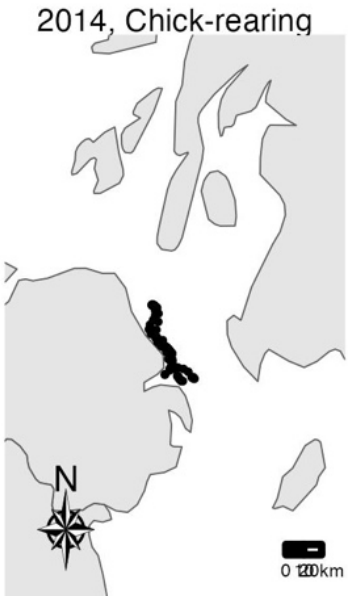

2014, Chick-rearing
N
0 120km


2014, Chick-rearing
N
0 120km

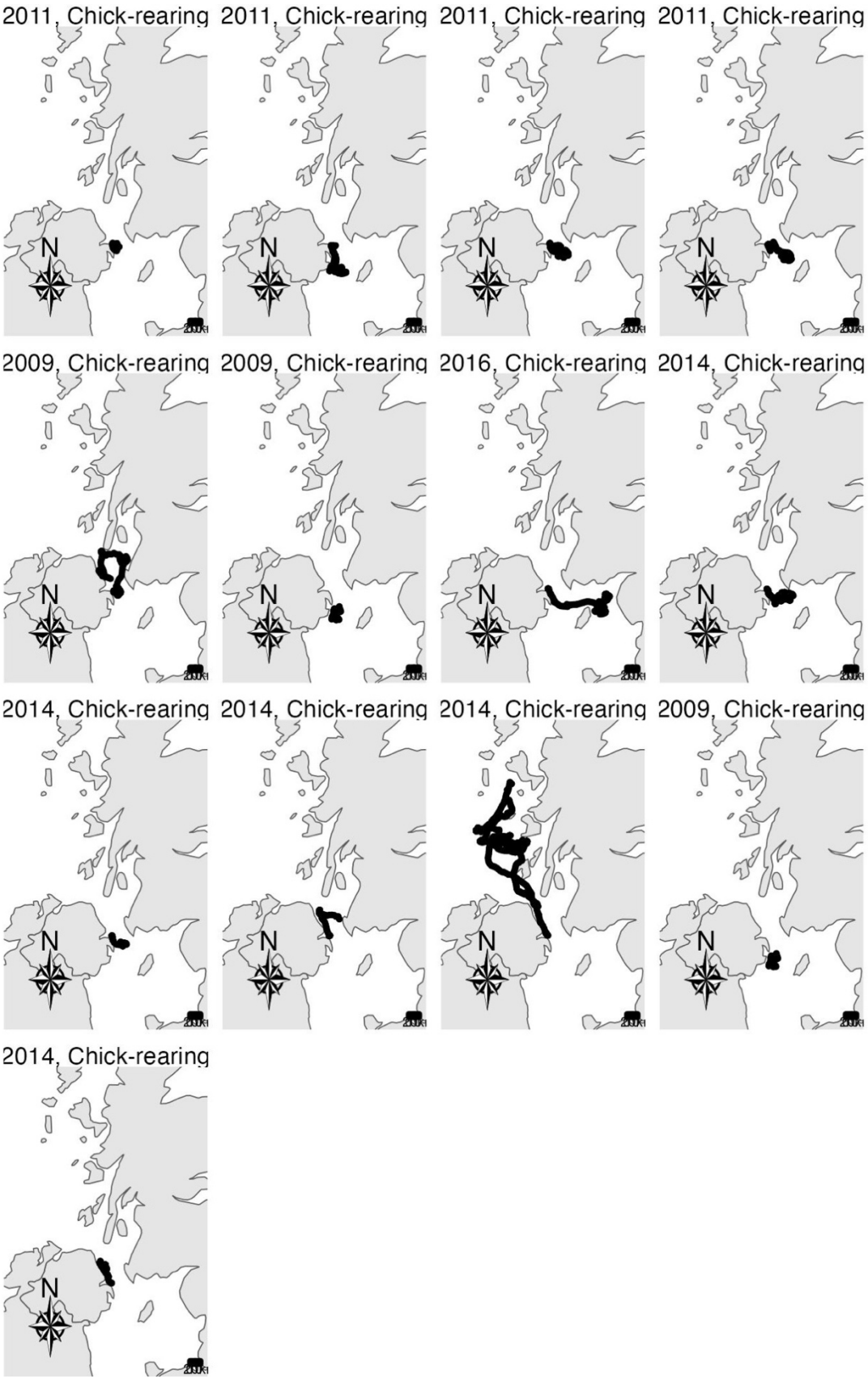

2014, Chick-rearing
N
0 120km


2014, Chick-rearing
N
0 120km

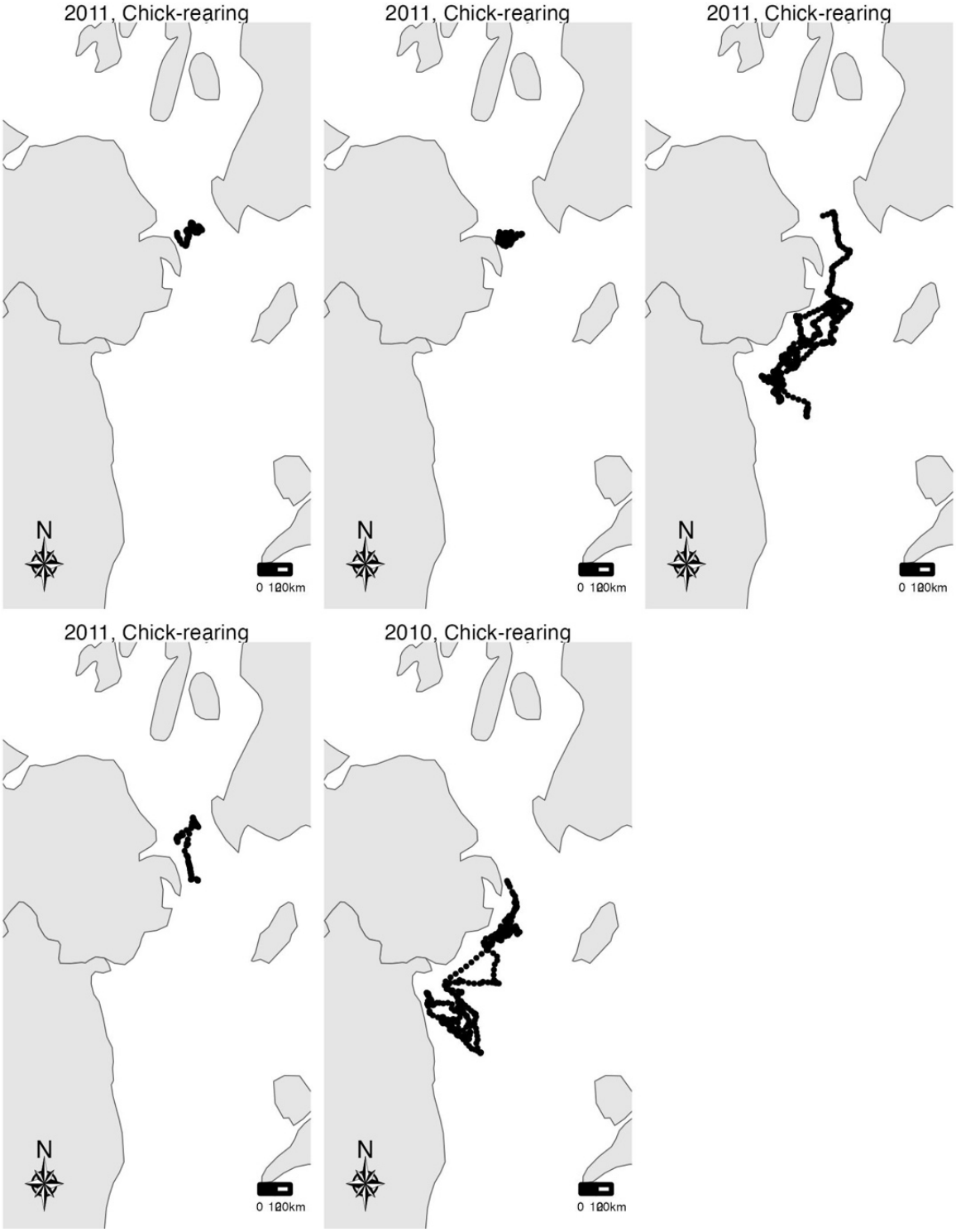

2014, Chick-rearing
N
0 120km


2014, Chick-rearing
N
0 120km

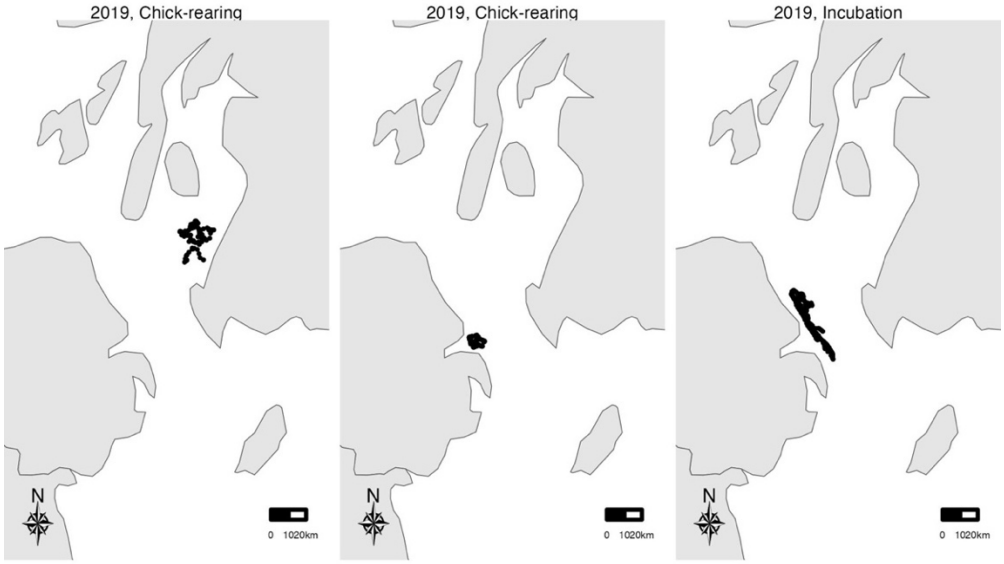
EG62538


2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2016, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2009, Chick-rearing
2014, Chick-rearing
N

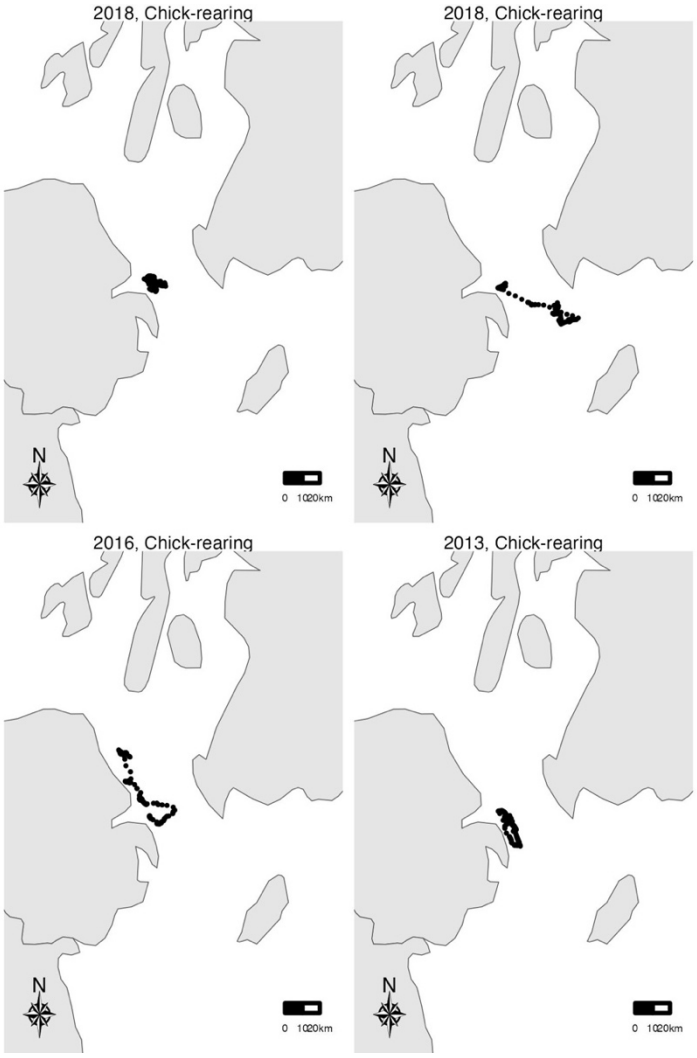
EG62542


2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2010, Chick-rearing
N
0 120km

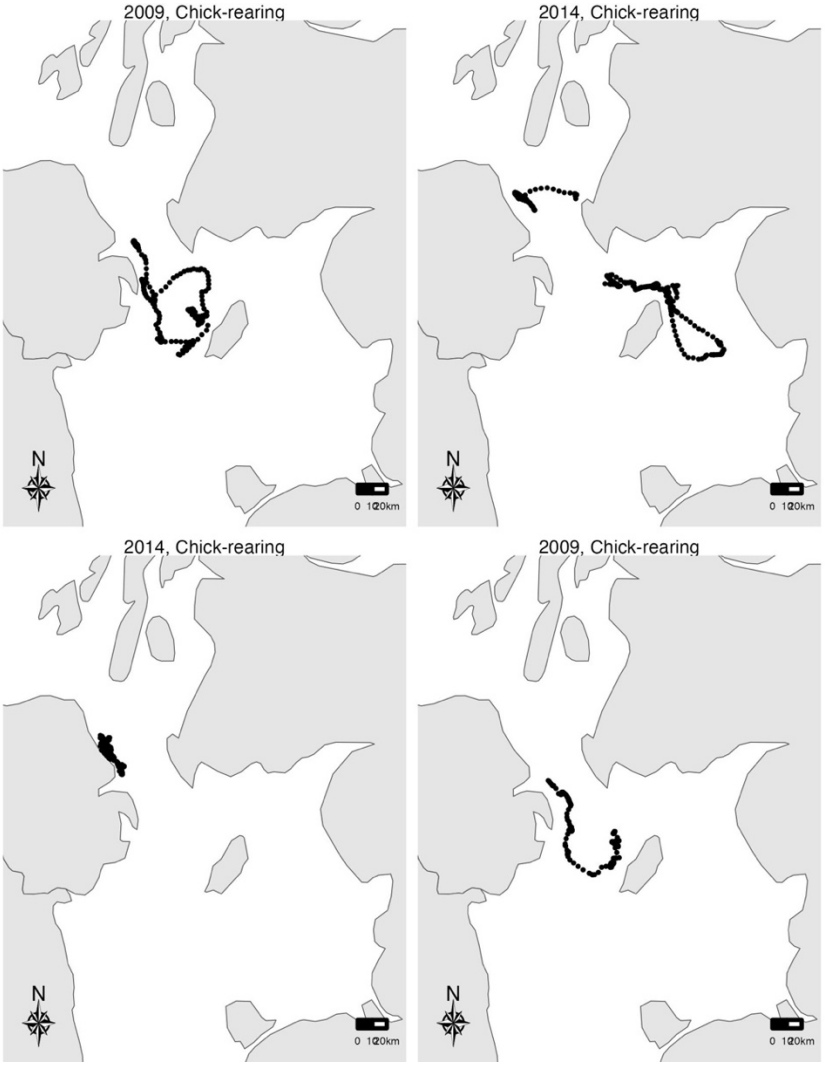
EG62692



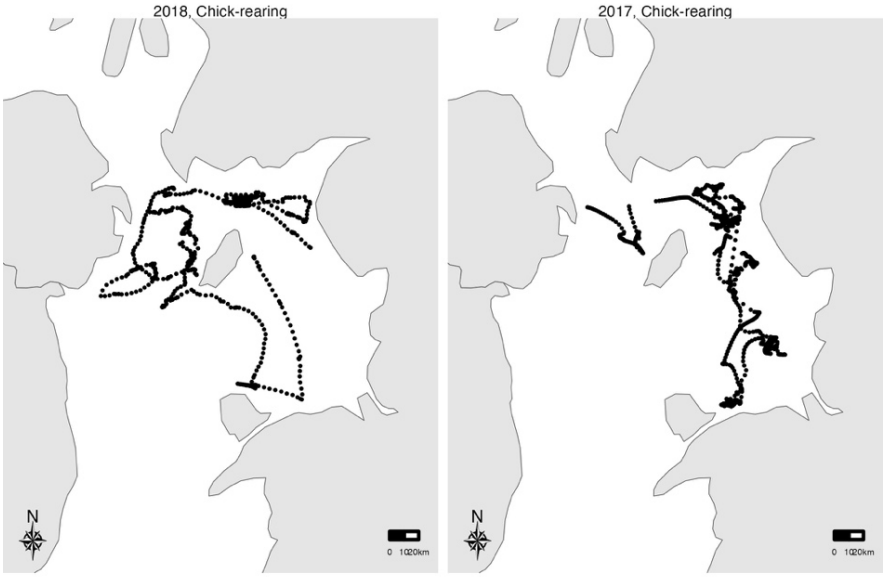
EG63126



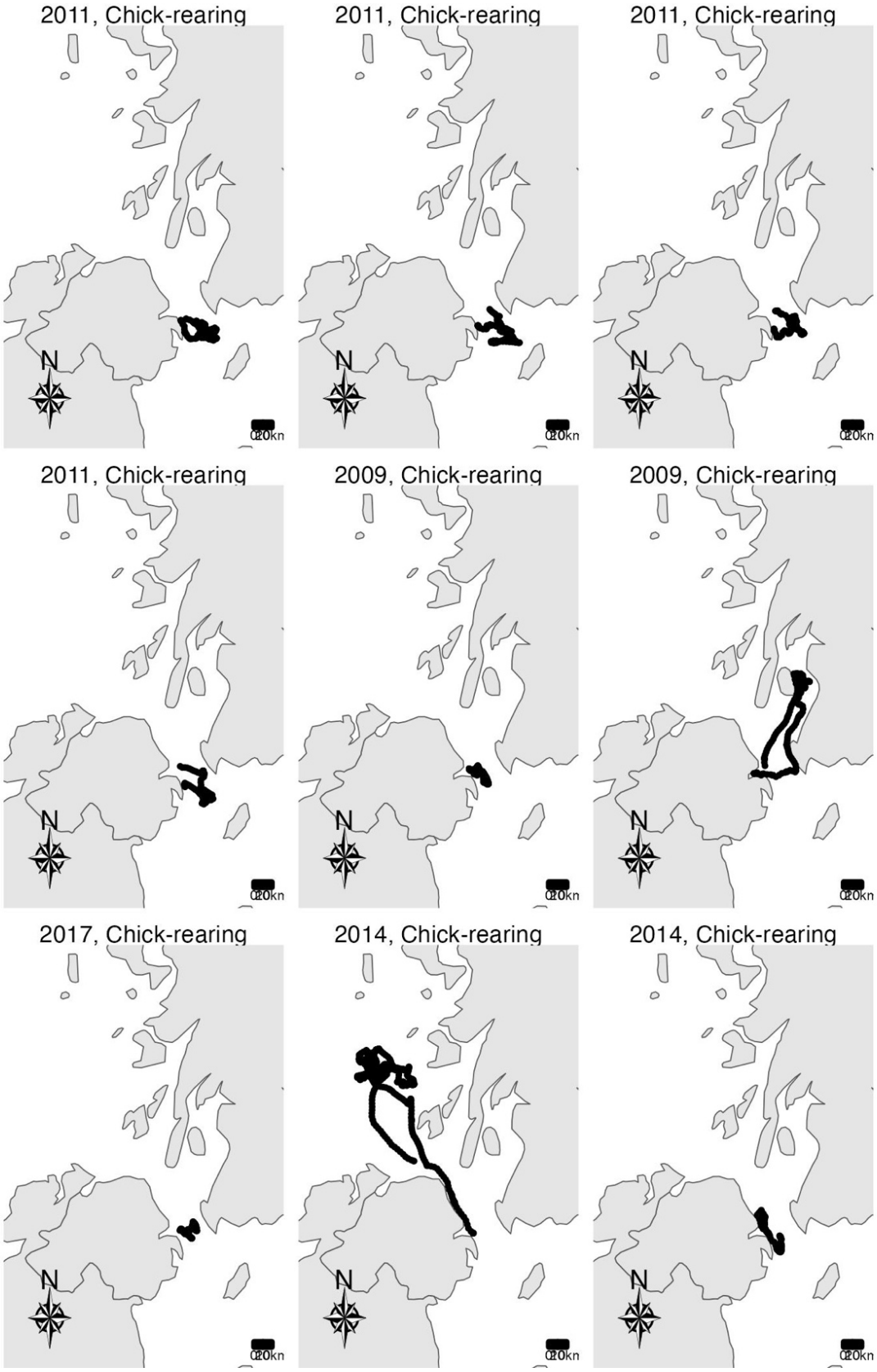
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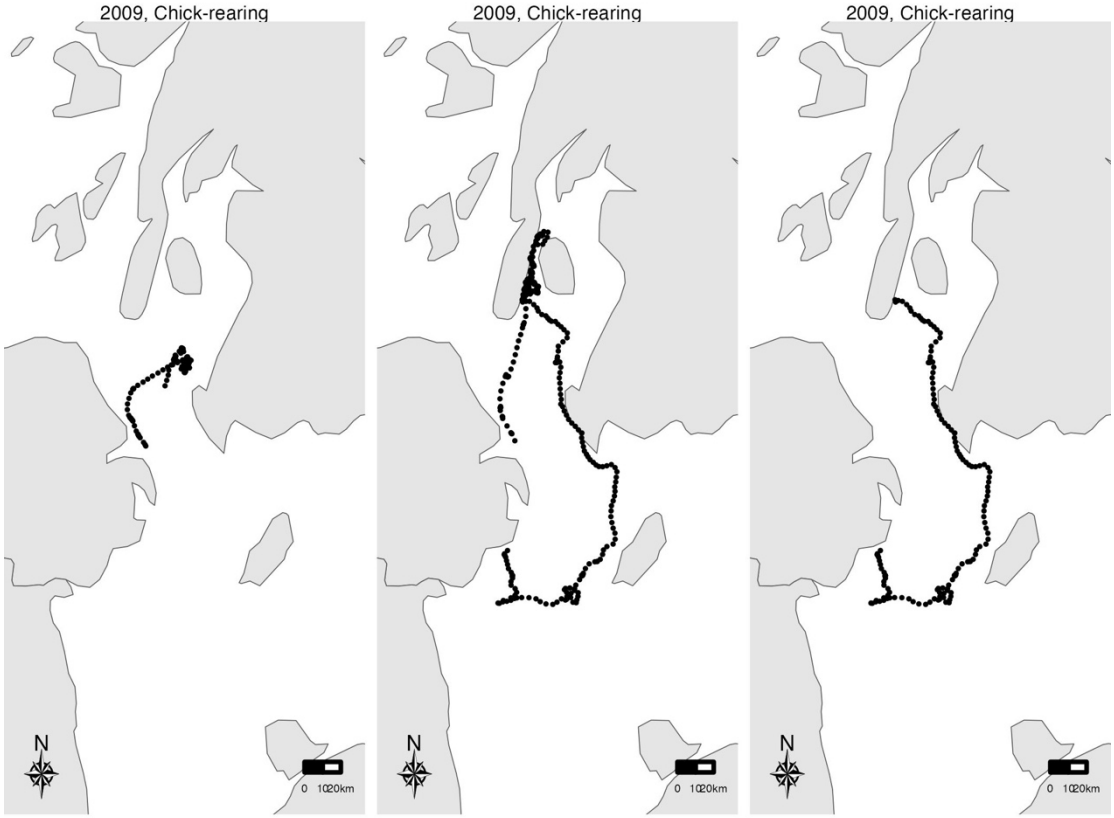
EG63777



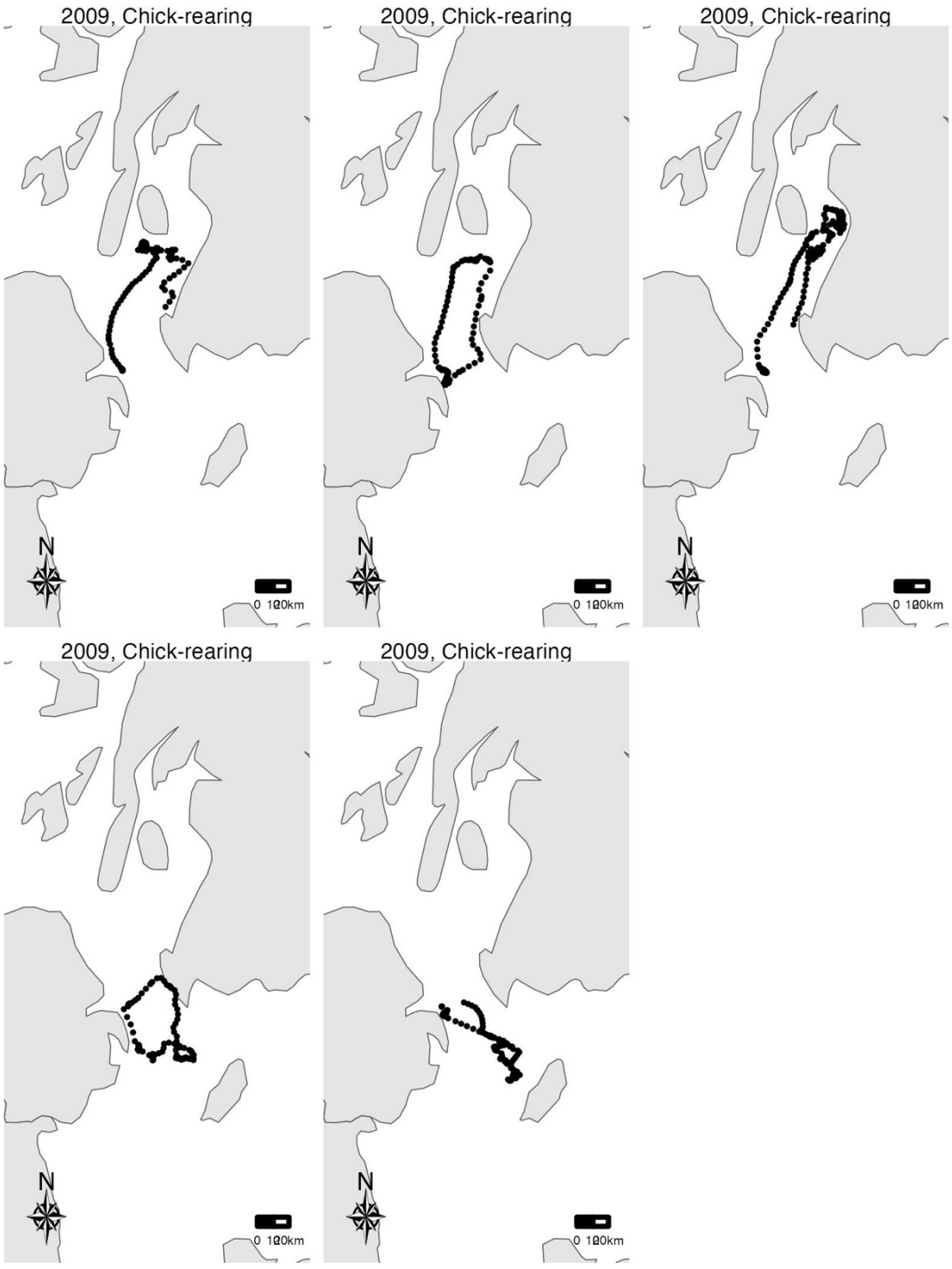
EG63782


2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2017, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
N
0 20 km

EG63794


2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km

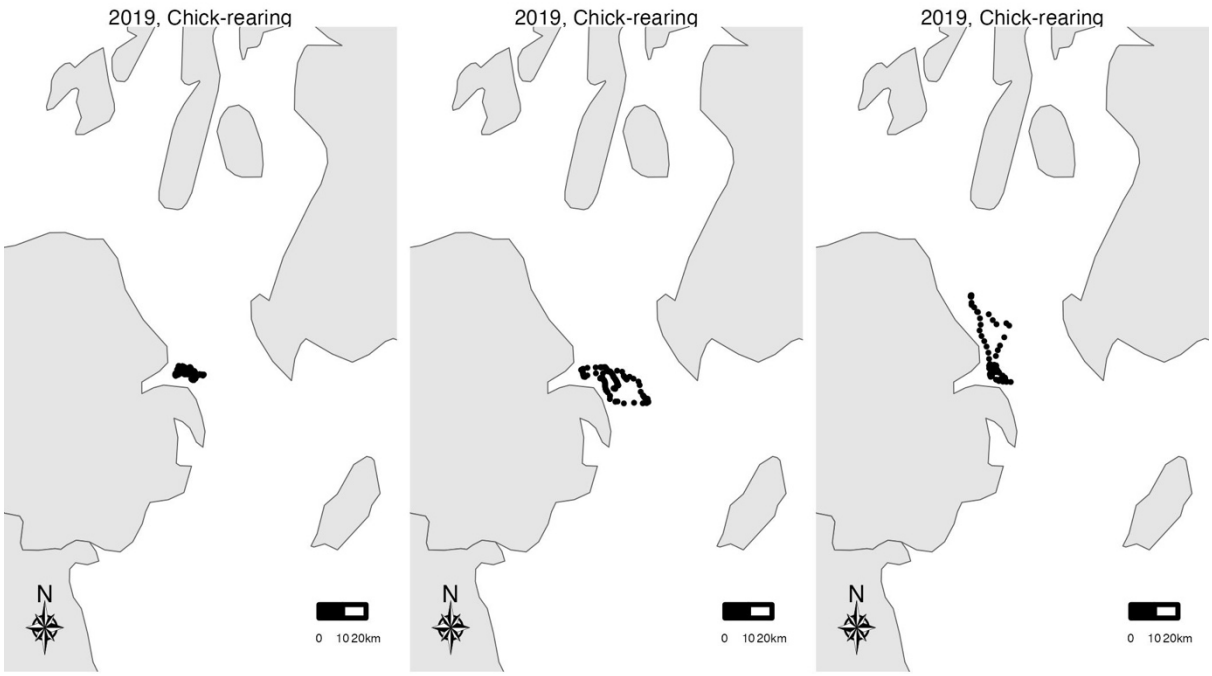
EG63865


2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
N
0 100km

EG63875



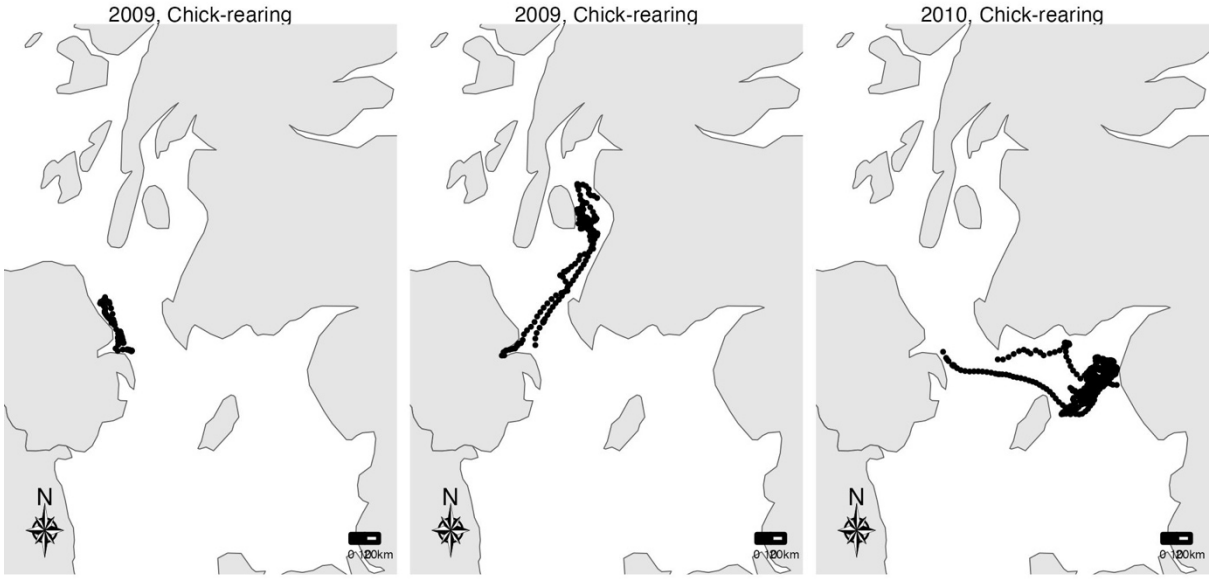
EG63891



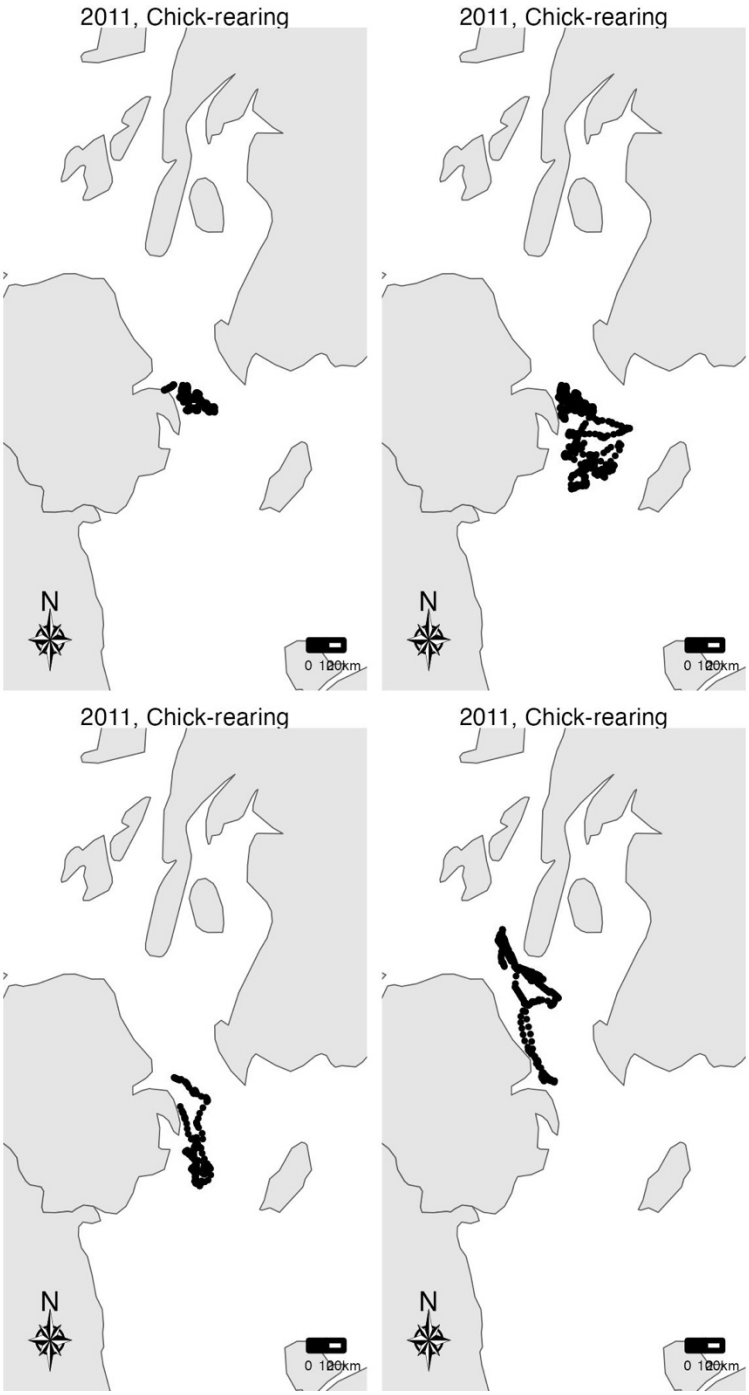
EG64824


2018, Chick-rearing
2018, Chick-rearing
2016, Chick-rearing
2017, Chick-rearing
2017, Chick-rearing
N
0 10 20km

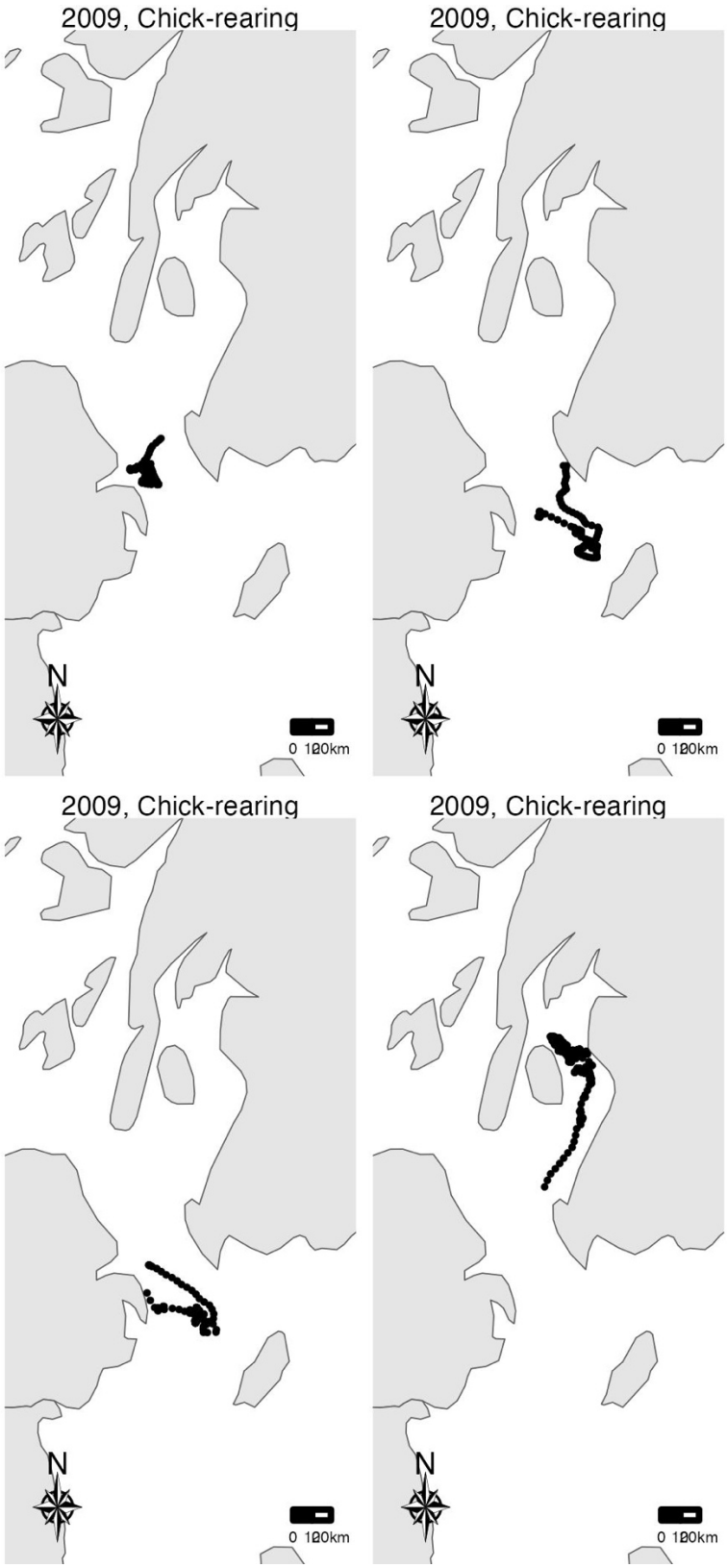
EG64896


2009, Chick-rearing
2009, Chick-rearing
2010, Chick-rearing
N
0 120km

EJ13879


2011, Chick-rearing
N
0 120km
2011, Chick-rearing
N
0 120km
2011, Chick-rearing
N
0 120km
2011, Chick-rearing
N
0 120km

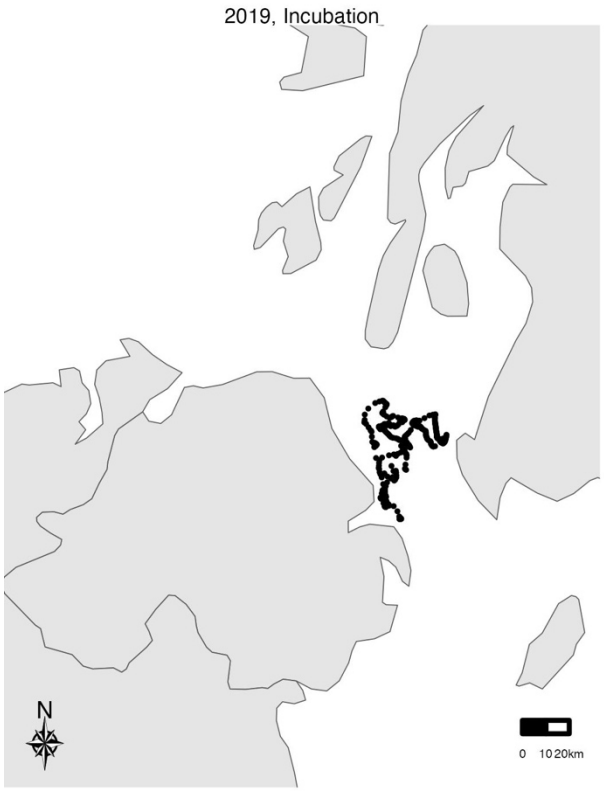
EJ14017

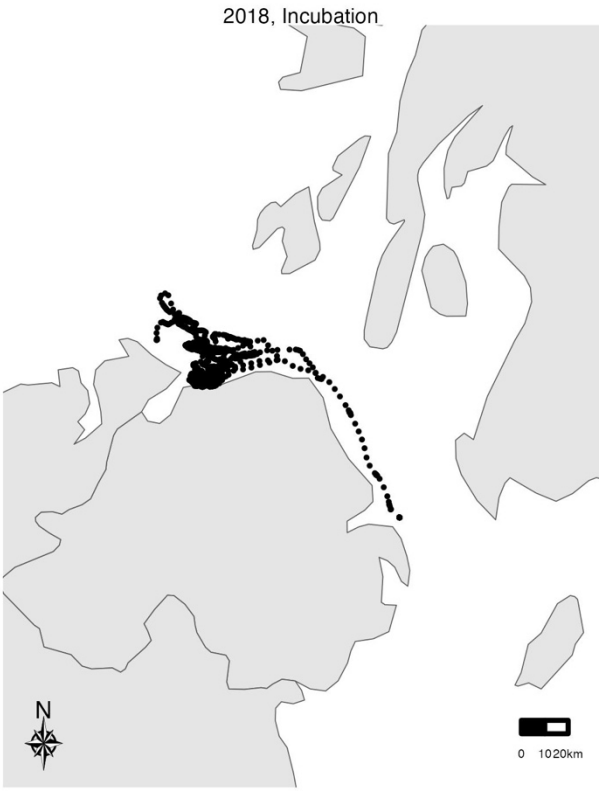

2009, Chick-rearing
N
0 120km
2009, Chick-rearing
N
0 120km
2009, Chick-rearing
N
0 120km
2009, Chick-rearing
N
0 120km

EJ14380

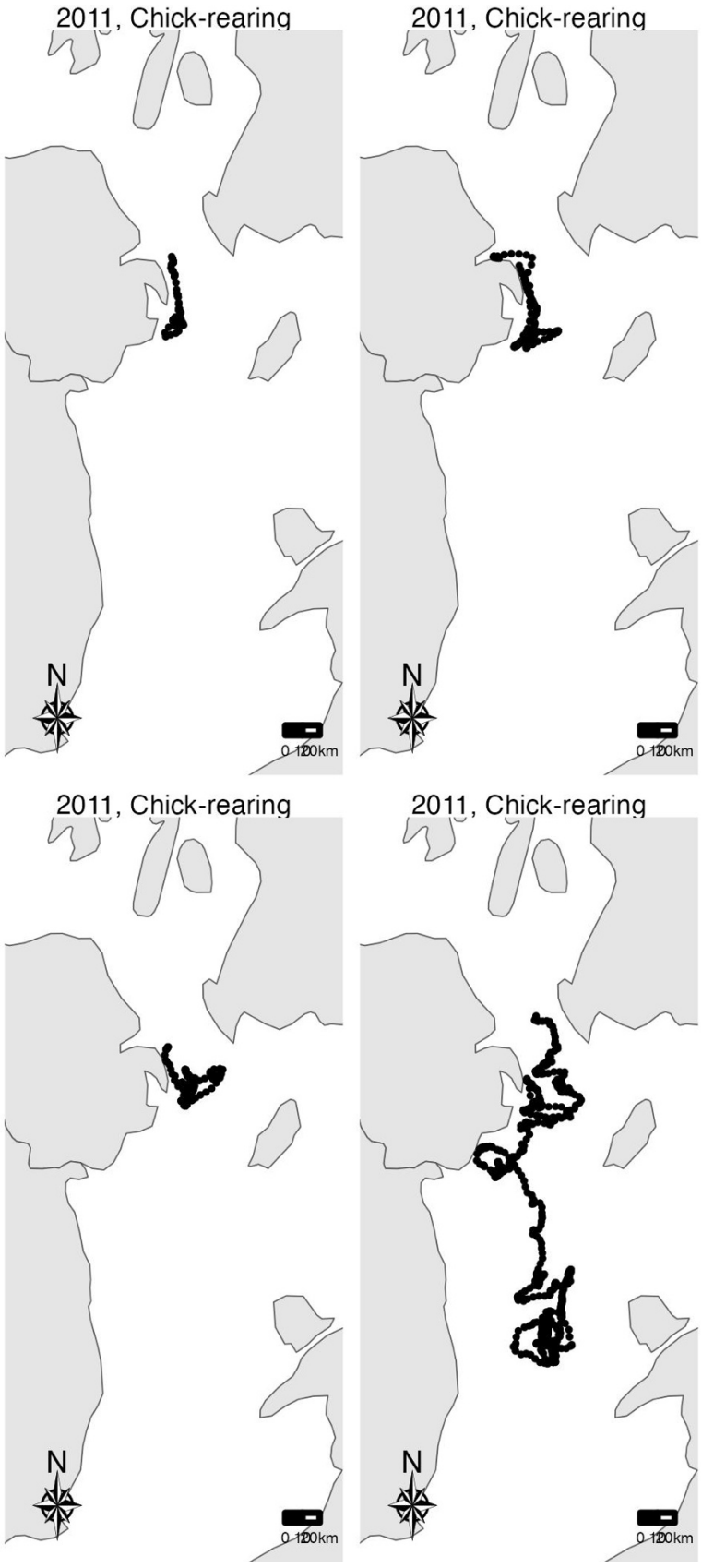

2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km

EJ95535

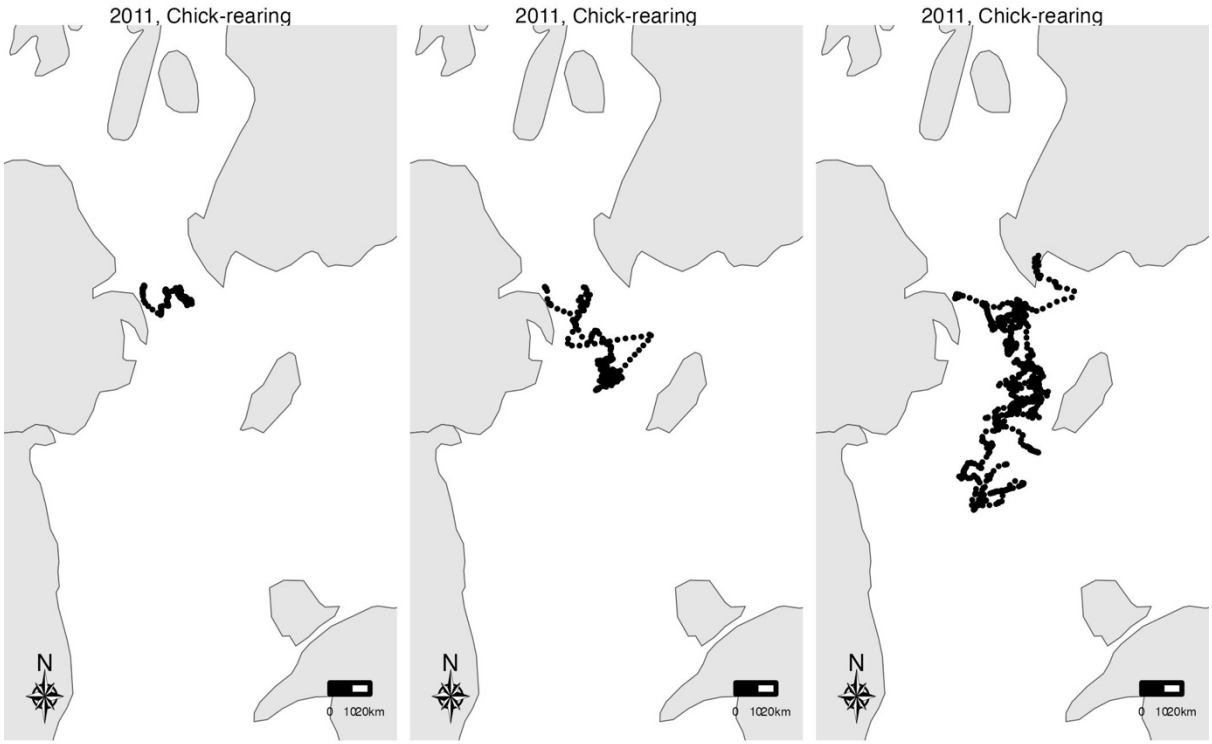




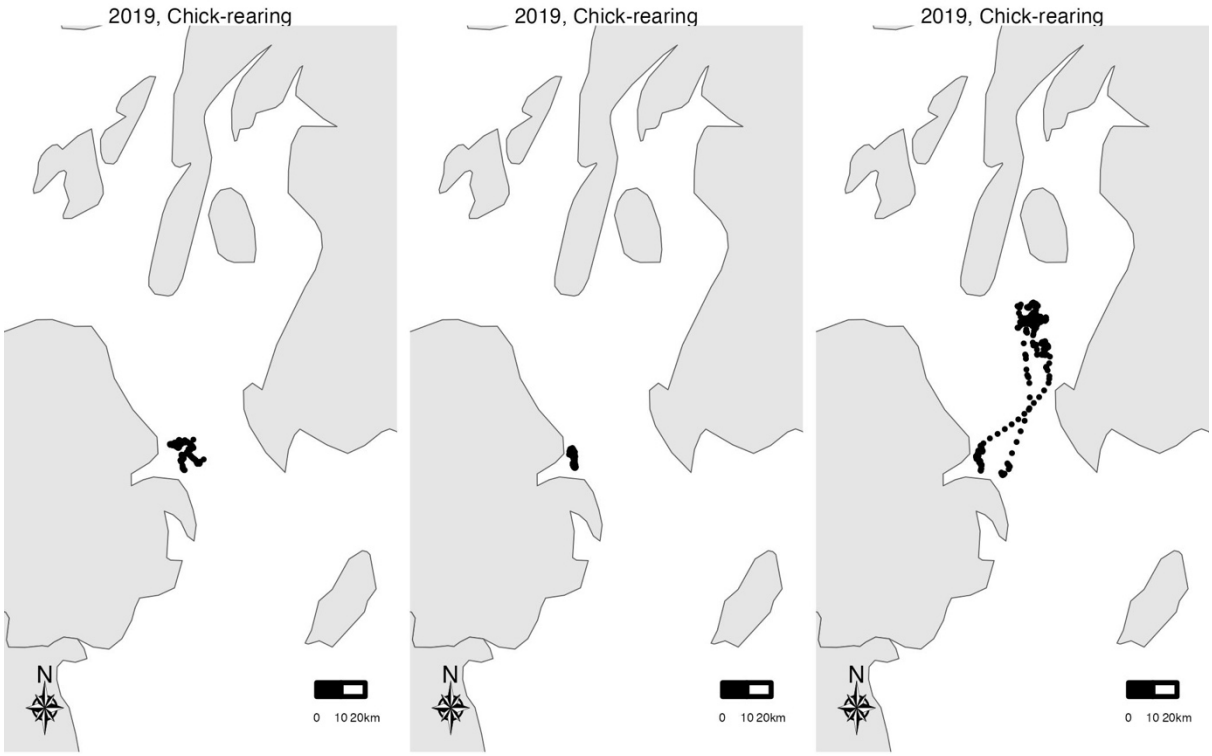
EL66084


2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
N
0 120km

EL66232



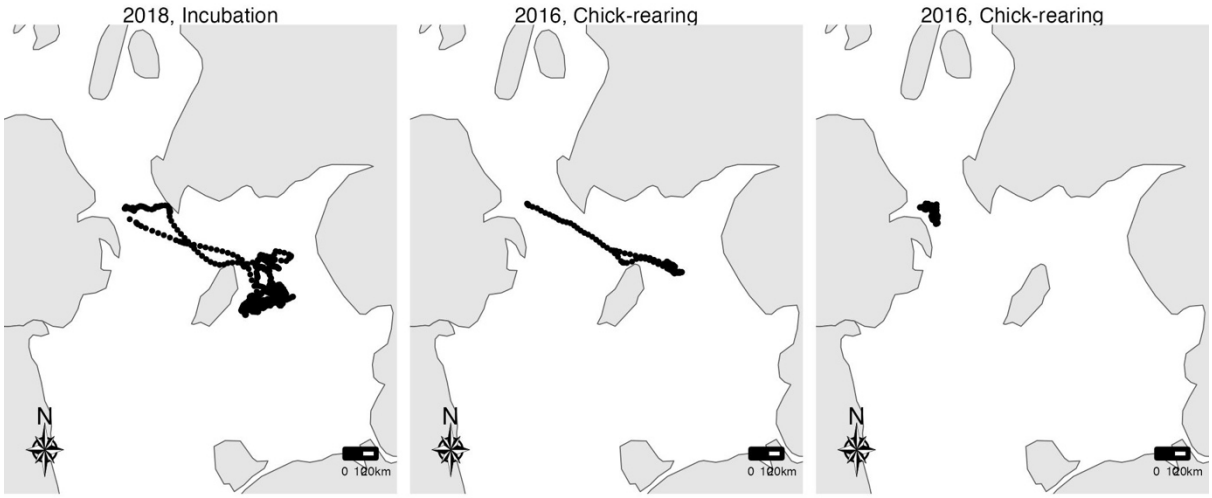
EL66654



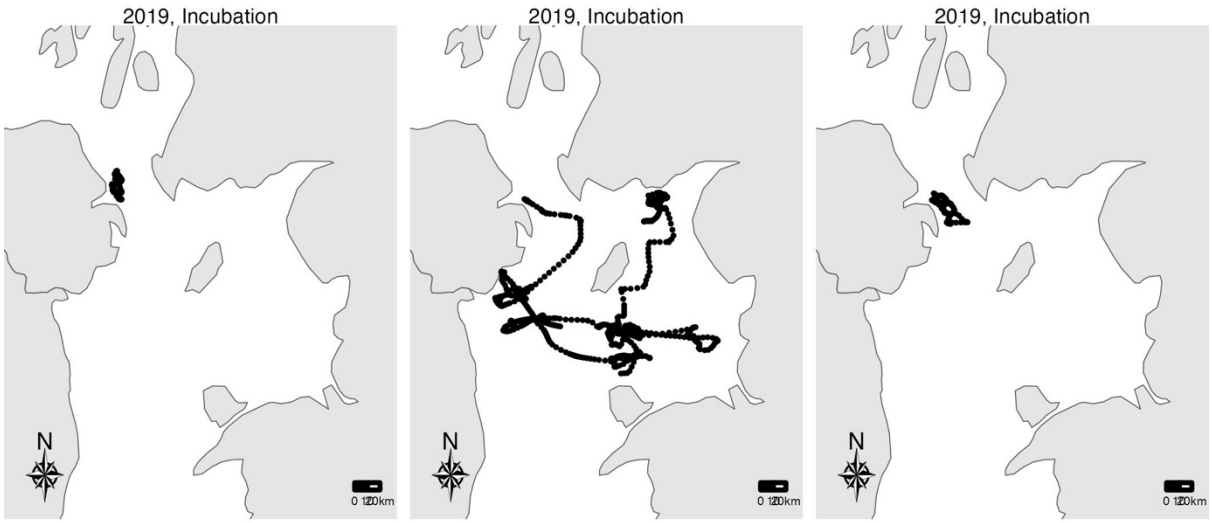
EL66919


2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2016, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
N
0 120 km

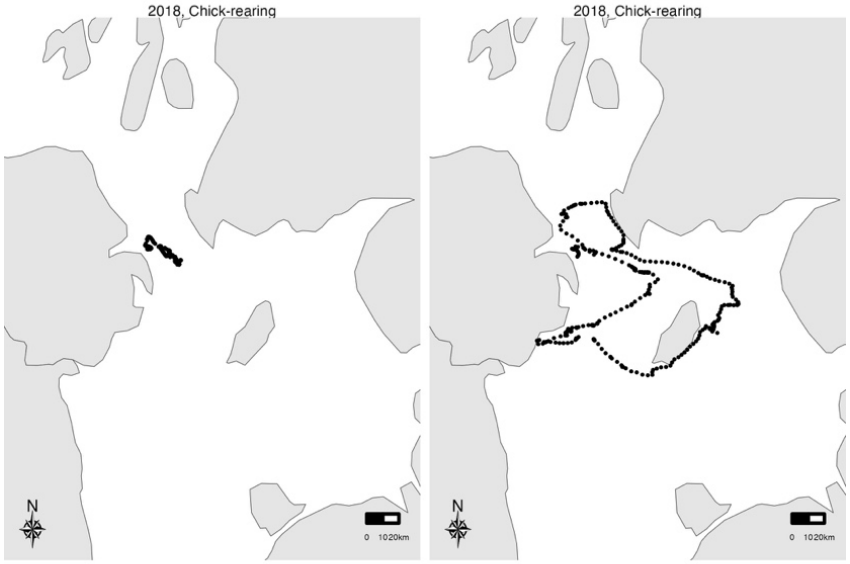
EL68236



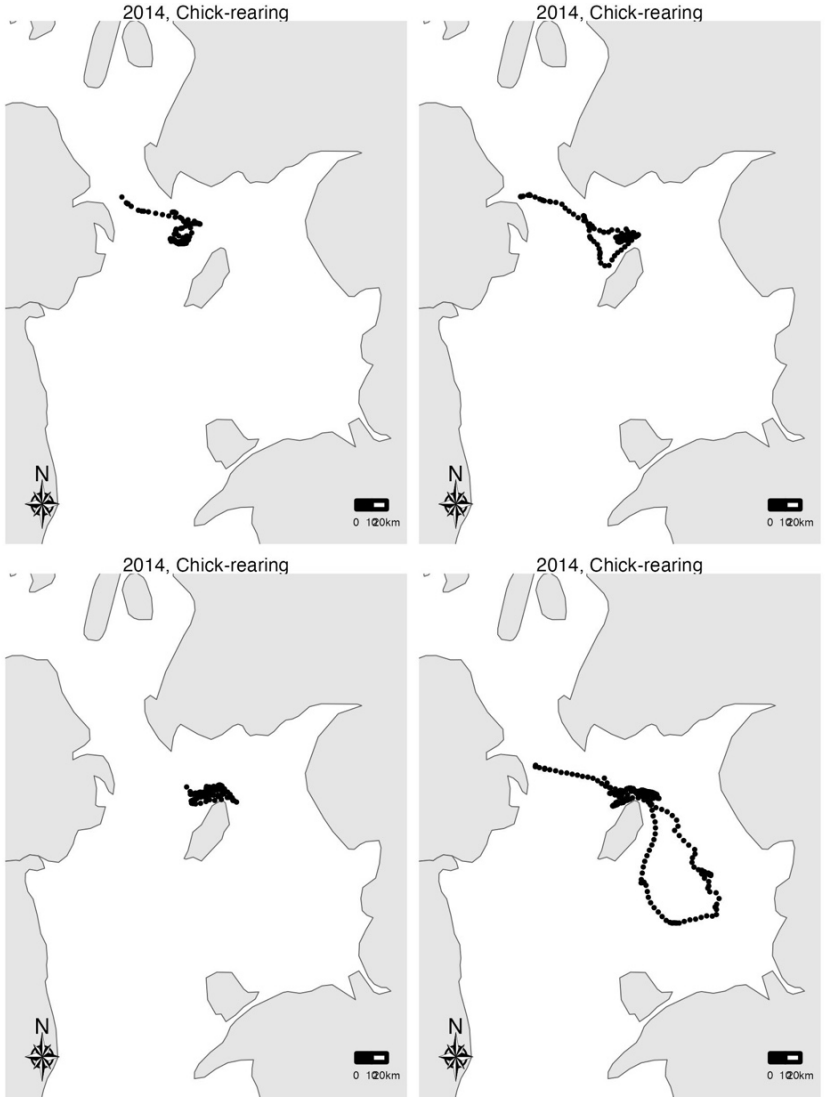
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EL90013



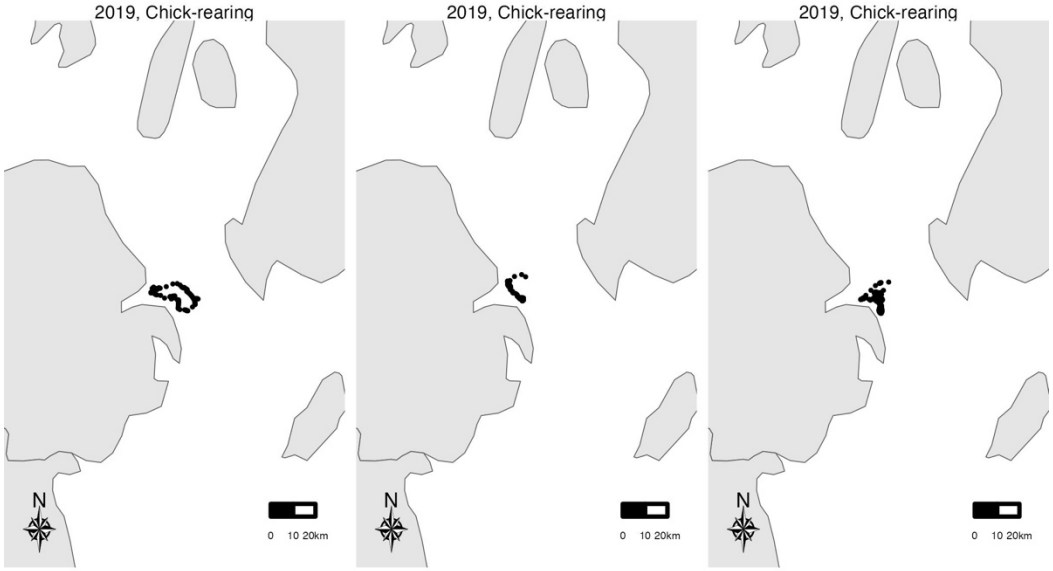
EL90359



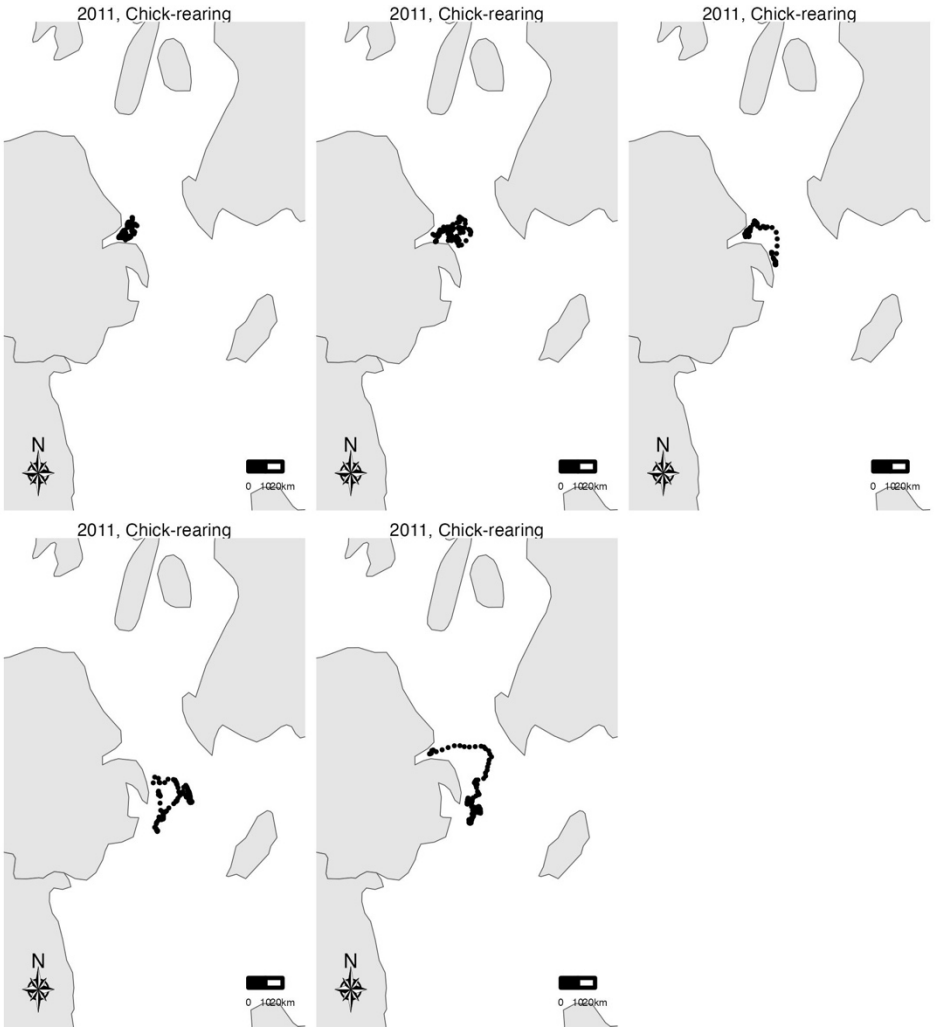
EL90719


2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2008, Chick-rearing
2008, Chick-rearing
2008, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2008, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
N
0 20km

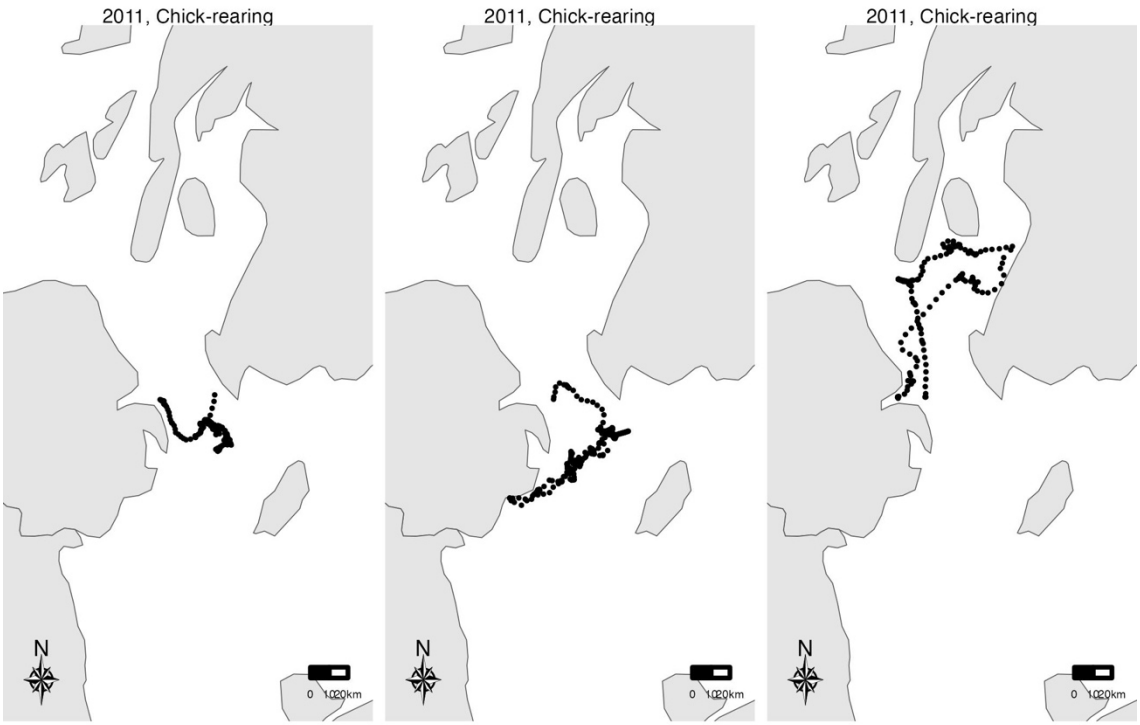
EL91214



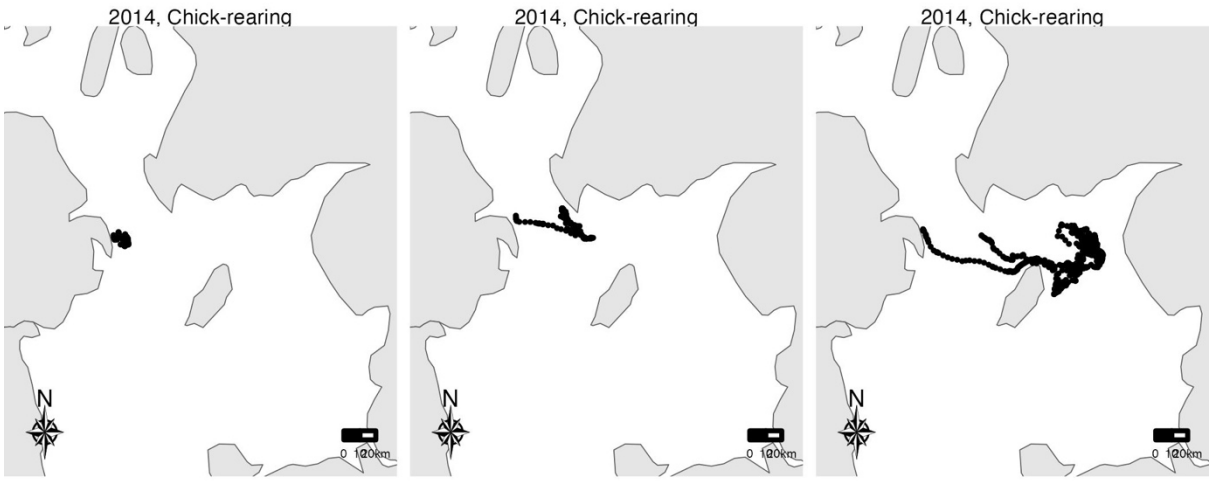
EL91269



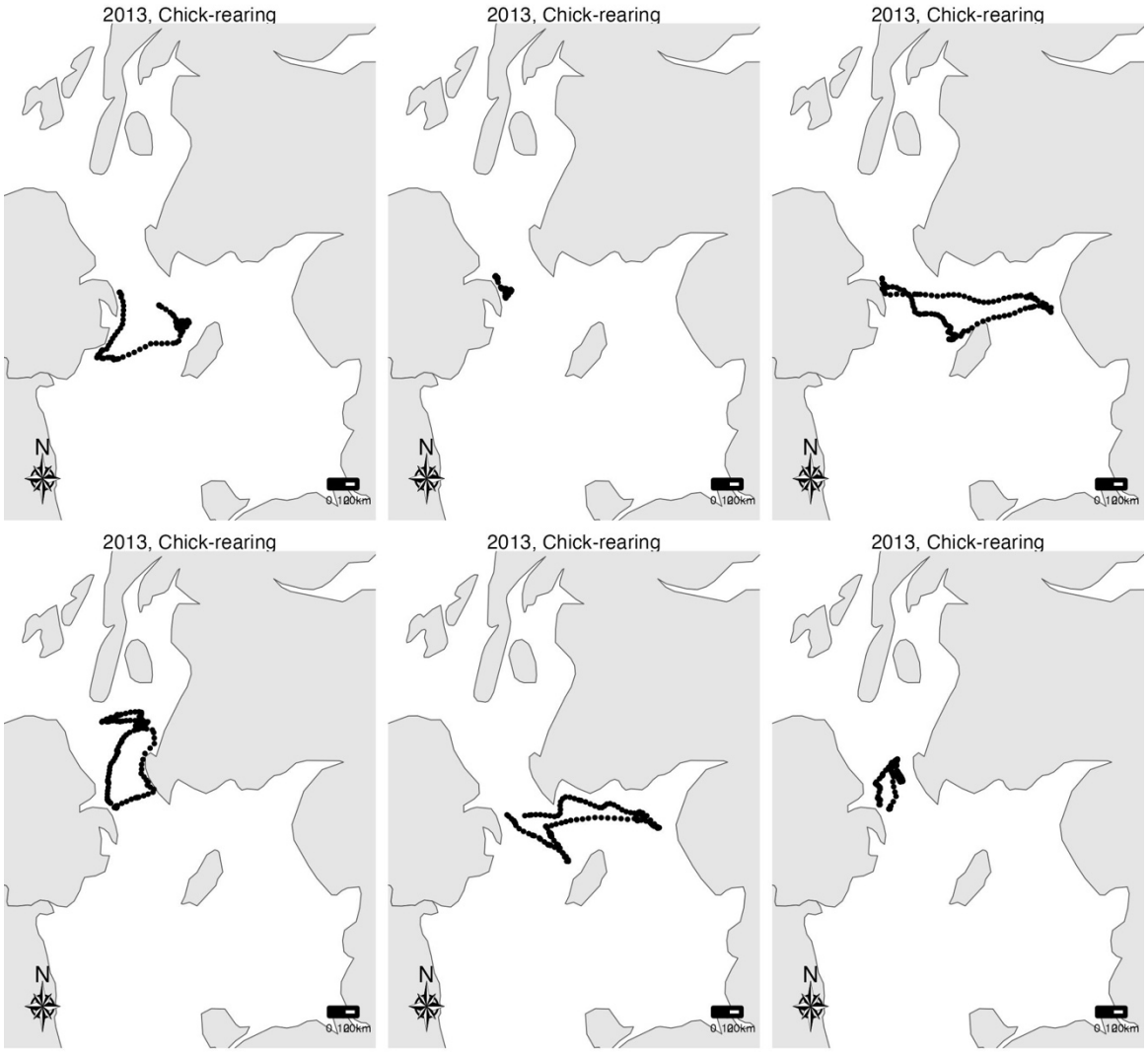
EL91505



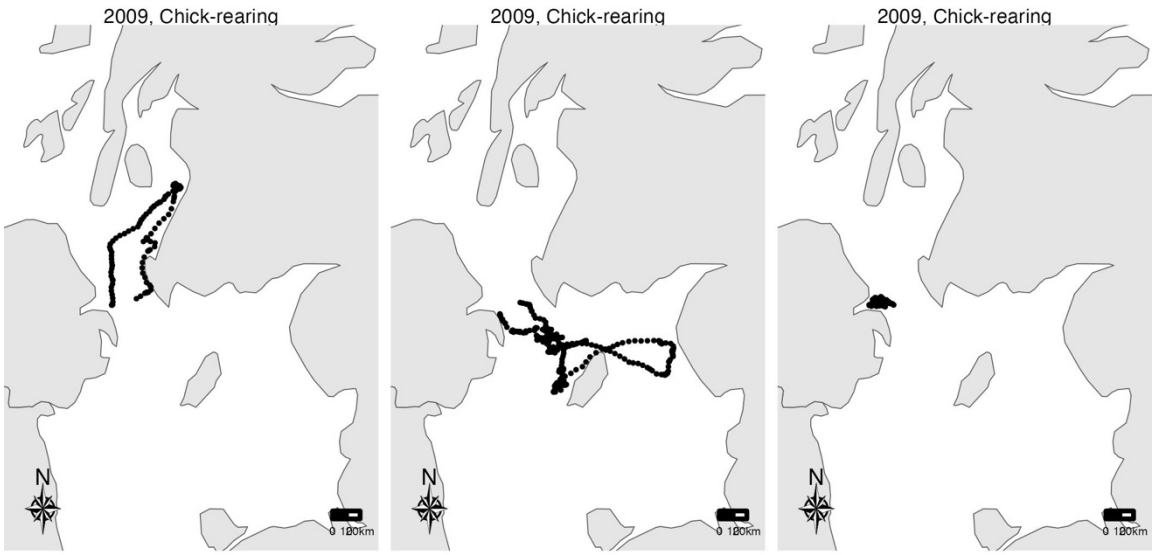
EL91692



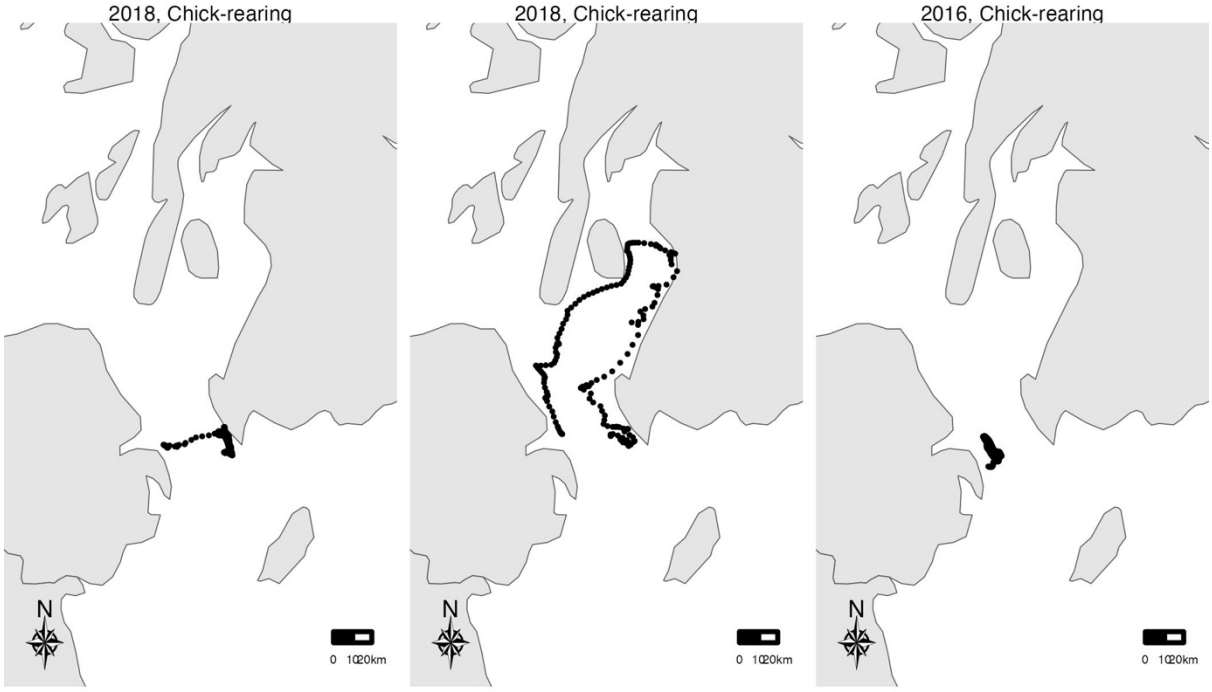
EL91698



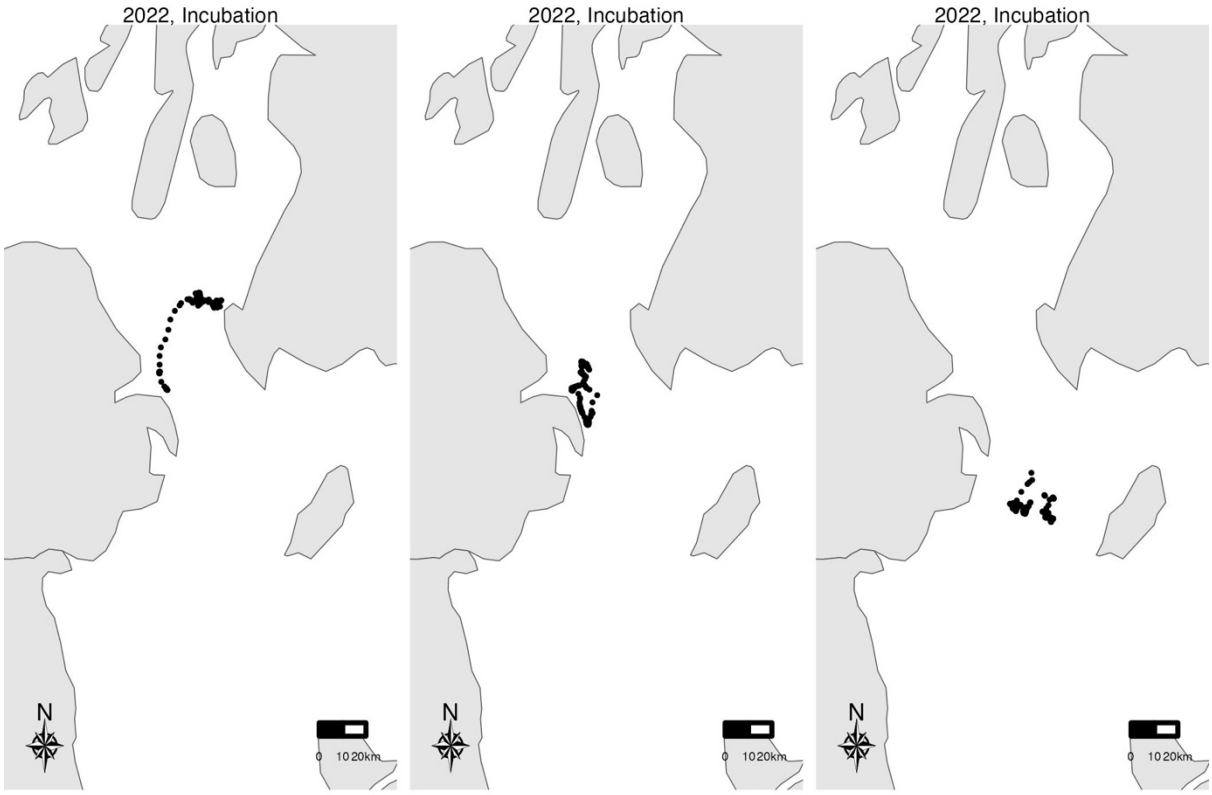
EL91737



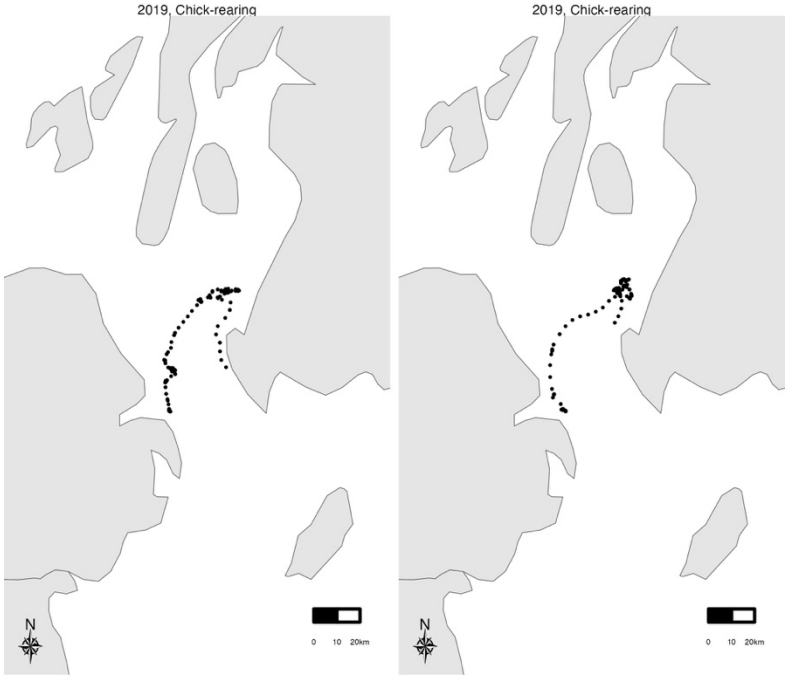
EL91756



EL91759



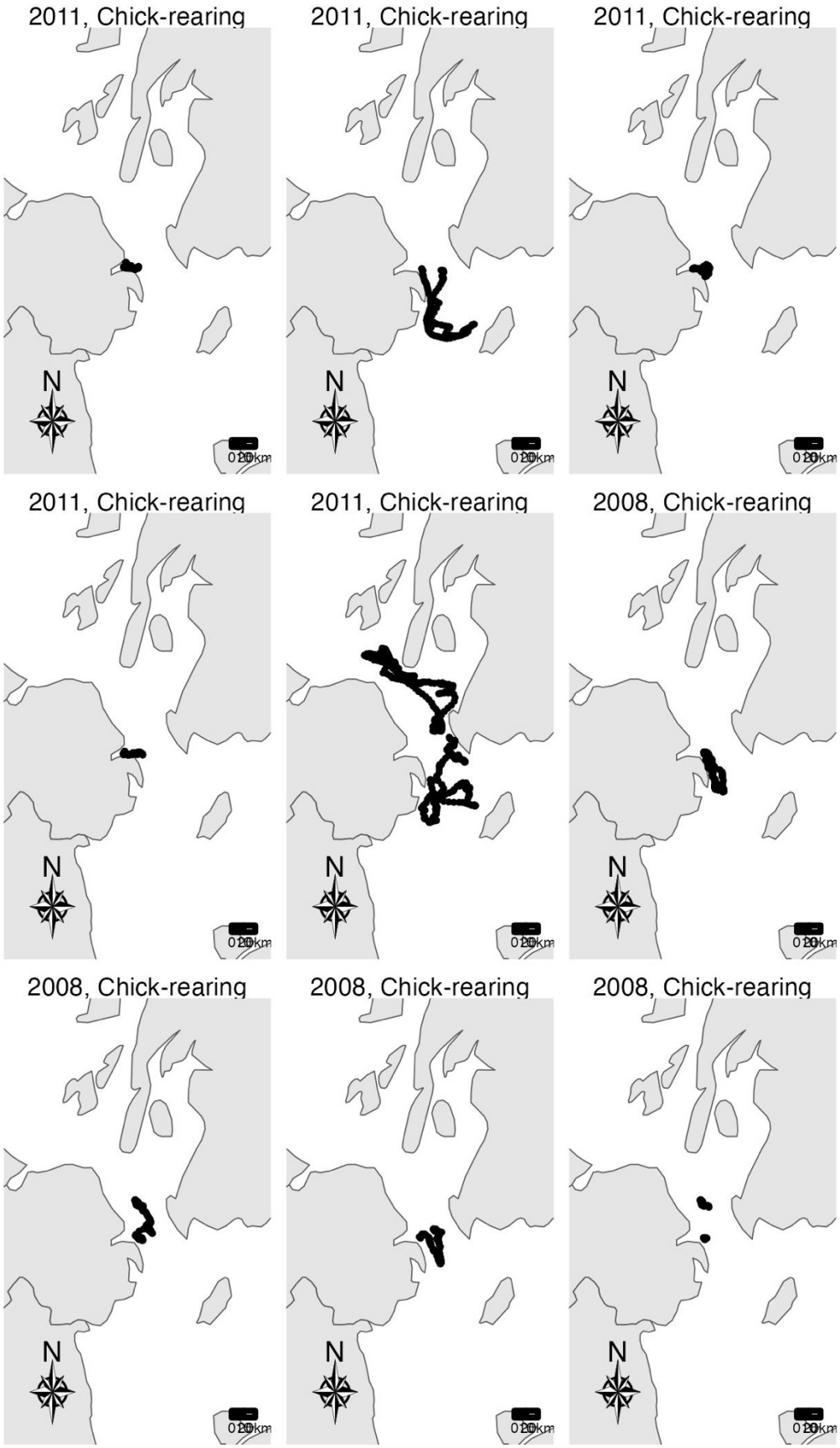
EL91908



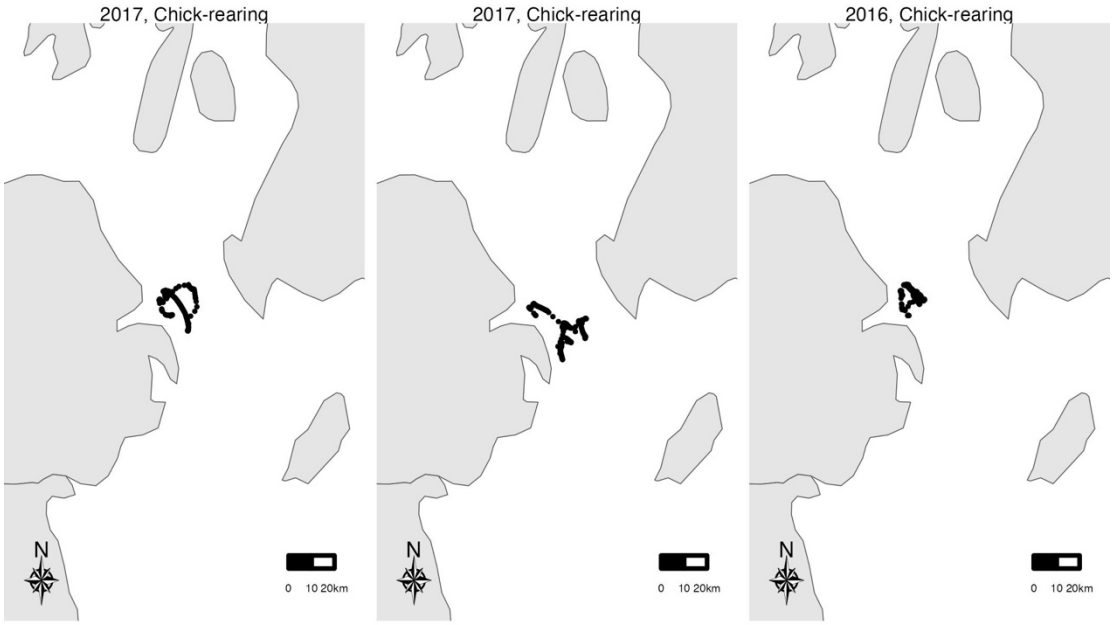
EL92310



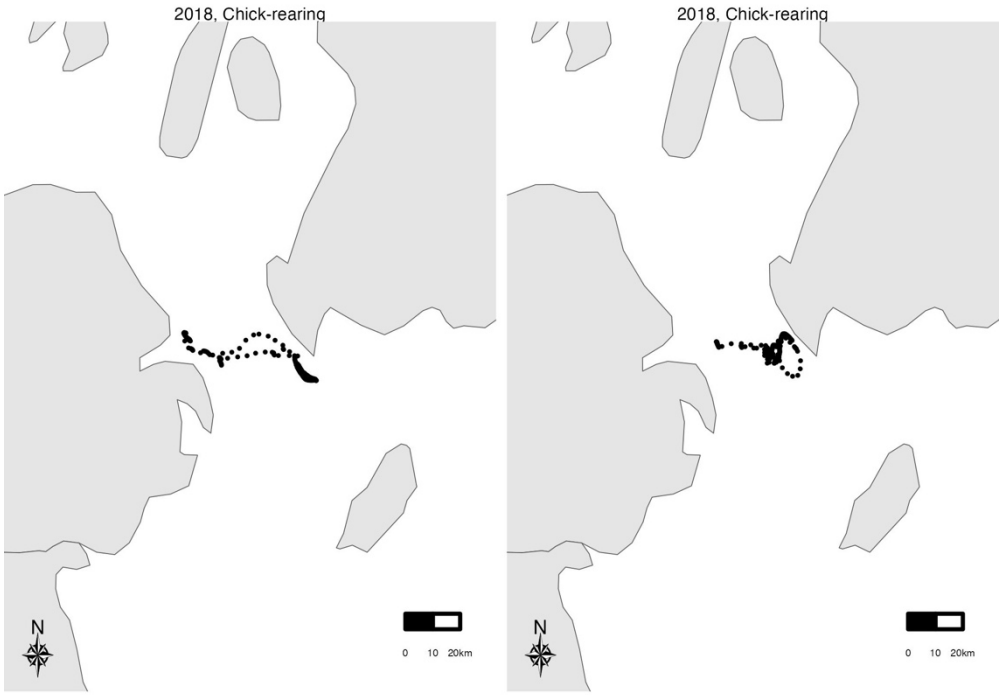
EL92575


2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2008, Chick-rearing
2008, Chick-rearing
2008, Chick-rearing
2008, Chick-rearing
N

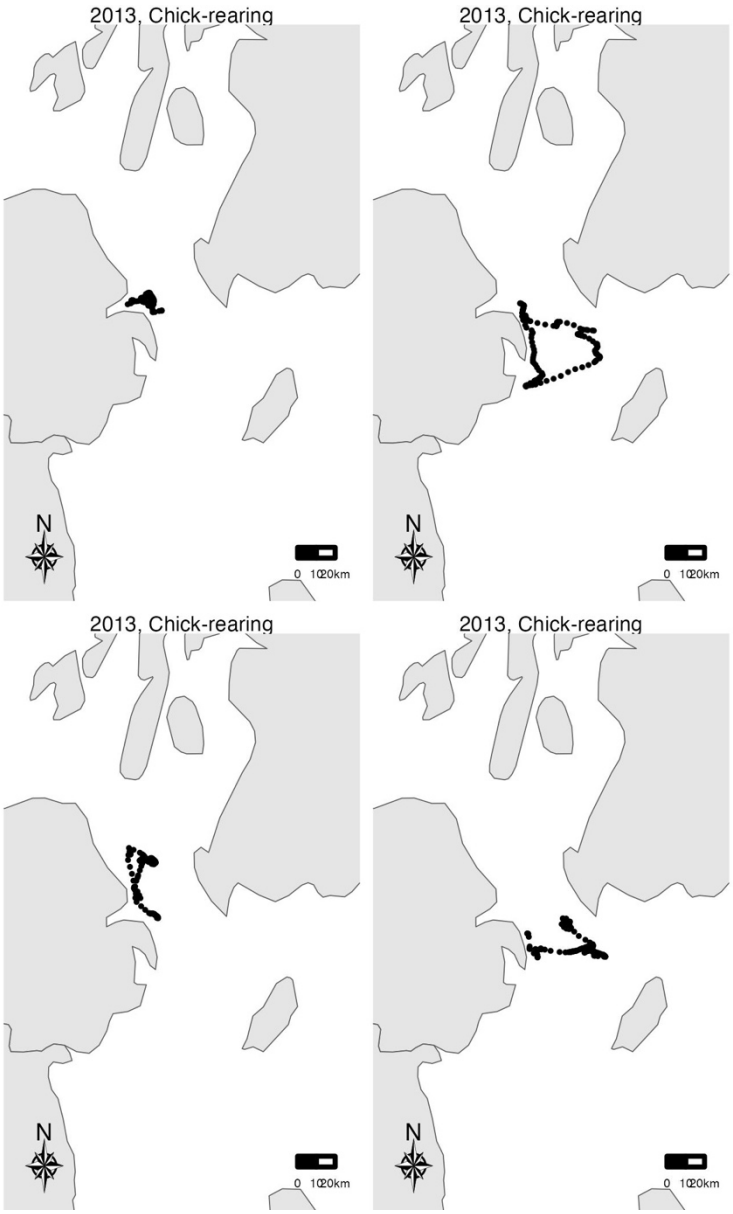
EL92631



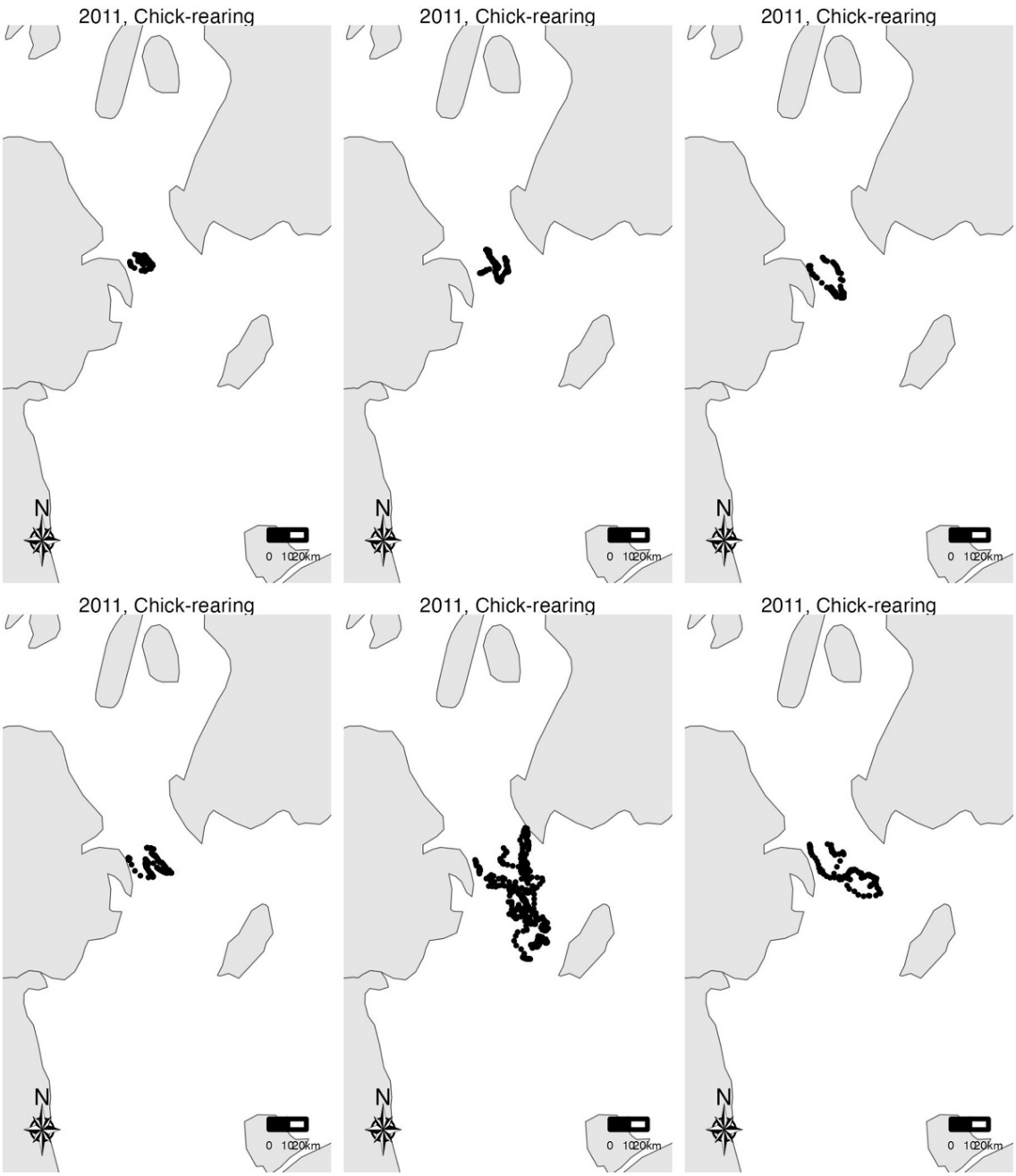
EL92637



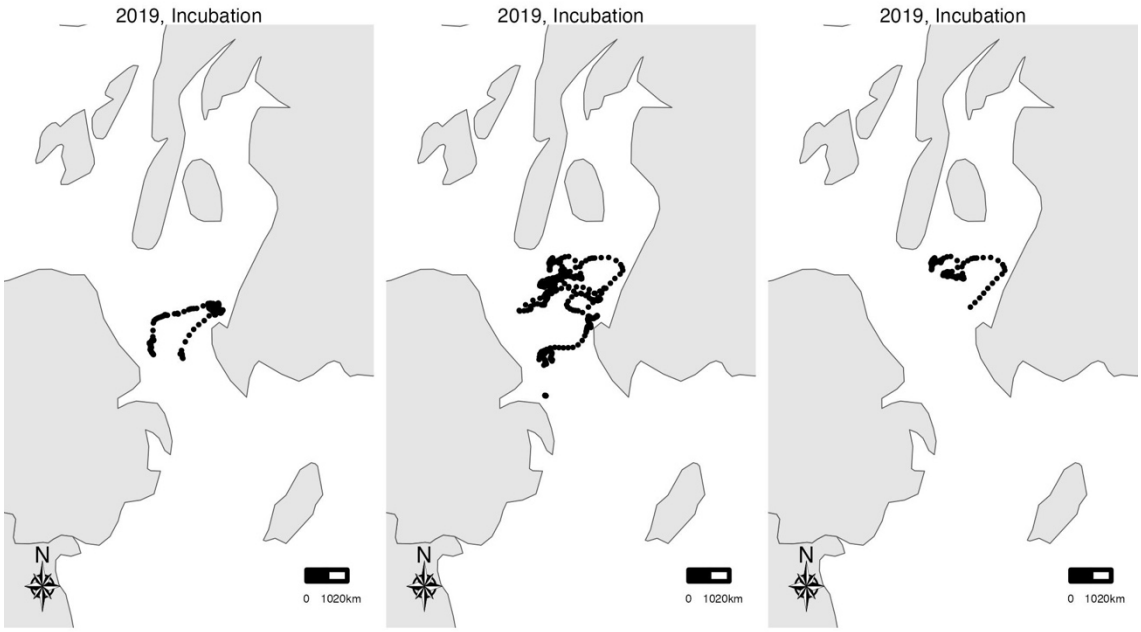
EL92680


2013, Chick-rearing
N
0 10 20km
2013, Chick-rearing
N
0 10 20km
2013, Chick-rearing
N
0 10 20km
2013, Chick-rearing
N
0 10 20km

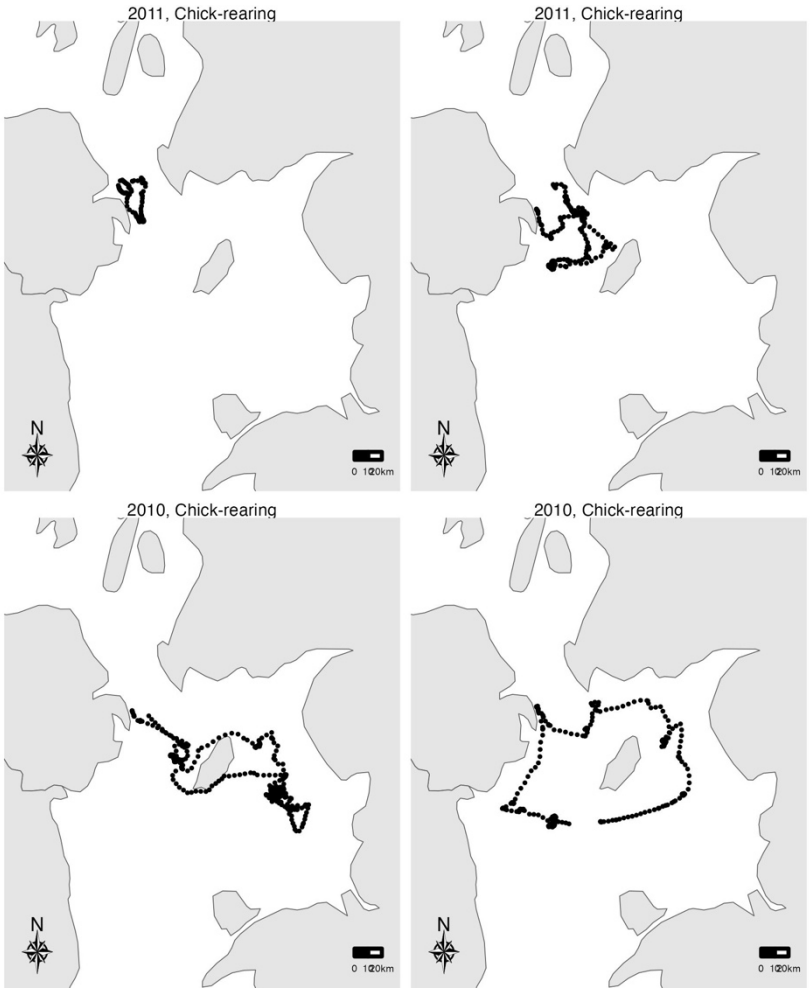
EN40606


2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
N
0 1020km

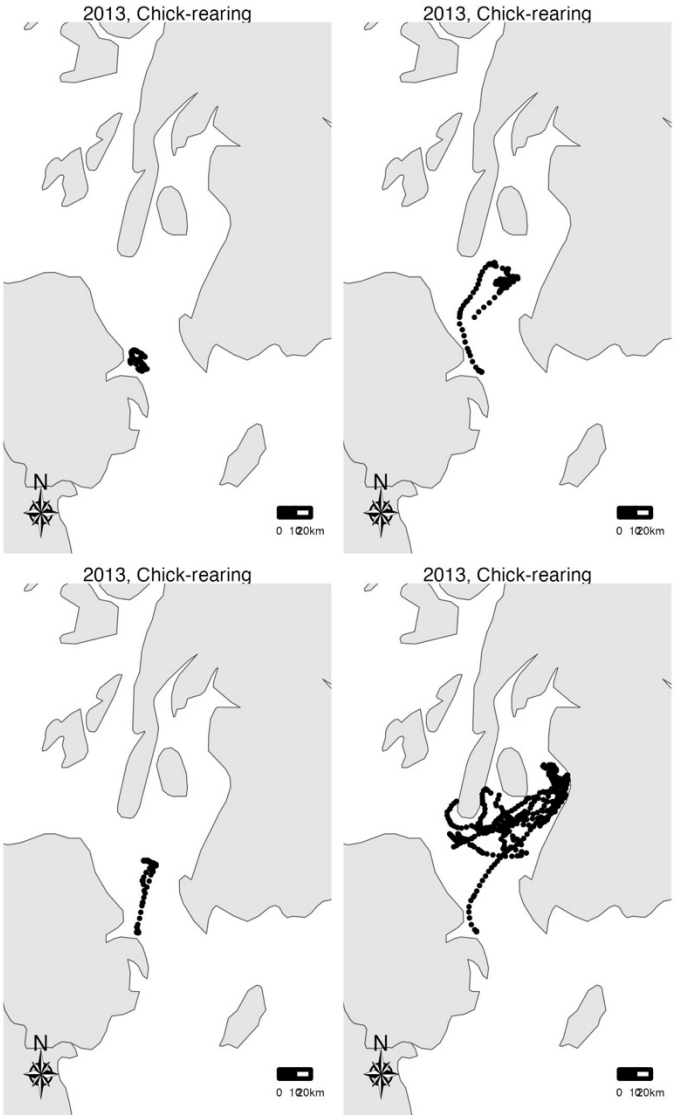
EN40728



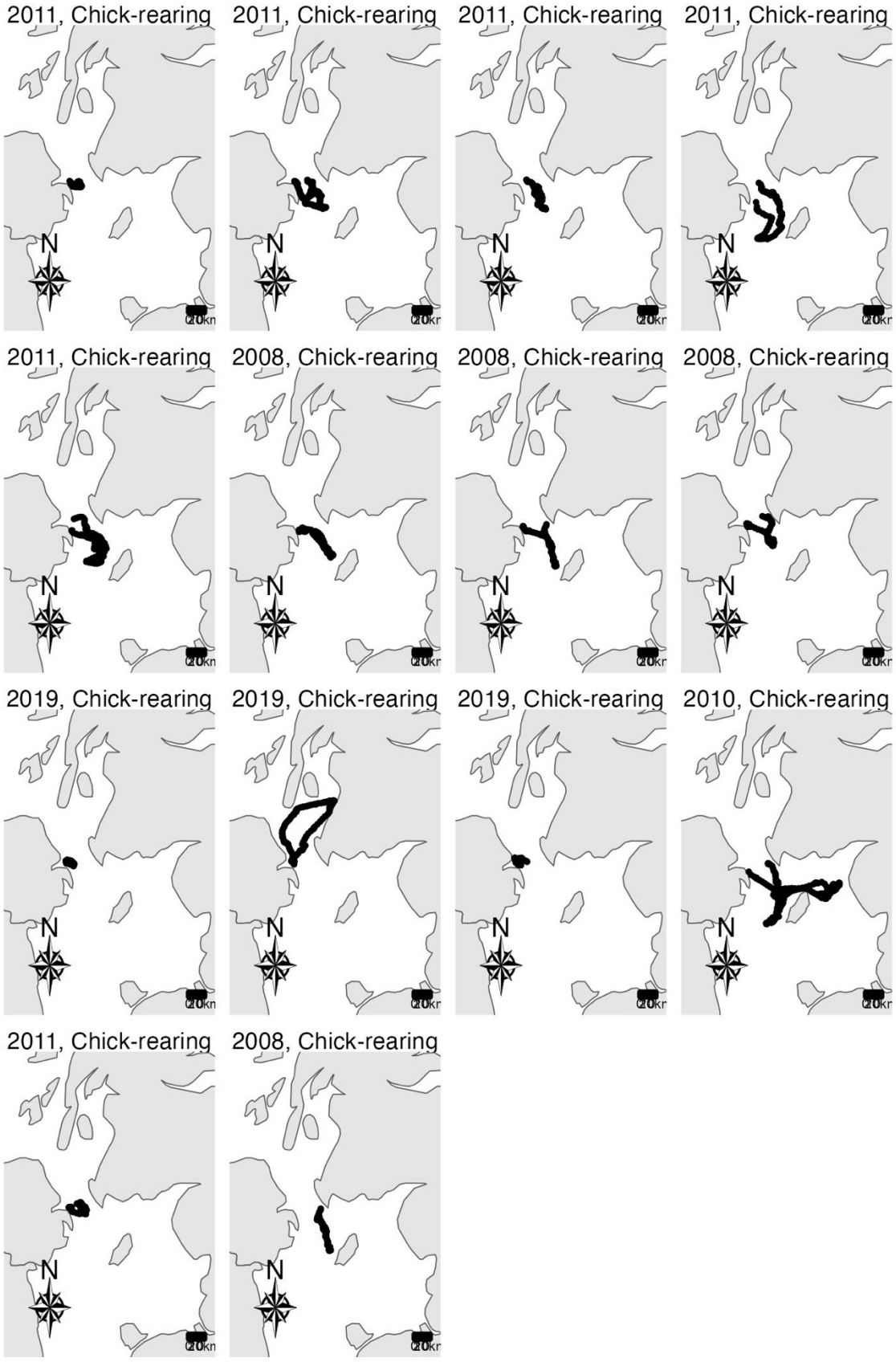
EN40781



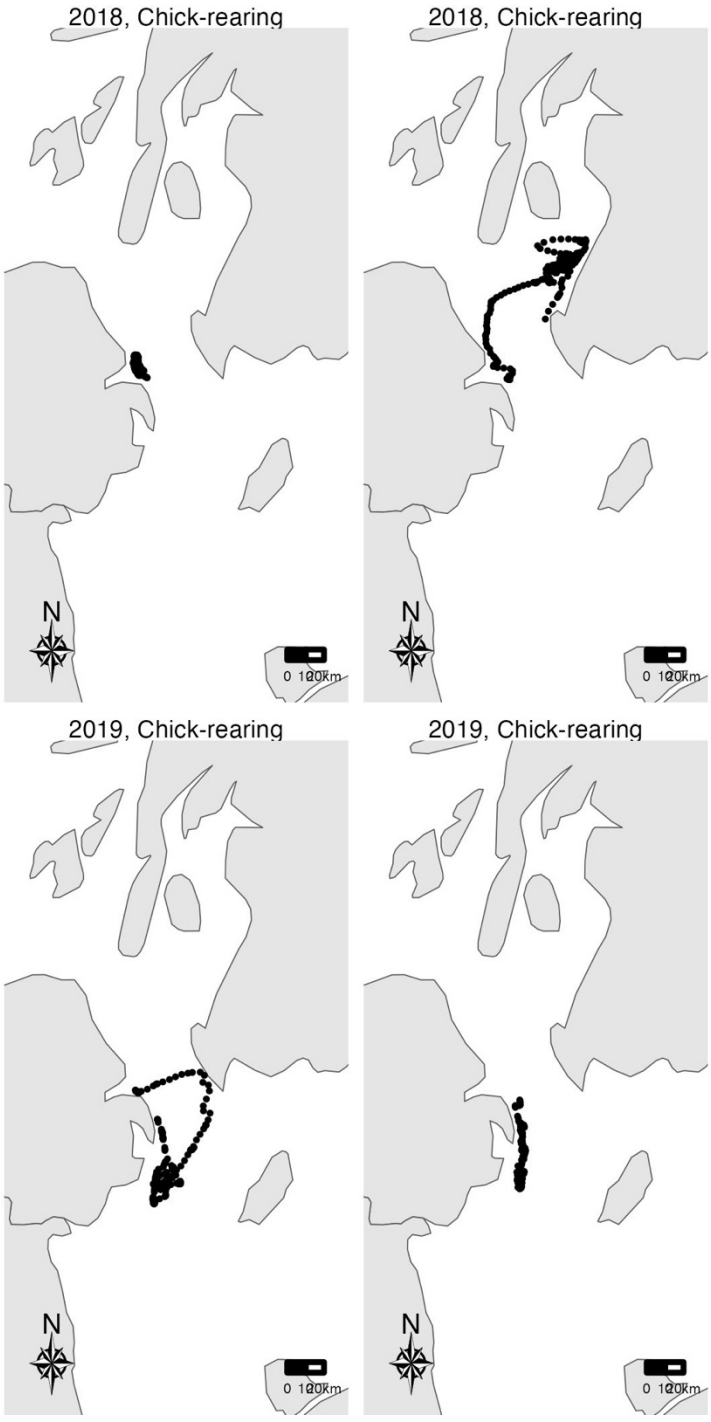
EN41585


2013, Chick-rearing
N
0 10 20km
2013, Chick-rearing
N
0 10 20km
2013, Chick-rearing
N
0 10 20km
2013, Chick-rearing
N
0 10 20km

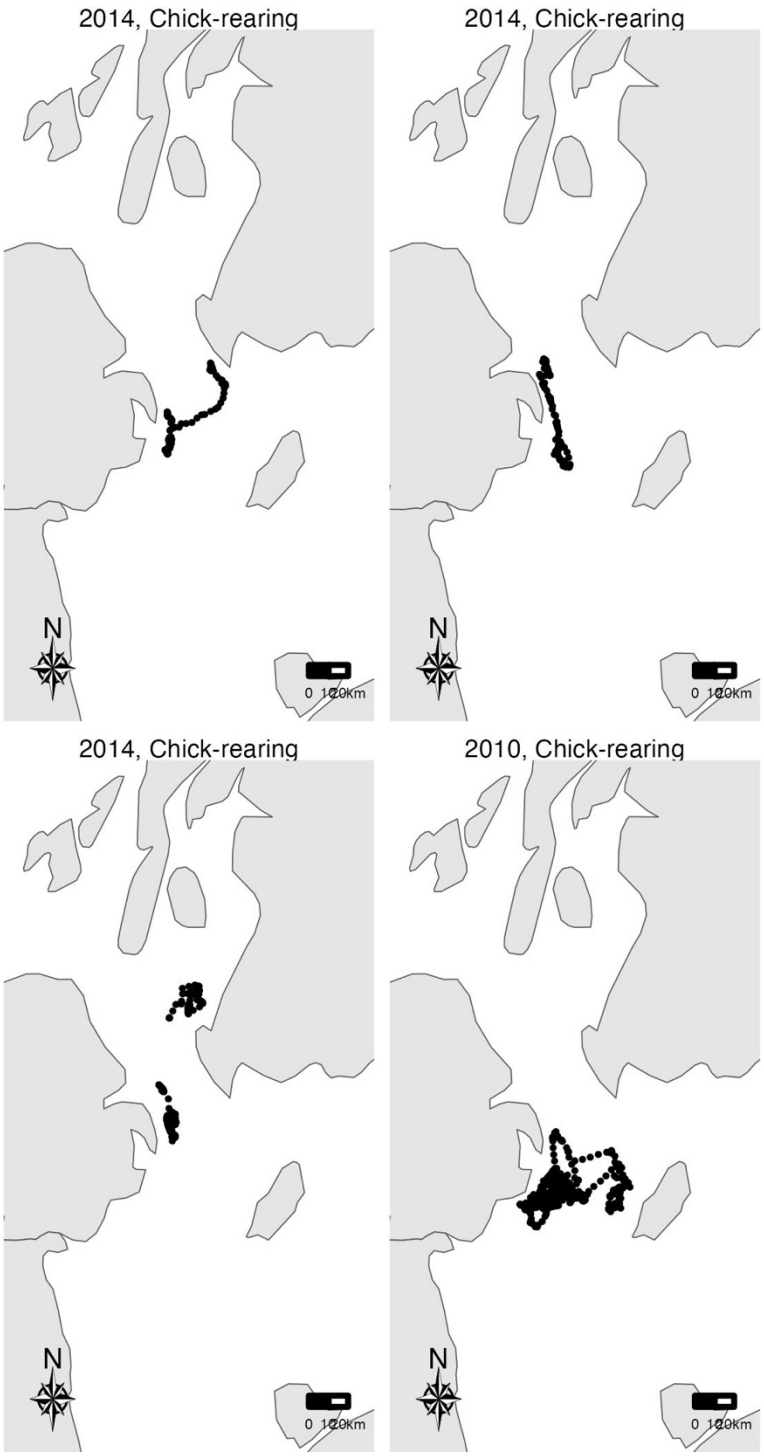
ER32302


2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2008, Chick-rearing
2008, Chick-rearing
2008, Chick-rearing
2019, Chick-rearing
2019, Chick-rearing
2019, Chick-rearing
2010, Chick-rearing
2011, Chick-rearing
2008, Chick-rearing
N

ER32400


2018, Chick-rearing
2018, Chick-rearing
2019, Chick-rearing
2019, Chick-rearing
N
0 100Km

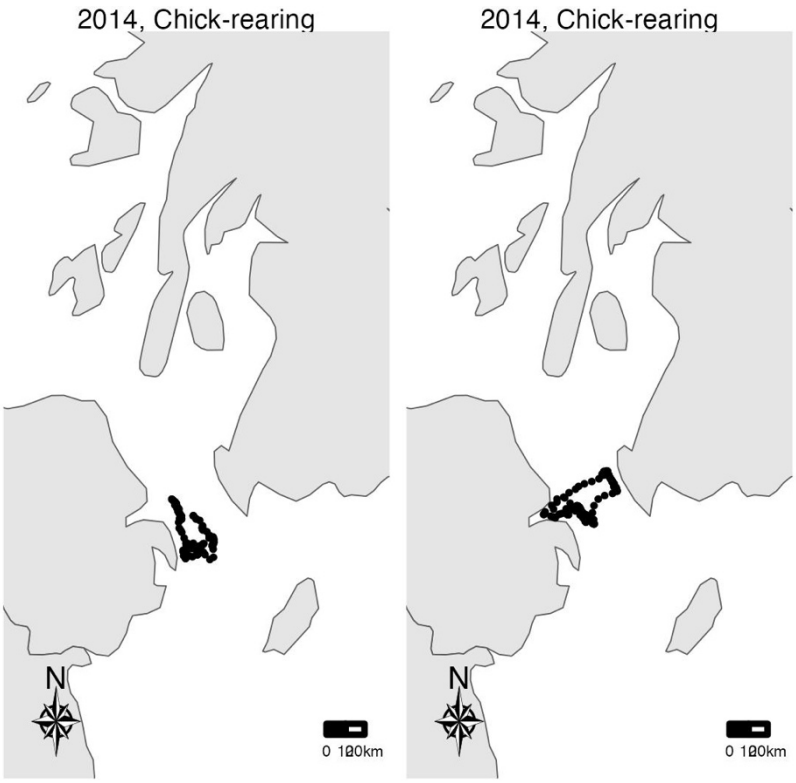
ER32877


2014, Chick-rearing
N
0 120km
2014, Chick-rearing
N
0 120km
2014, Chick-rearing
N
0 120km
2010, Chick-rearing
N
0 120km

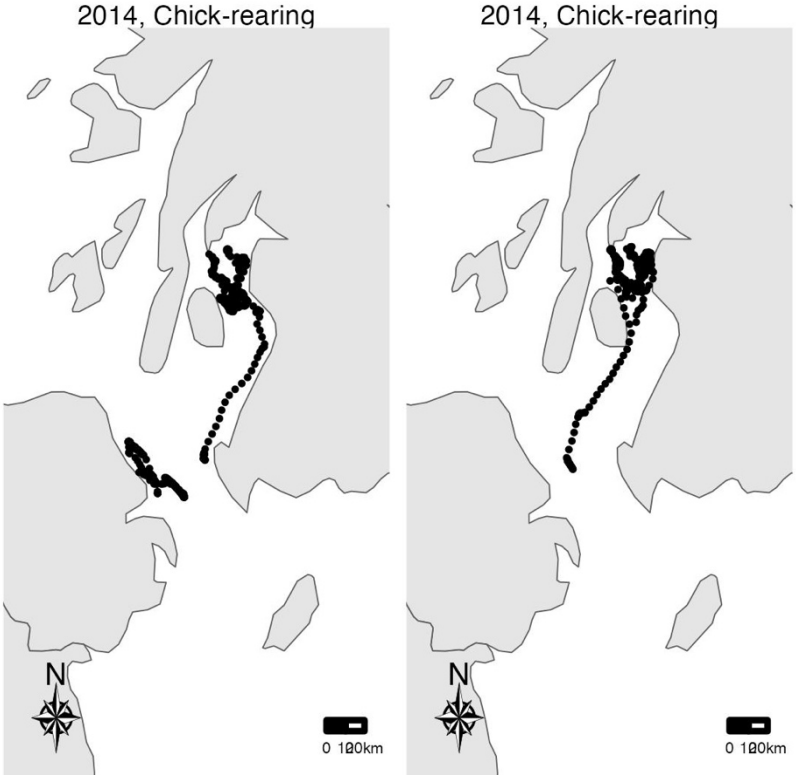
ER32917


2018, Incubation
2021, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2010, Chick-rearing
2010, Chick-rearing
2019, Chick-rearing
2019, Chick-rearing
N

ER33064

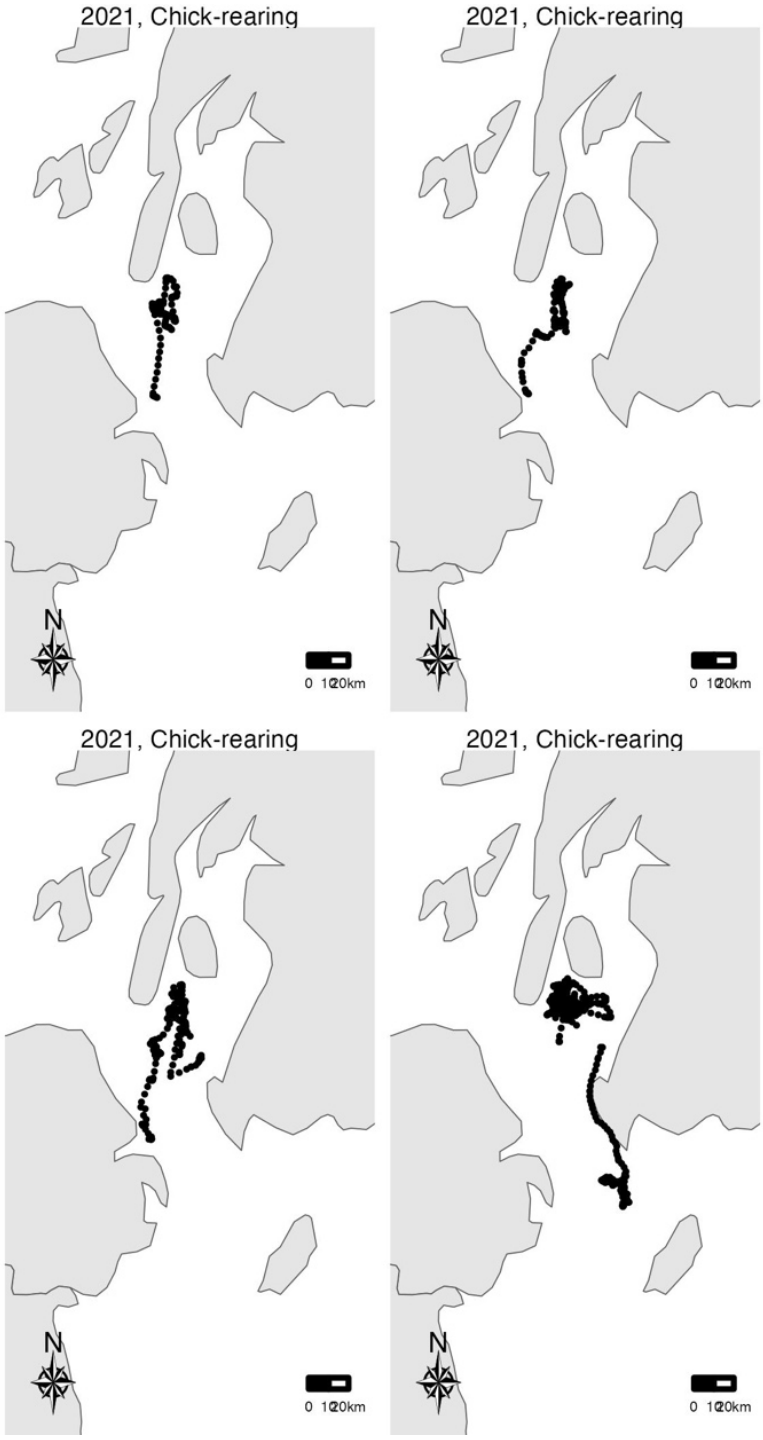

2014, Chick-rearing
N
0 120km

2014, Chick-rearing
N
0 120km

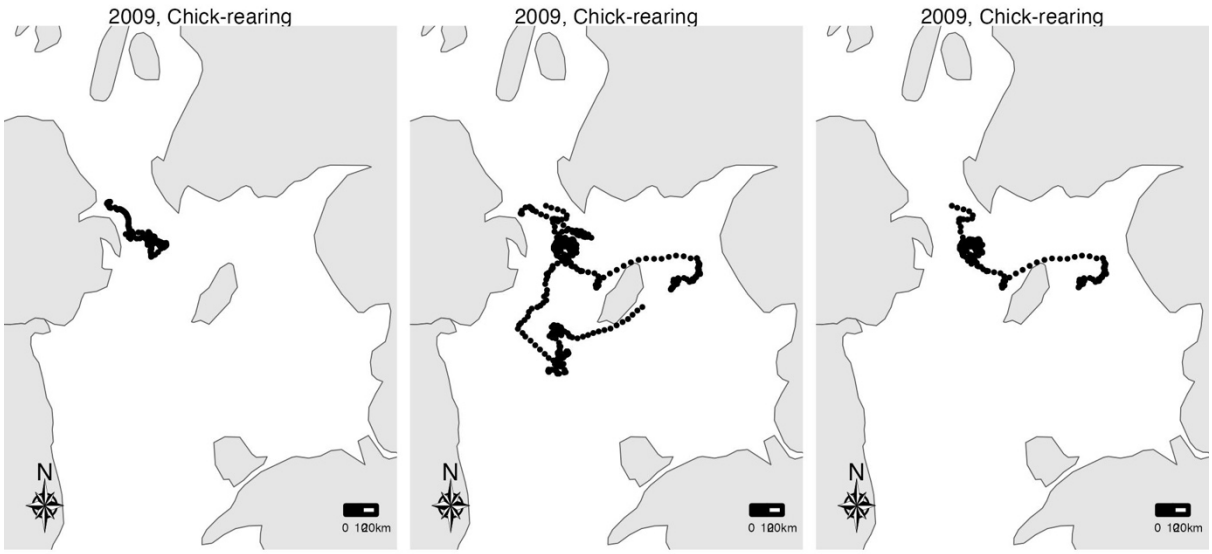

2014, Chick-rearing
N
0 120km

2014, Chick-rearing
N
0 120km

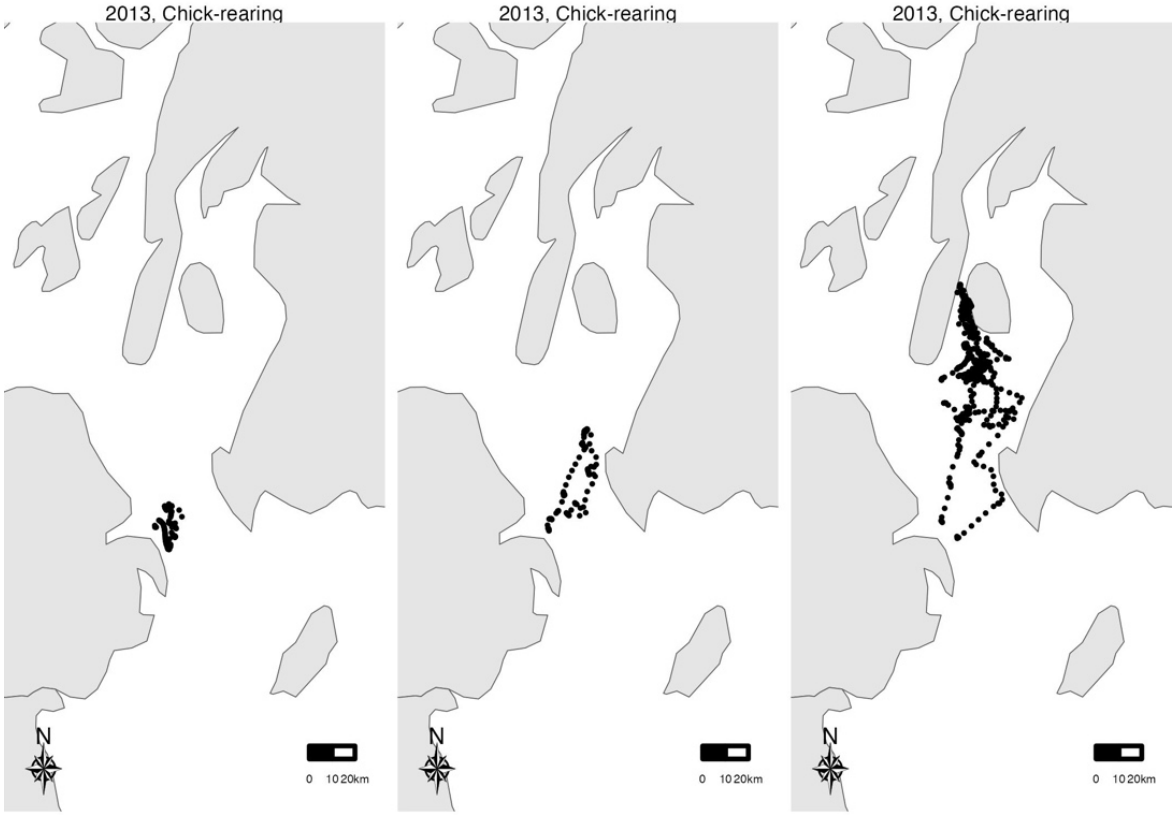
ER33520


2021, Chick-rearing
N
0 10 20km
2021, Chick-rearing
N
0 10 20km
2021, Chick-rearing
N
0 10 20km
2021, Chick-rearing
N
0 10 20km

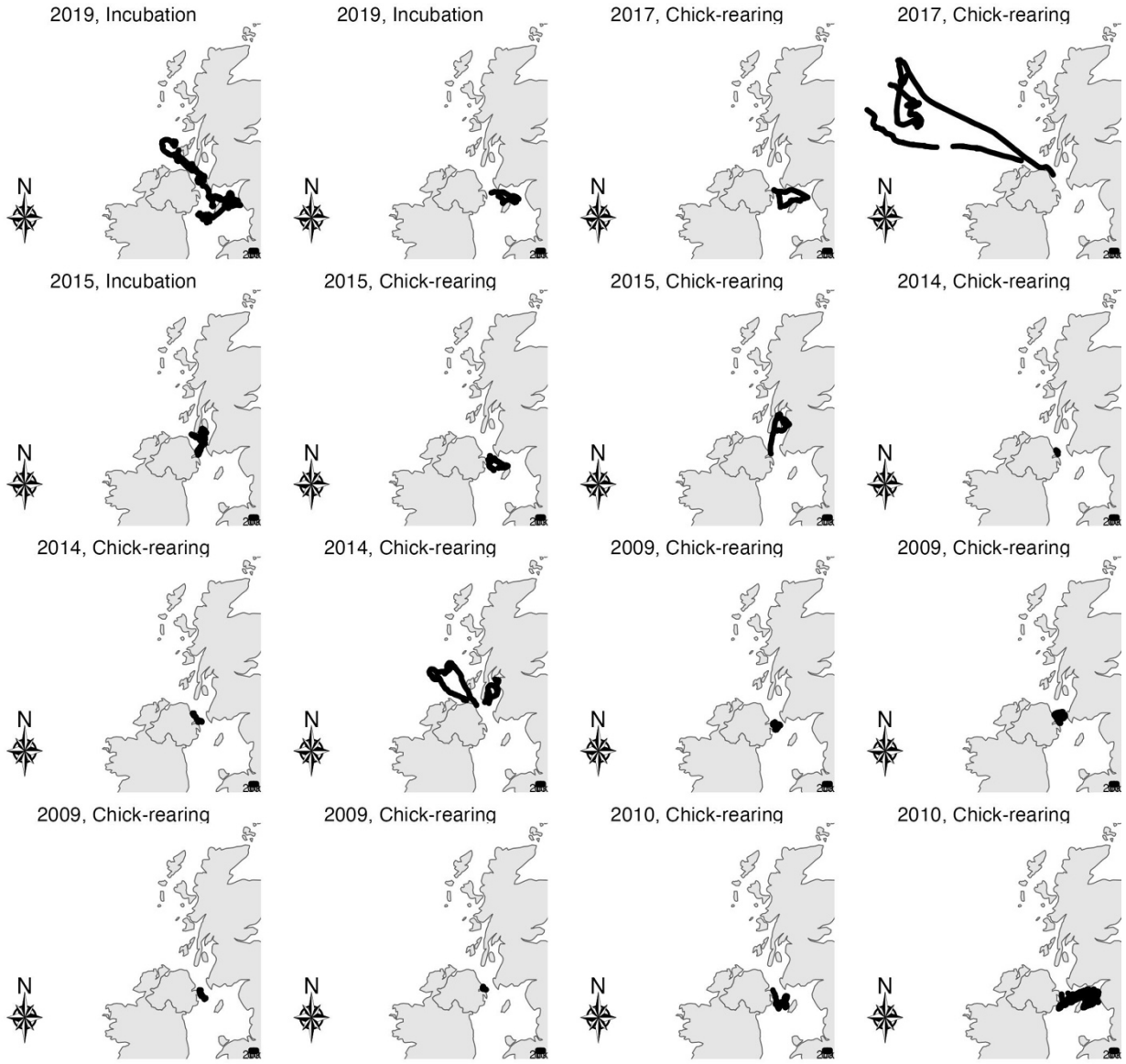
ER33585



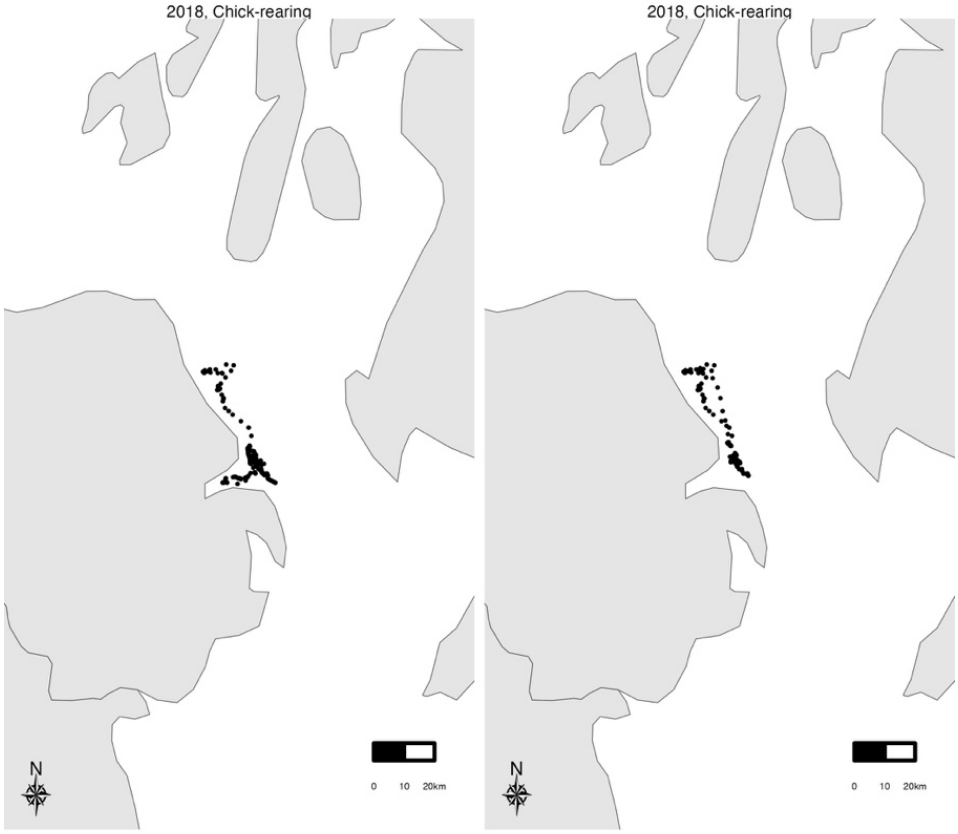
ER33809



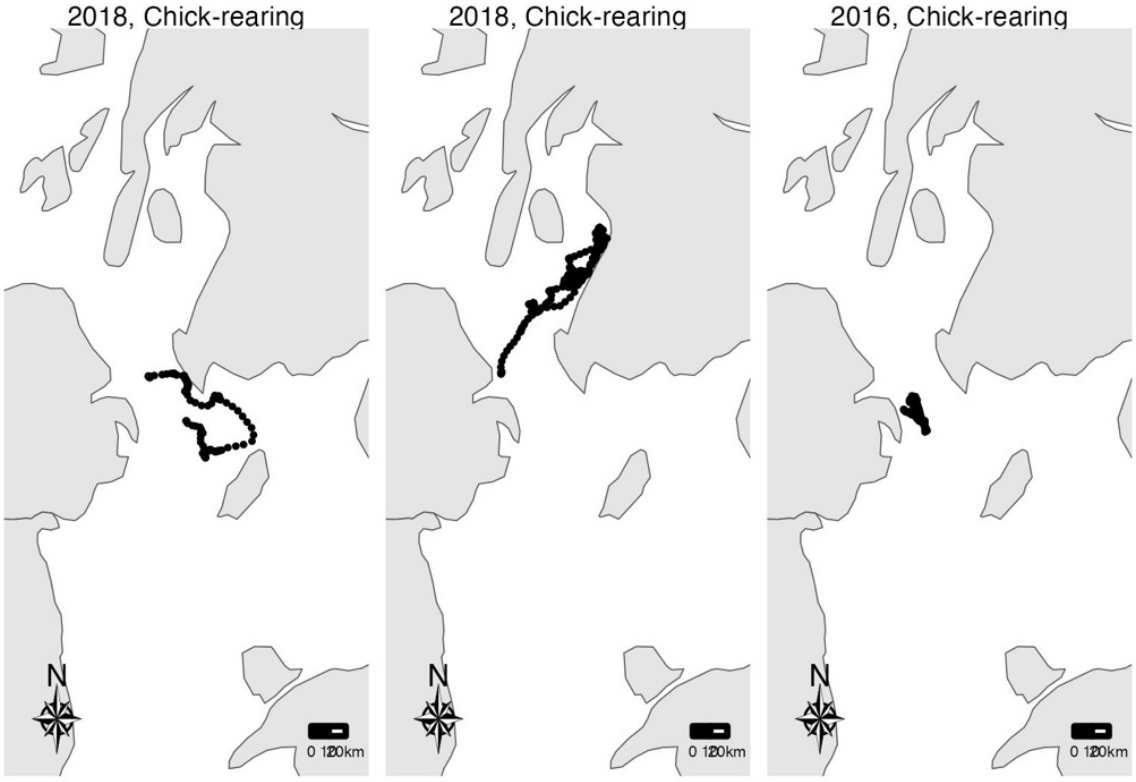
ES11008

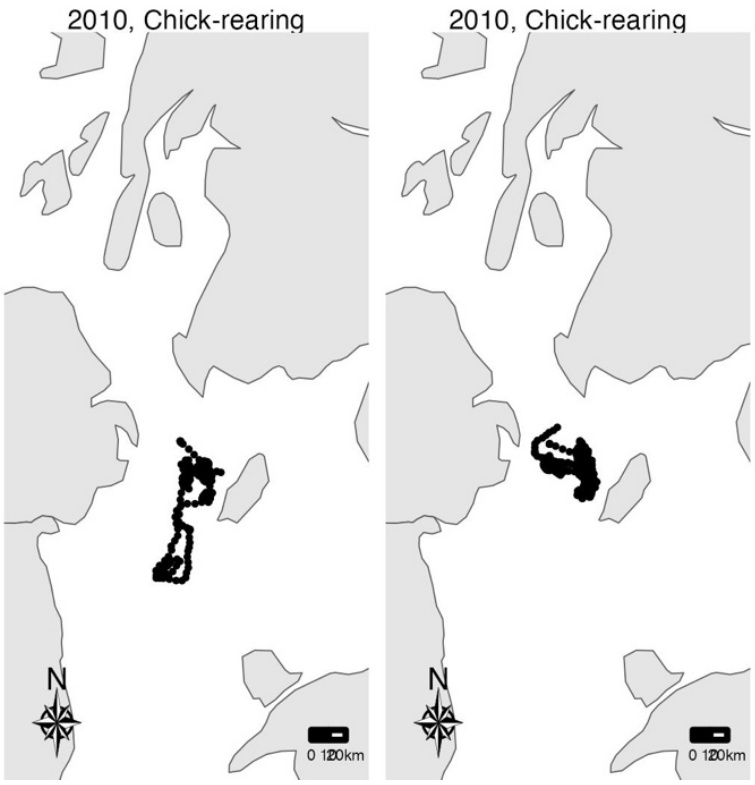

2019, Incubation
2019, Incubation
2017, Chick-rearing
2017, Chick-rearing
2015, Incubation
2015, Chick-rearing
2015, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2010, Chick-rearing
2010, Chick-rearing
N

ES11126

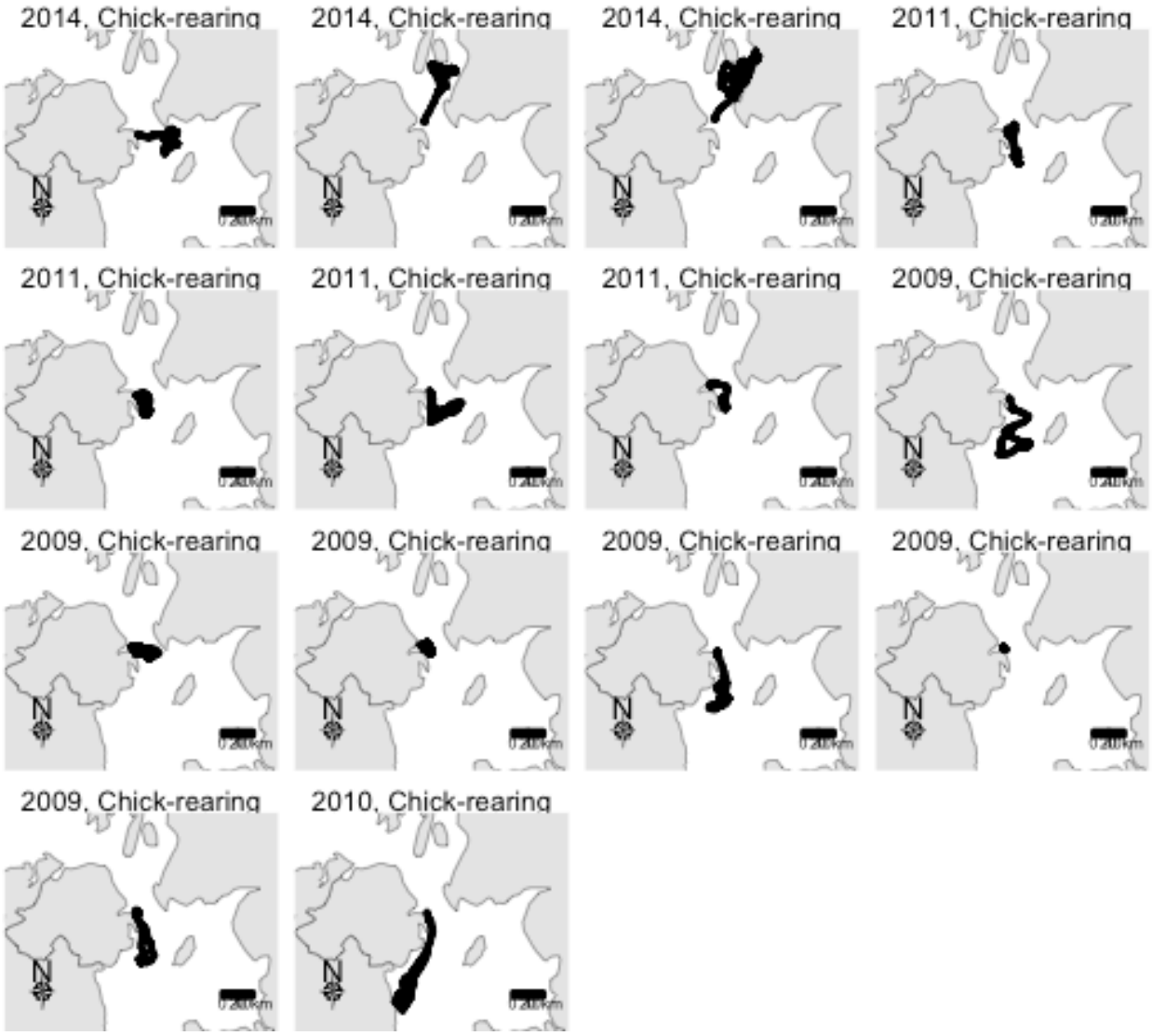


ES11339


2018, Chick-rearing
2018, Chick-rearing
2016, Chick-rearing
N
0 120km

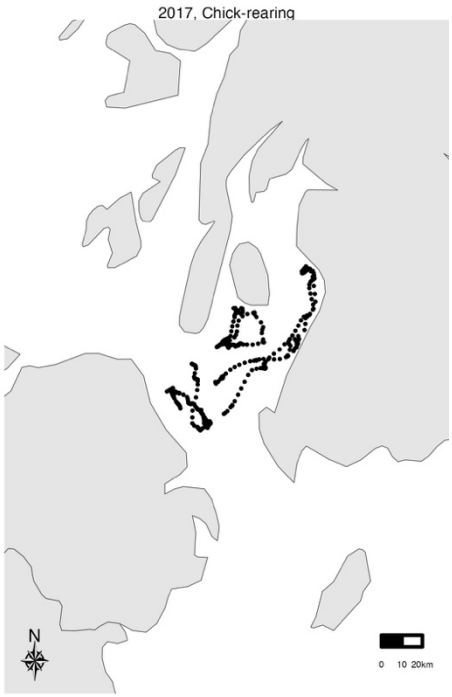

2010, Chick-rearing
2010, Chick-rearing
N
0 120km

ES11902

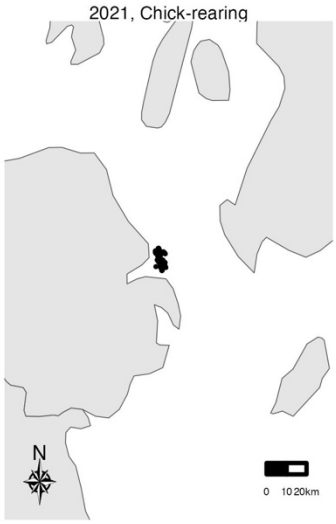

2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2010, Chick-rearing

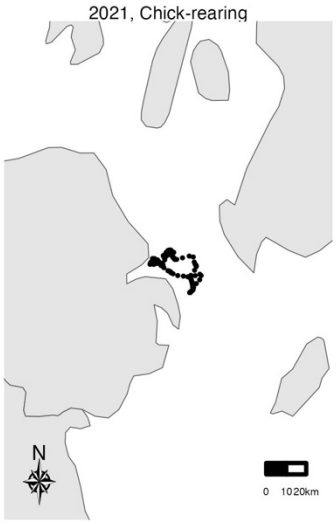
ES11999

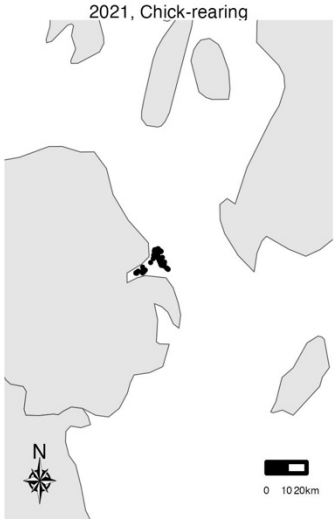


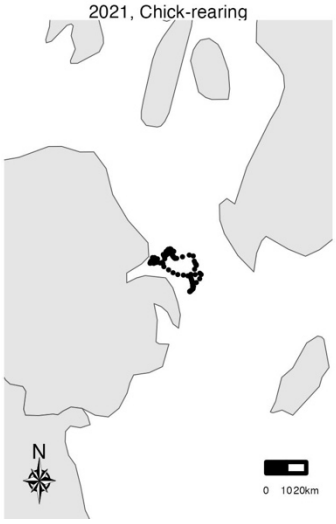


ES61047





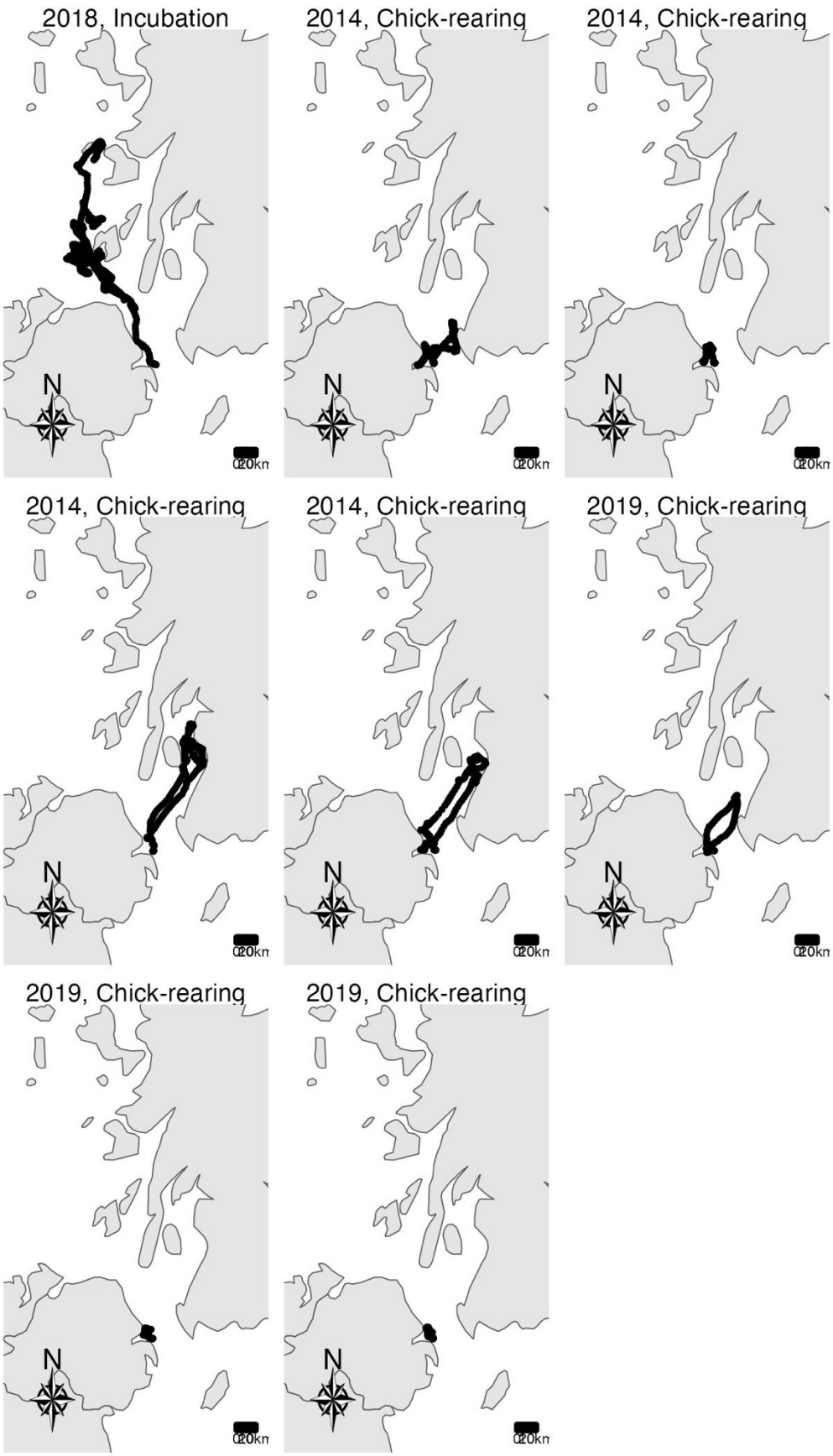




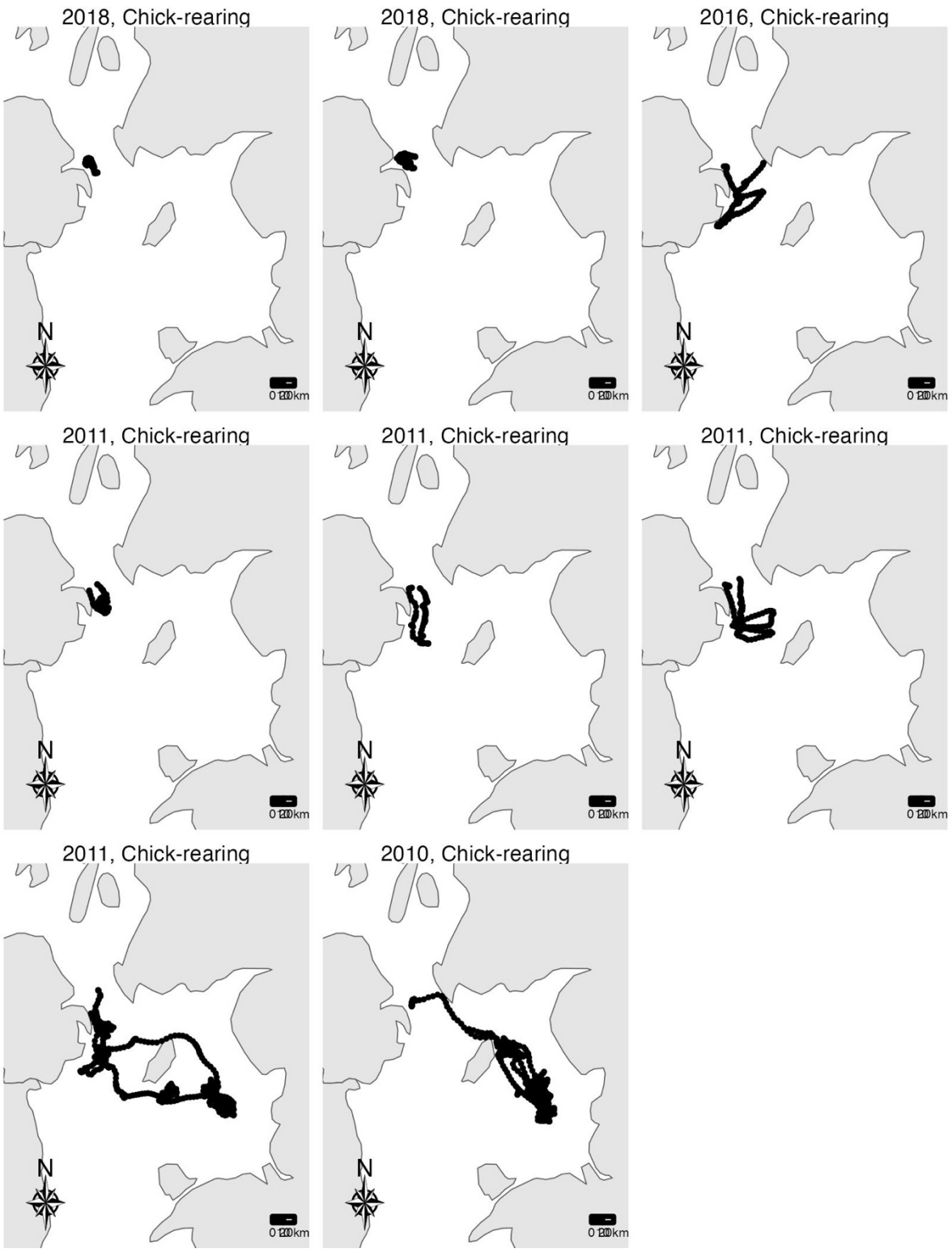
ET00079


2018, Chick-rearing
2018, Chick-rearing
2017, Chick-rearing
2017, Chick-rearing
2017, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2009, Chick-rearing
2010, Chick-rearing
2018, Chick-rearing
N
0 20km

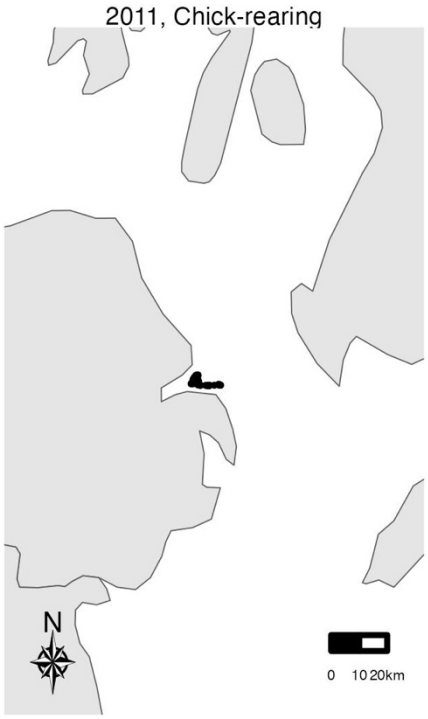
ET00289

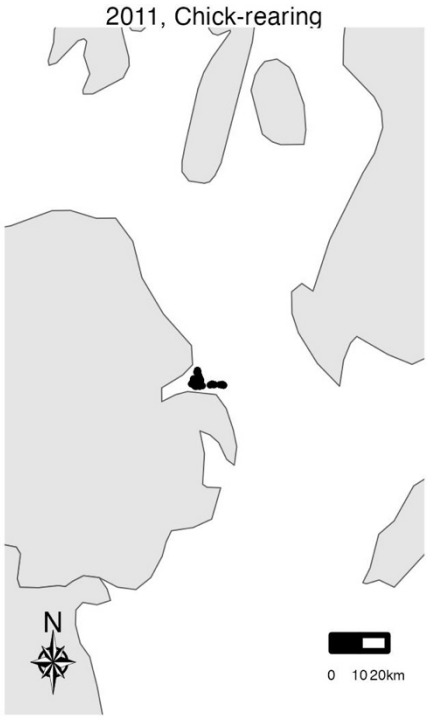

2018, Incubation
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2019, Chick-rearing
2019, Chick-rearing
2019, Chick-rearing
N
0 20km

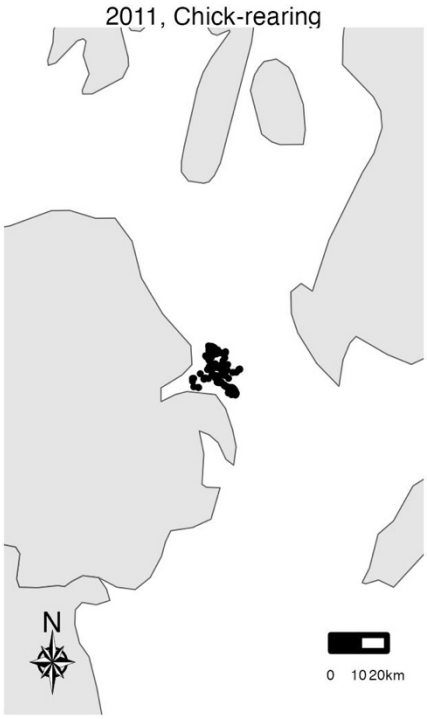
ET00604

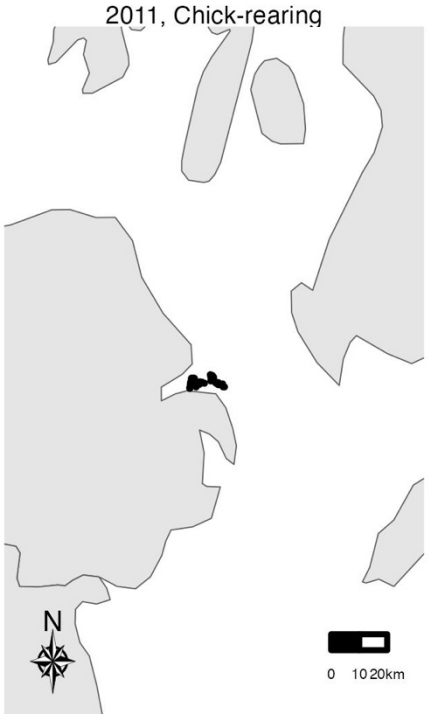

2018, Chick-rearing
2018, Chick-rearing
2016, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2011, Chick-rearing
2010, Chick-rearing
N
0 120 240 km

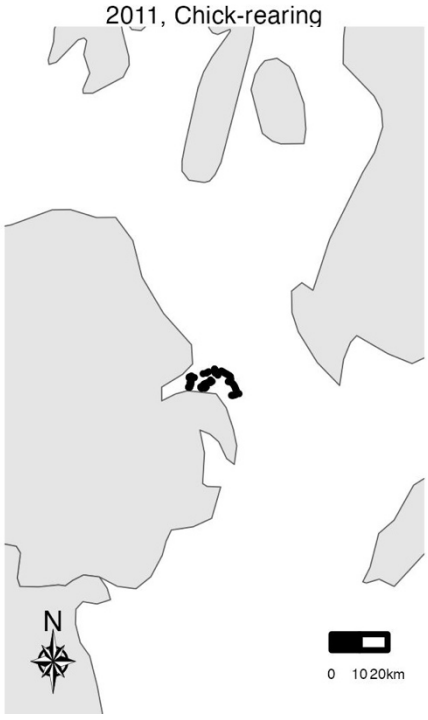
ET00717


2011, Chick-rearing
N
0 10 20km

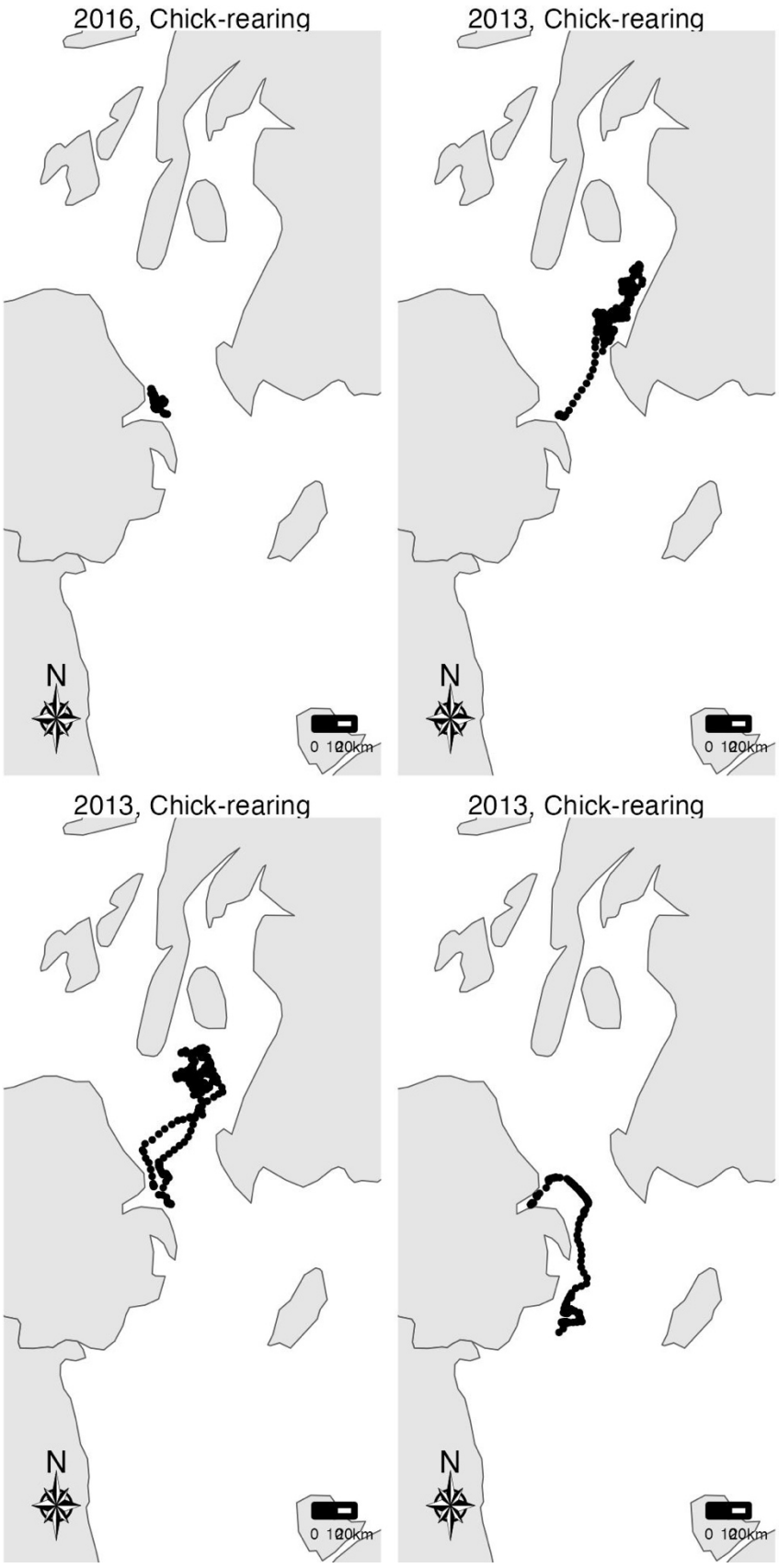

2011, Chick-rearing
N
0 10 20km


2011, Chick-rearing
N
0 10 20km

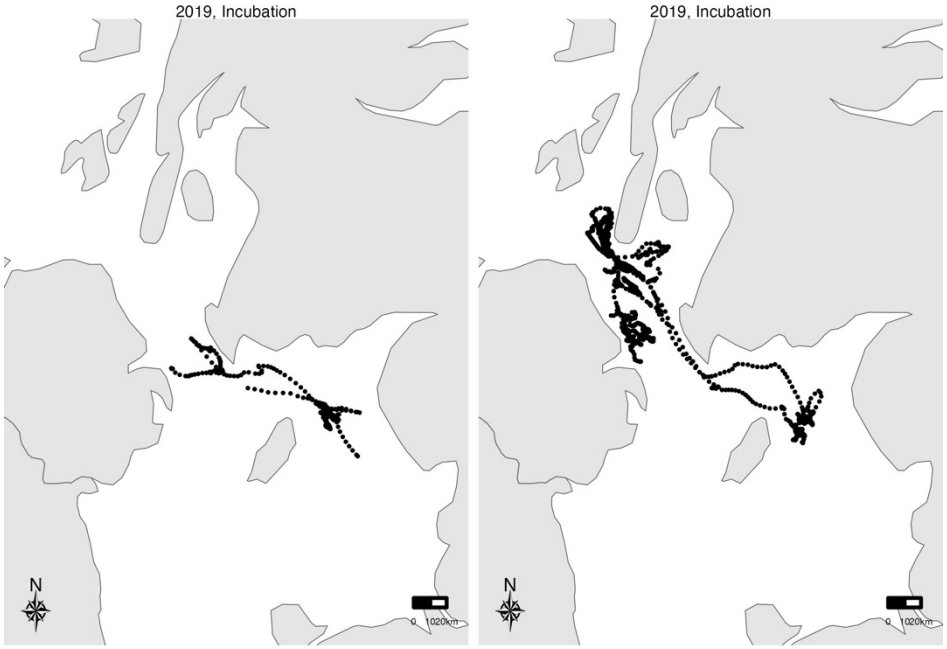

2011, Chick-rearing
N
0 10 20km


2011, Chick-rearing
N
0 10 20km

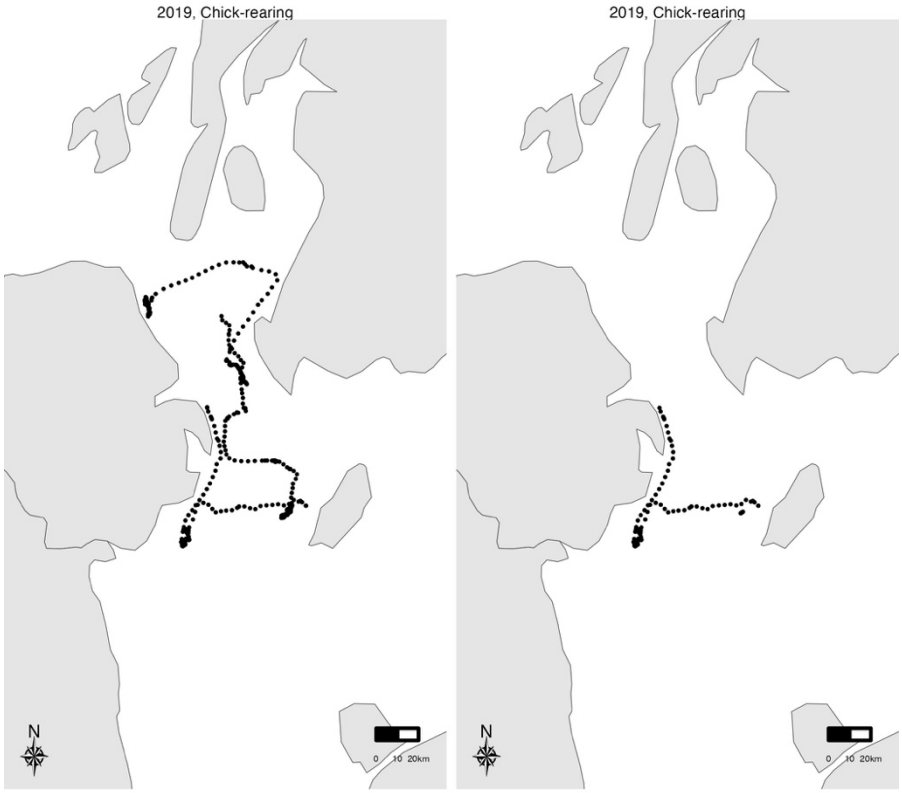
ET00739


2016, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
N
0 120km

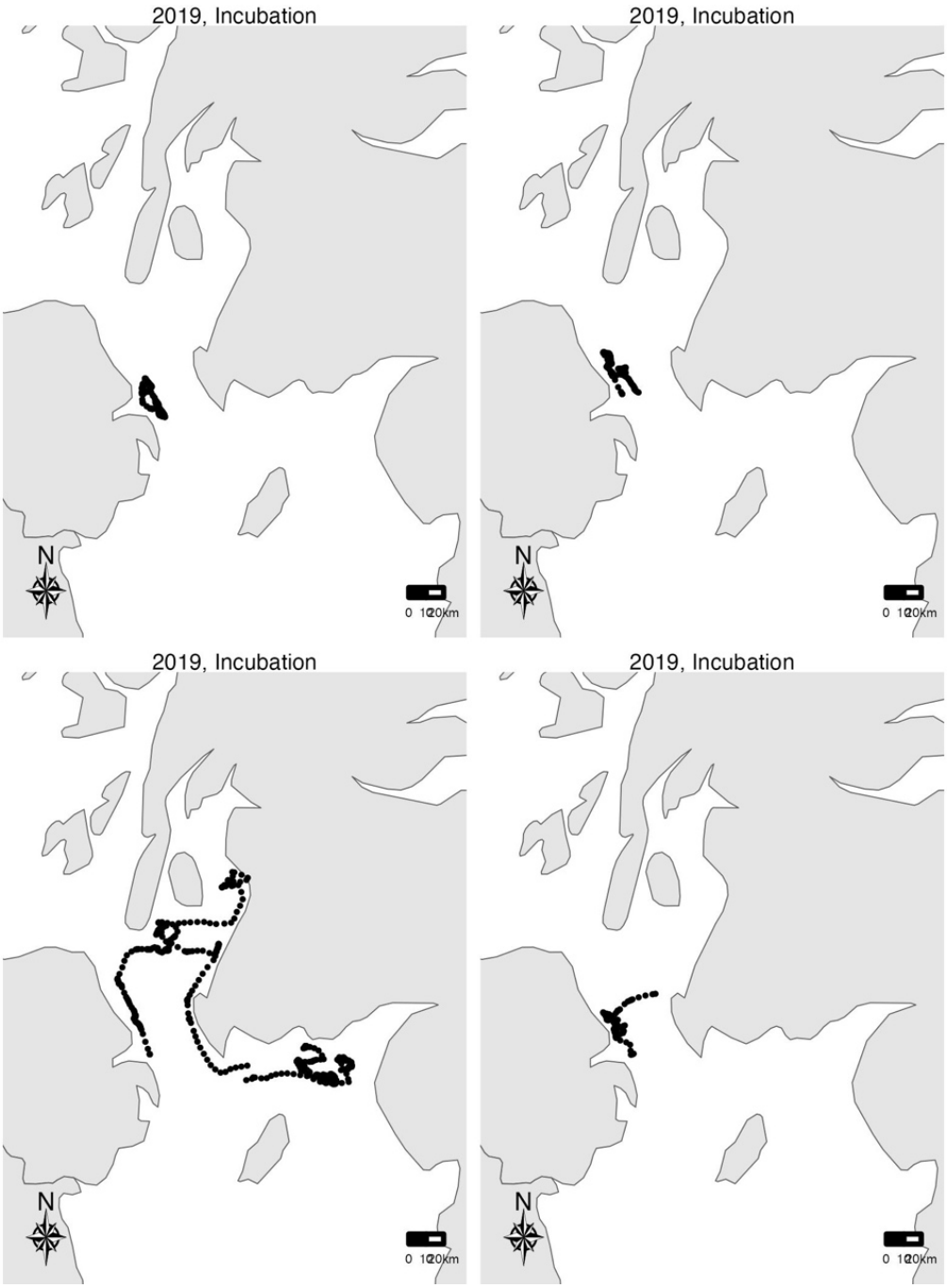
ET00935



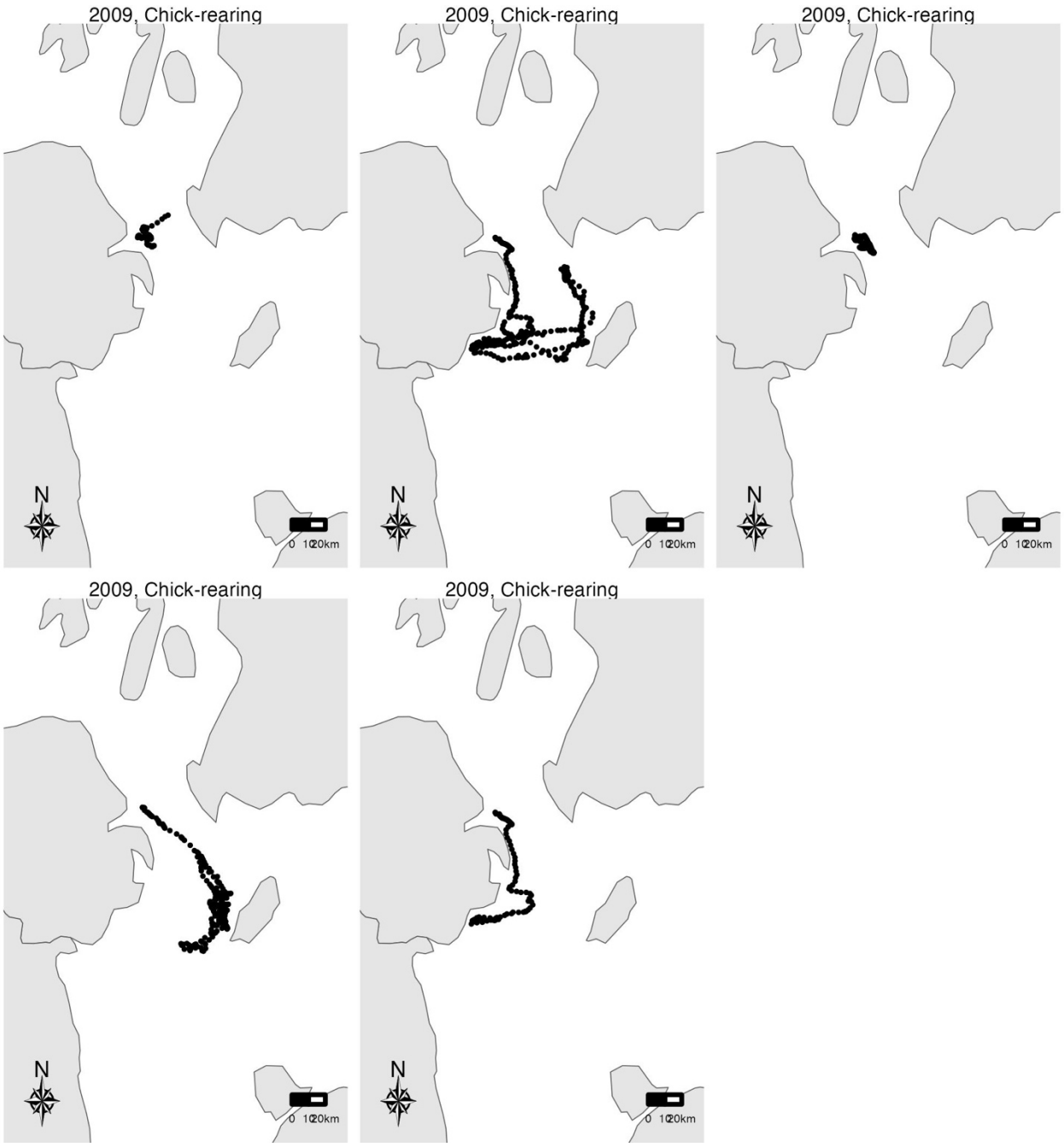
ET00957



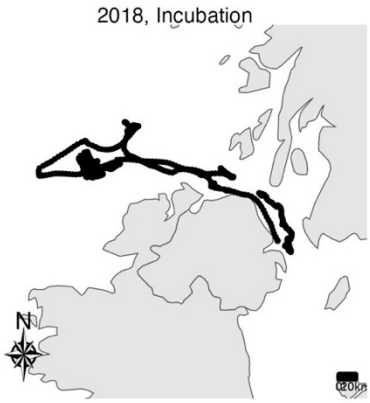
ET01125

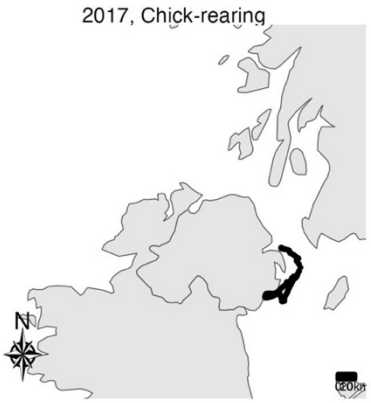

2019, Incubation
2019, Incubation
2019, Incubation
2019, Incubation
N
0 120km

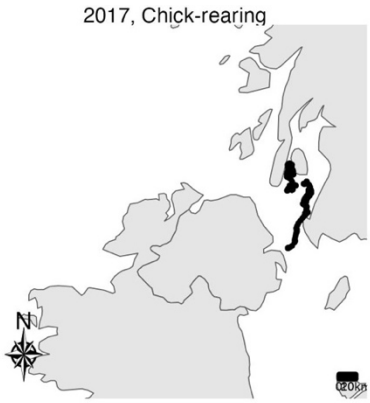
ET01379


2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km
2009, Chick-rearing
N
0 10 20km

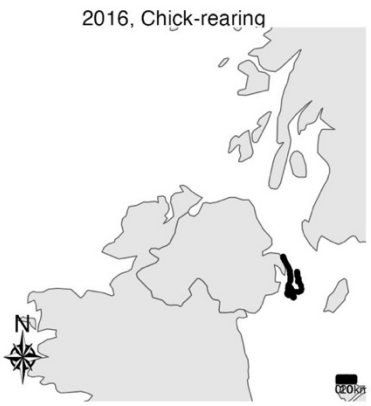
ET01468

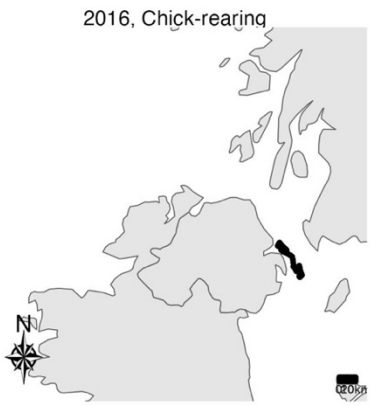

2018, Incubation
N
20km

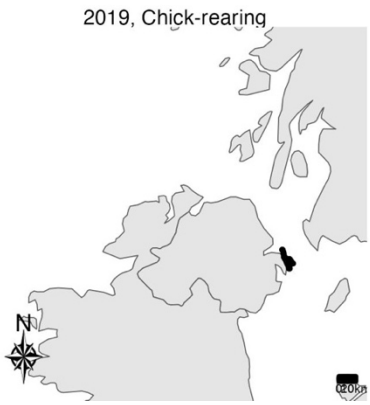

2017, Chick-rearing
N
20km


2017, Chick-rearing
N
20km

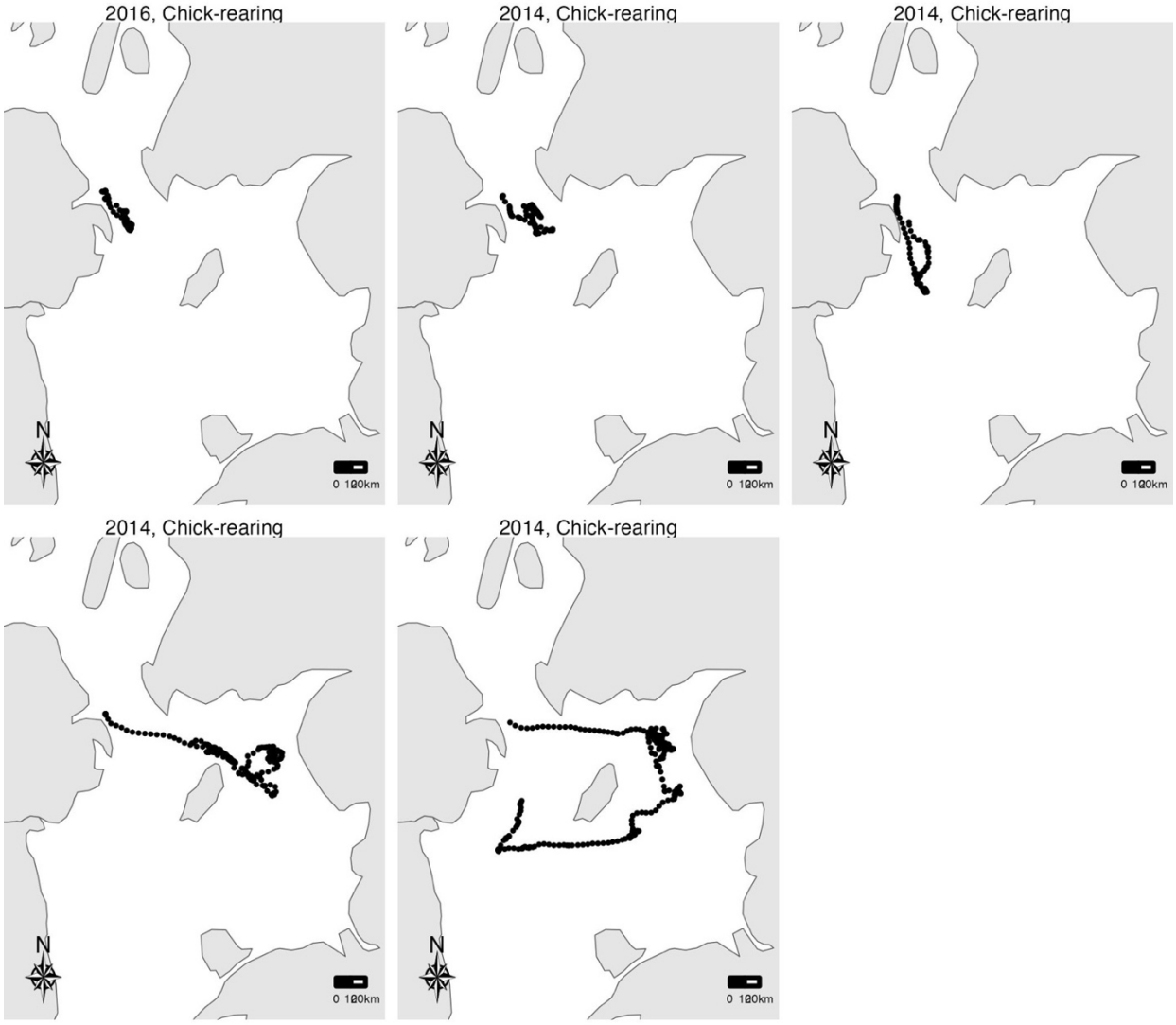

2016, Chick-rearing
N
20km


2016, Chick-rearing
N
20km

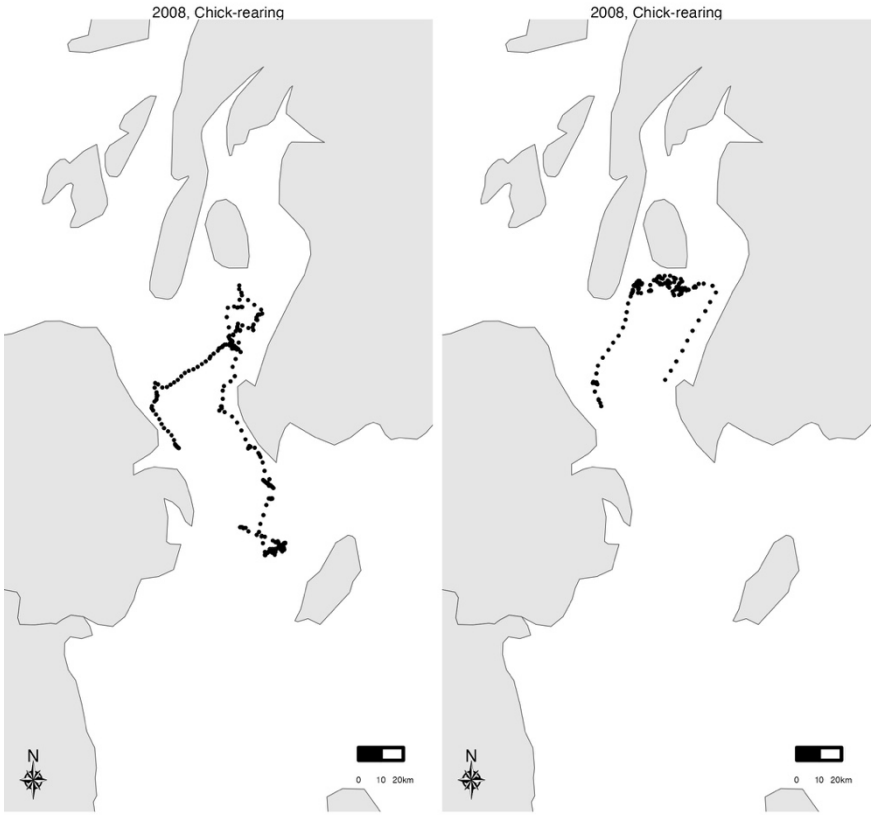

2016, Chick-rearing
N
20km


2019, Chick-rearing
N
20km

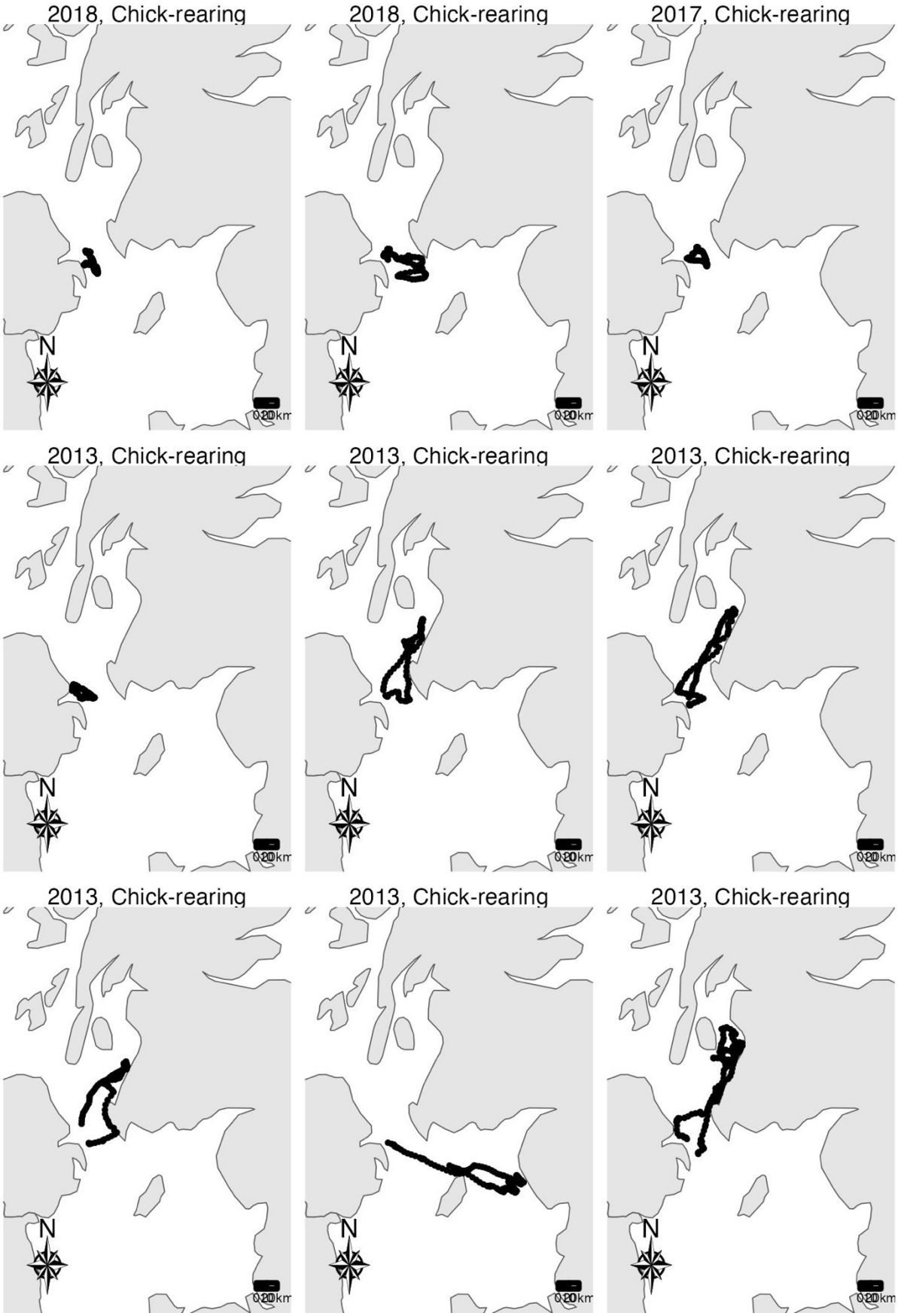
ET01506


2016, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
N
0 100km

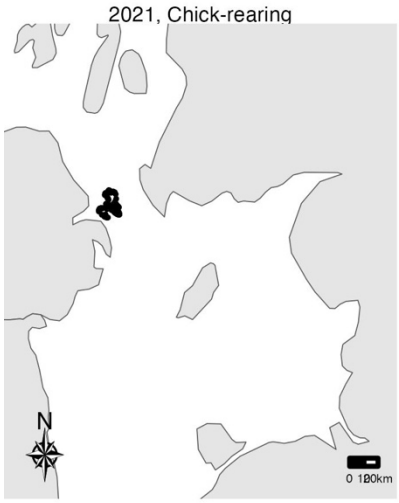
ET01744

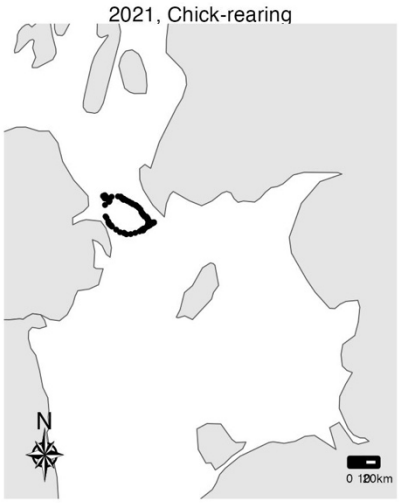


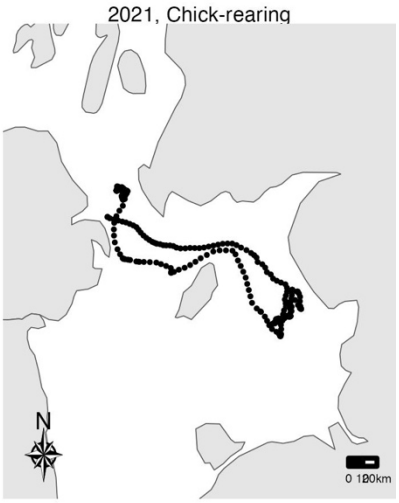
ET01819


2018, Chick-rearing
2018, Chick-rearing
2017, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
2013, Chick-rearing
N
0 20 km

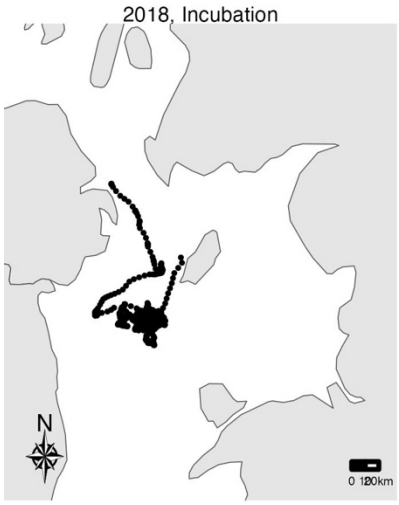
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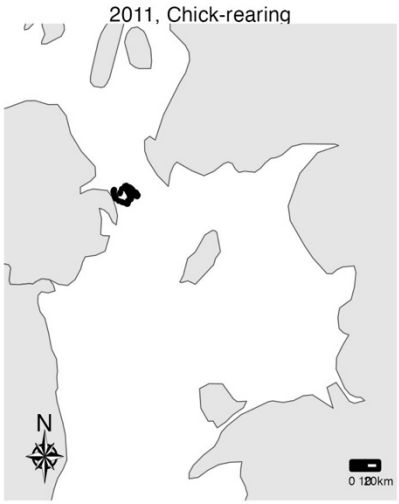




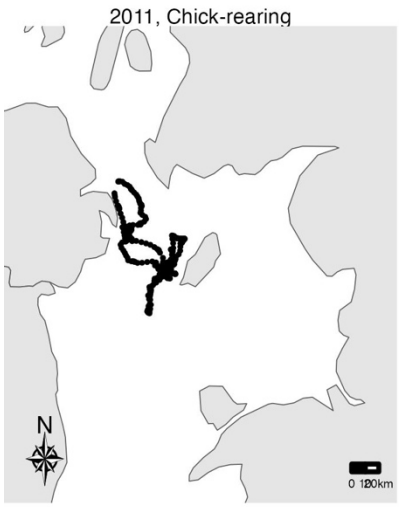


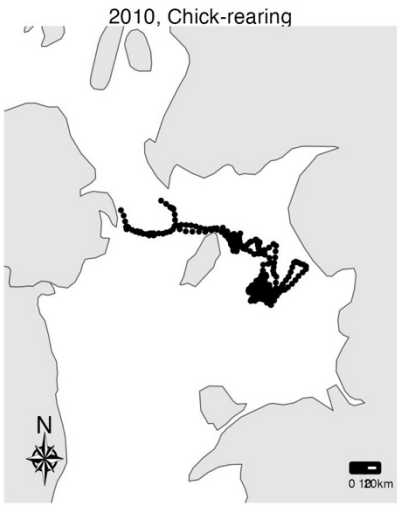
ET02264



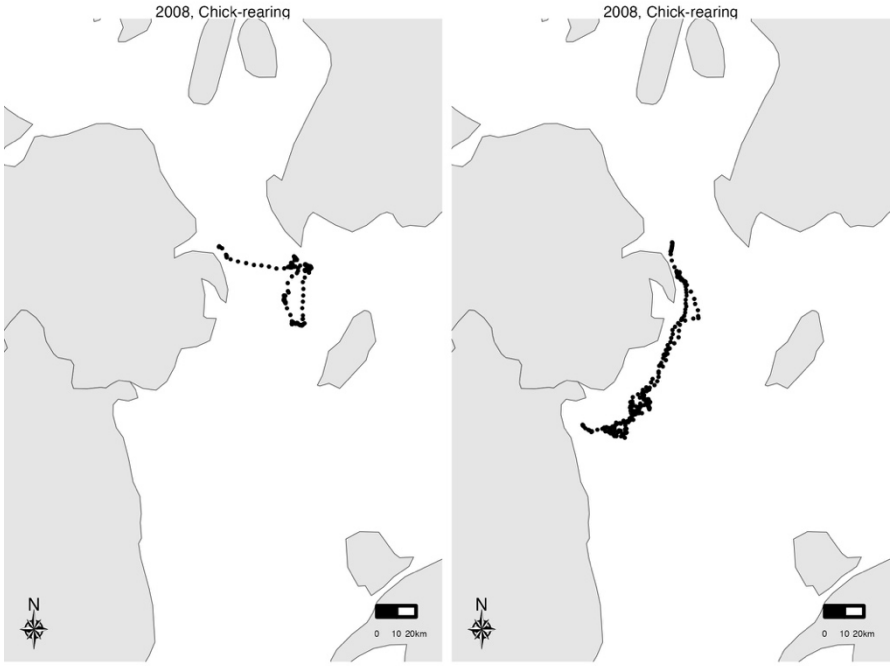




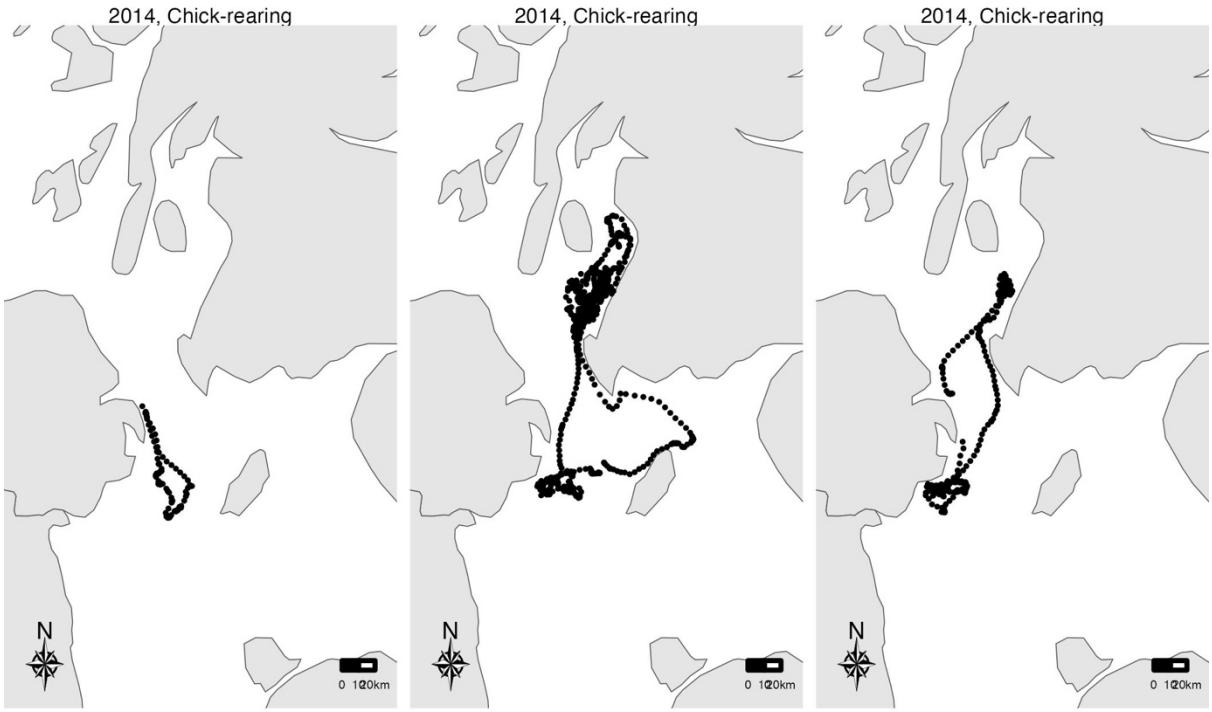




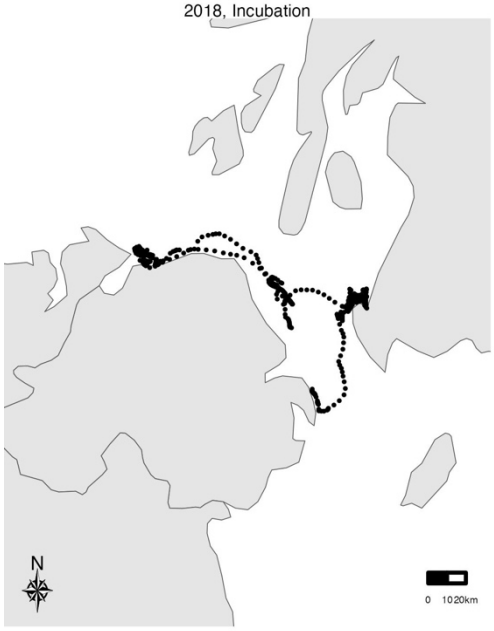
ET02445

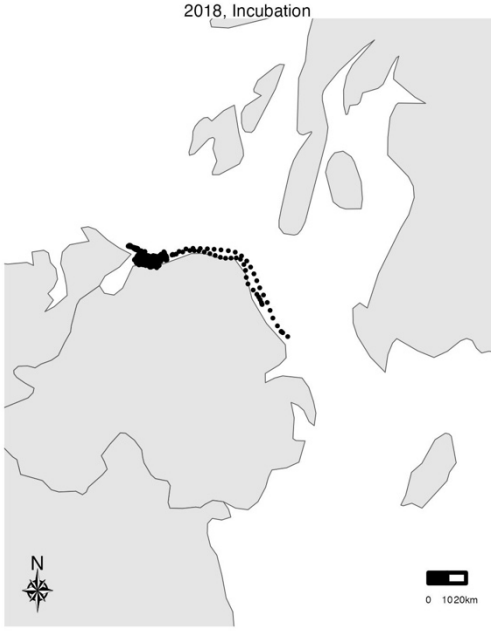


ET02708

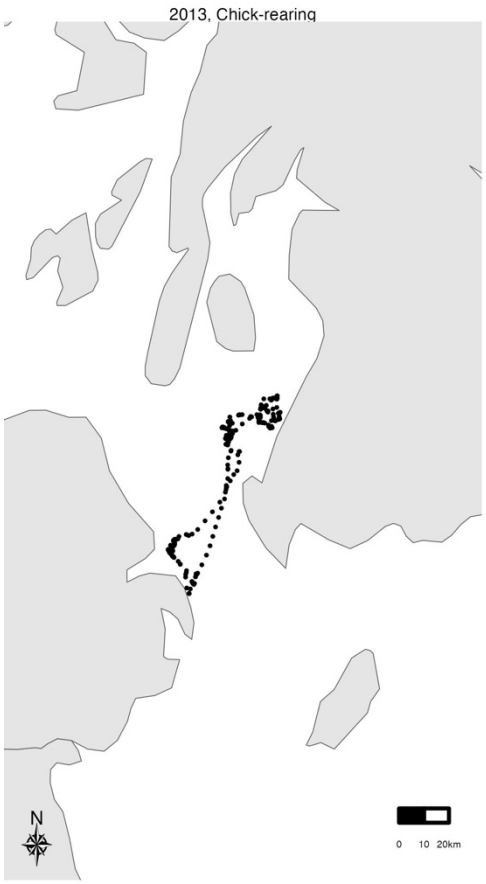


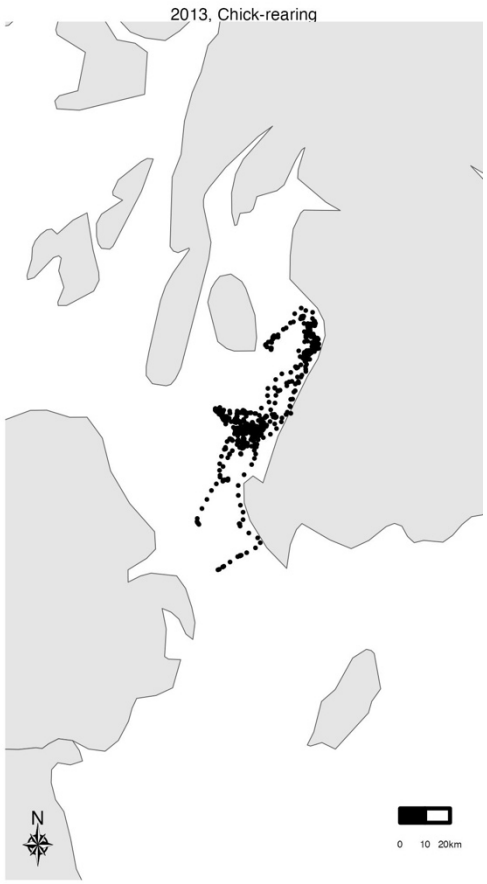
ET013165





EW82387

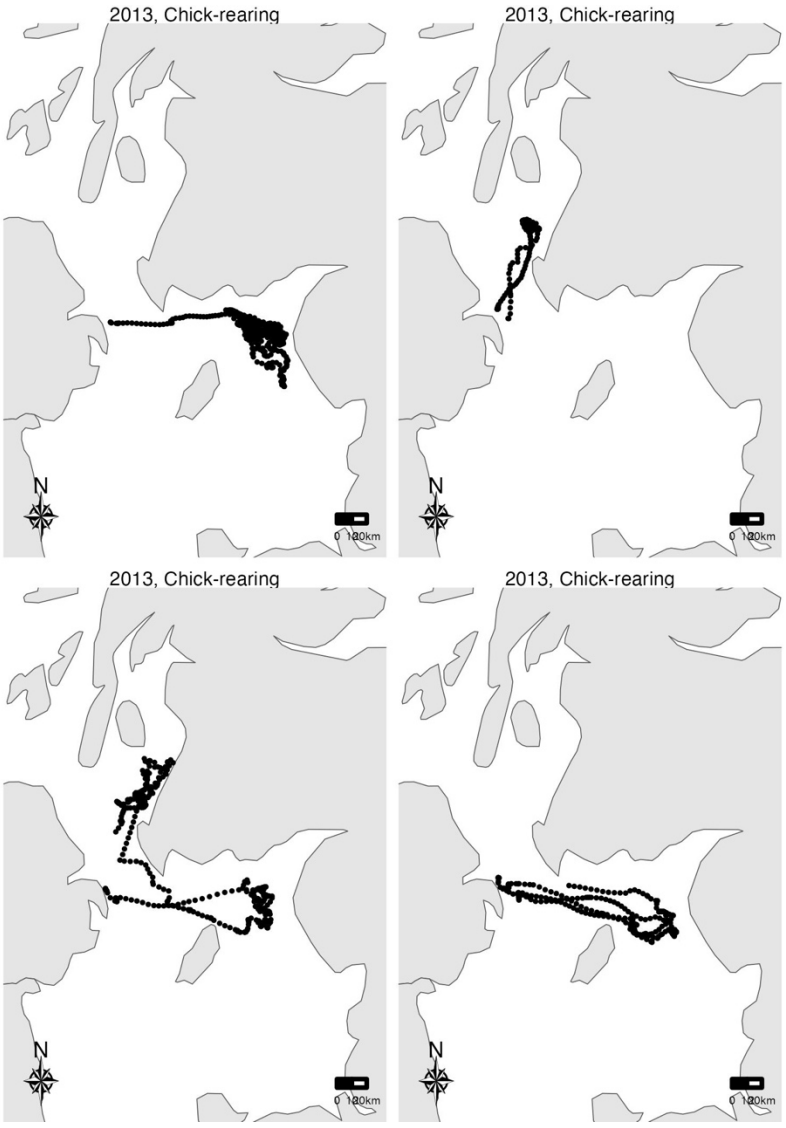




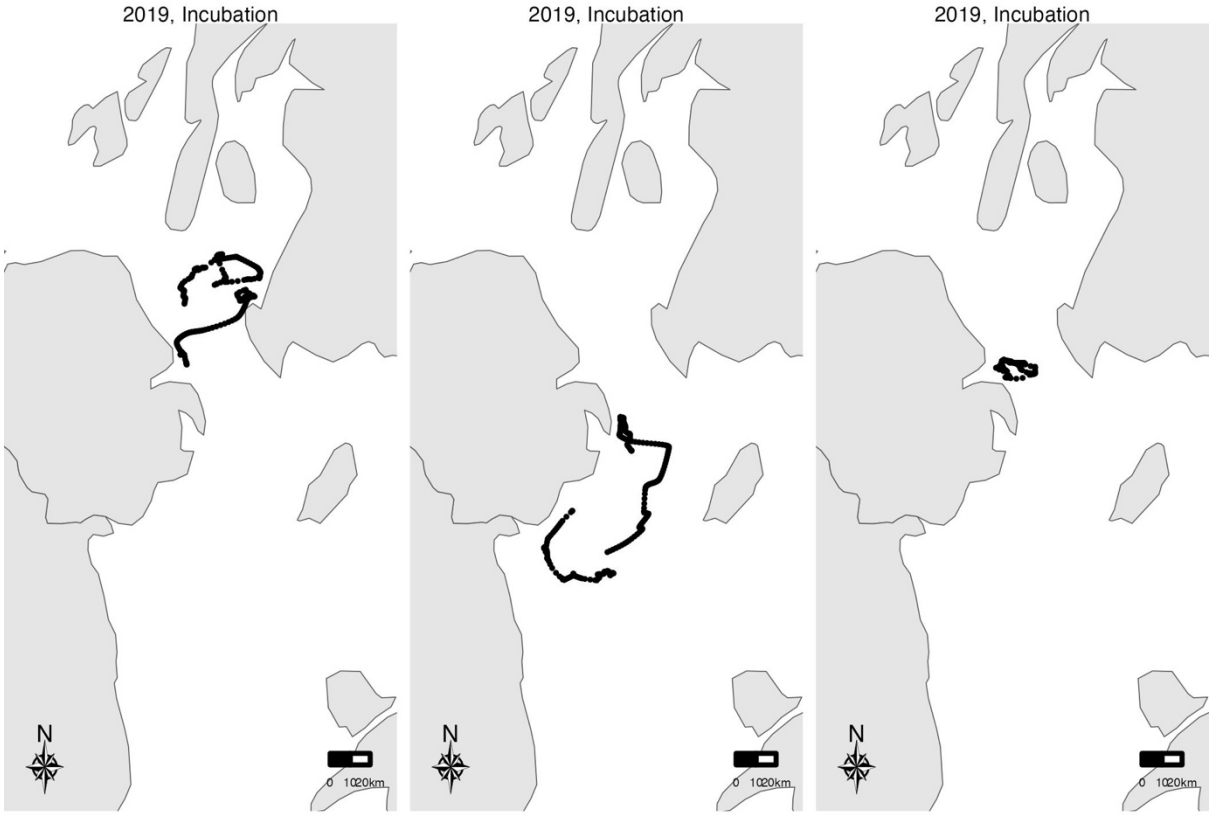
EW82438



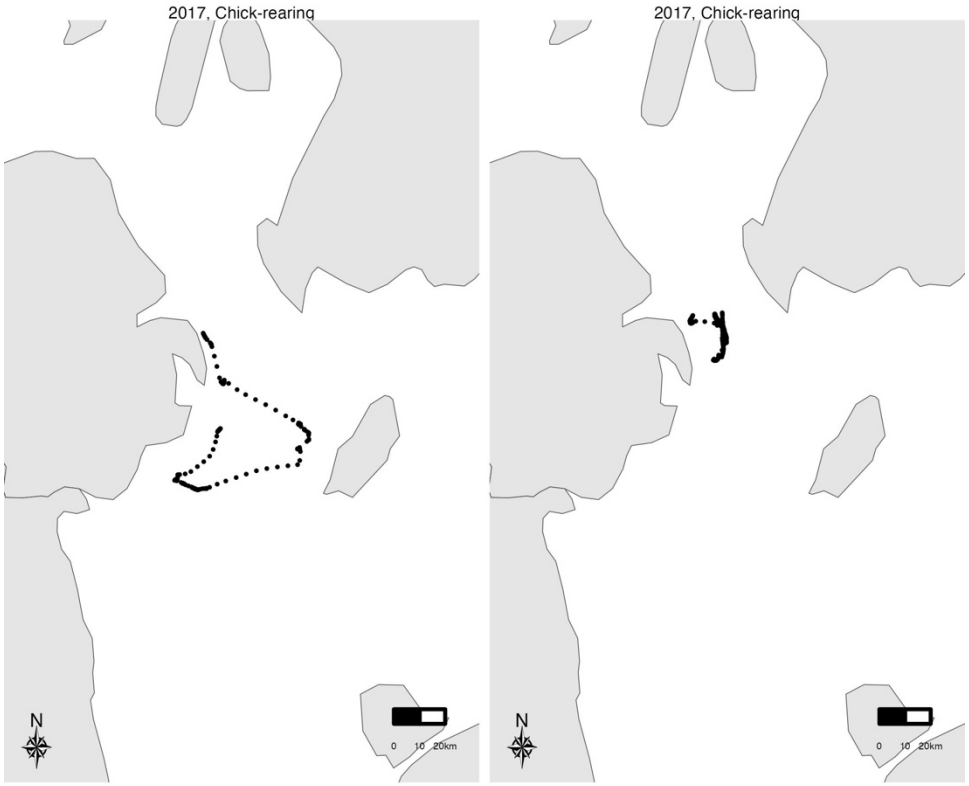
EW82658



EW82682



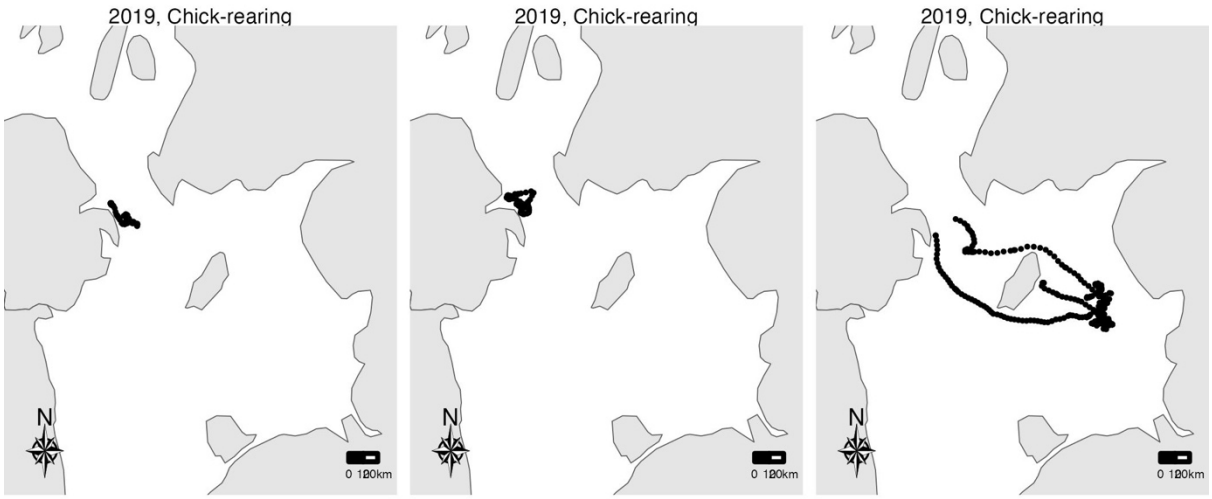
EW82837



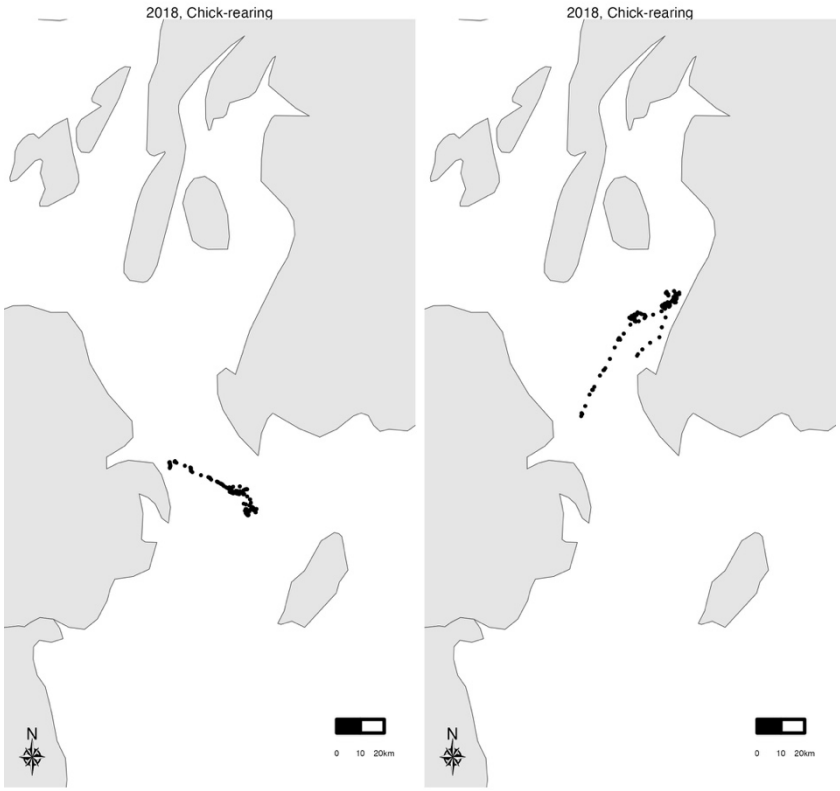
EW88721


2019, Chick-rearing
N
0 10 20km
2019, Chick-rearing
N
0 10 20km
2019, Chick-rearing
N
0 10 20km
2019, Chick-rearing
N
0 10 20km
2019, Chick-rearing
N
0 10 20km

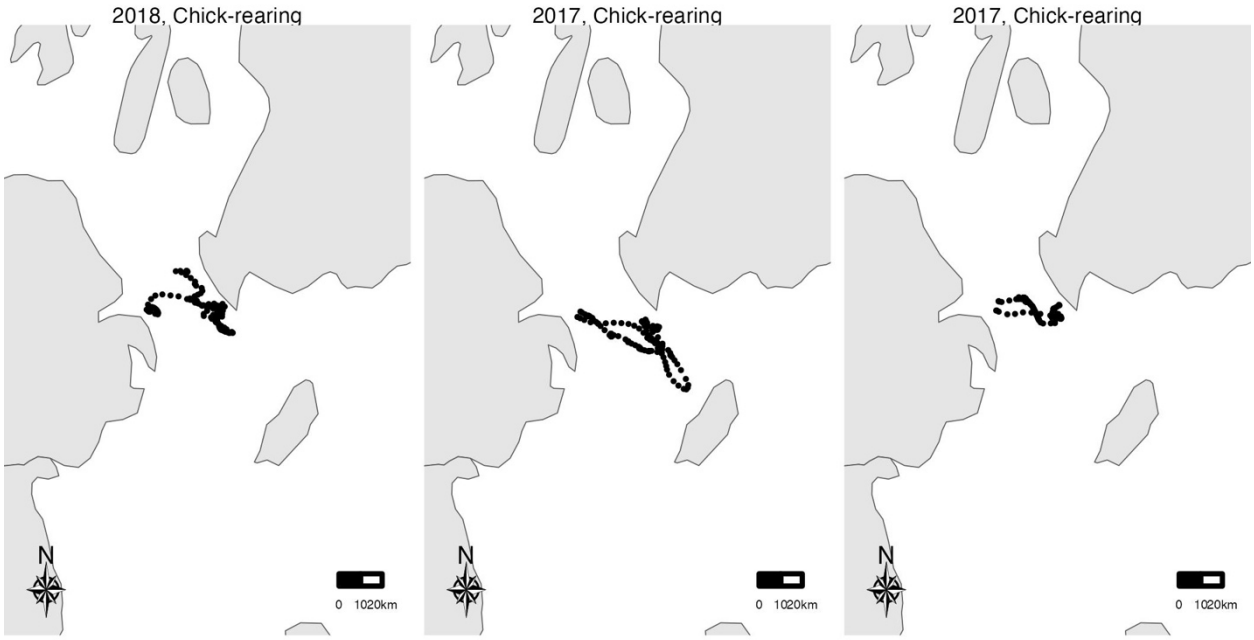
EX00604



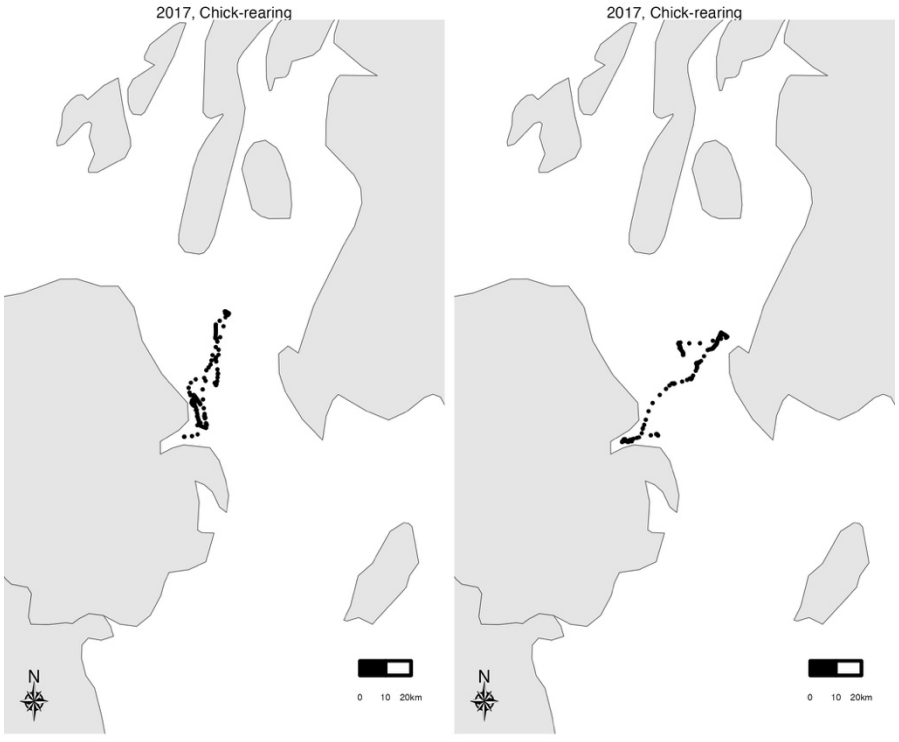
EX60866



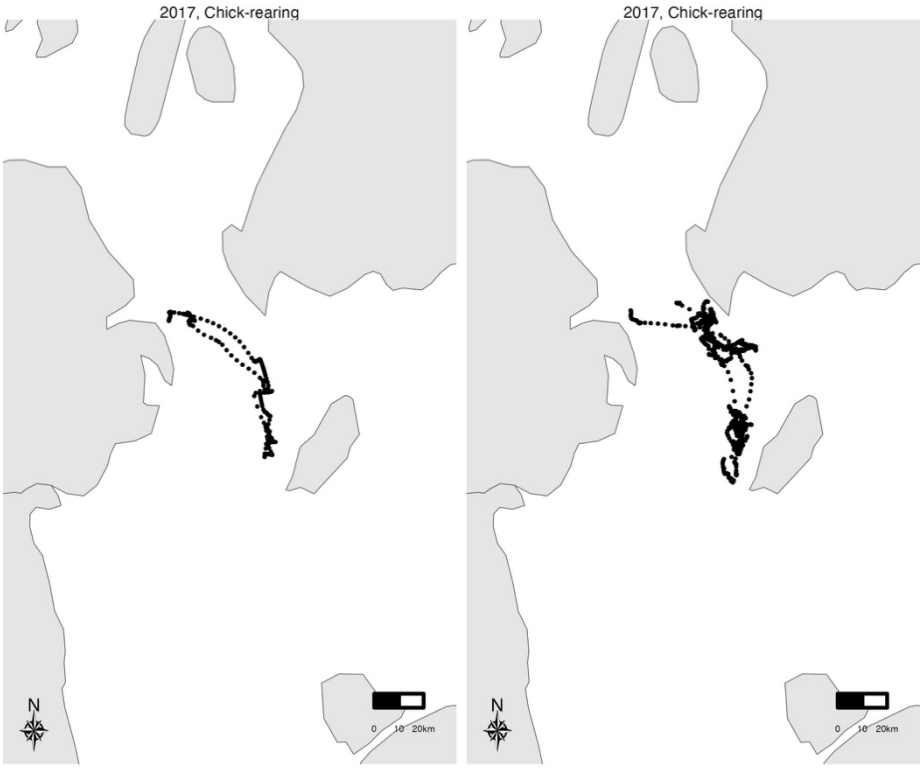
EX61160



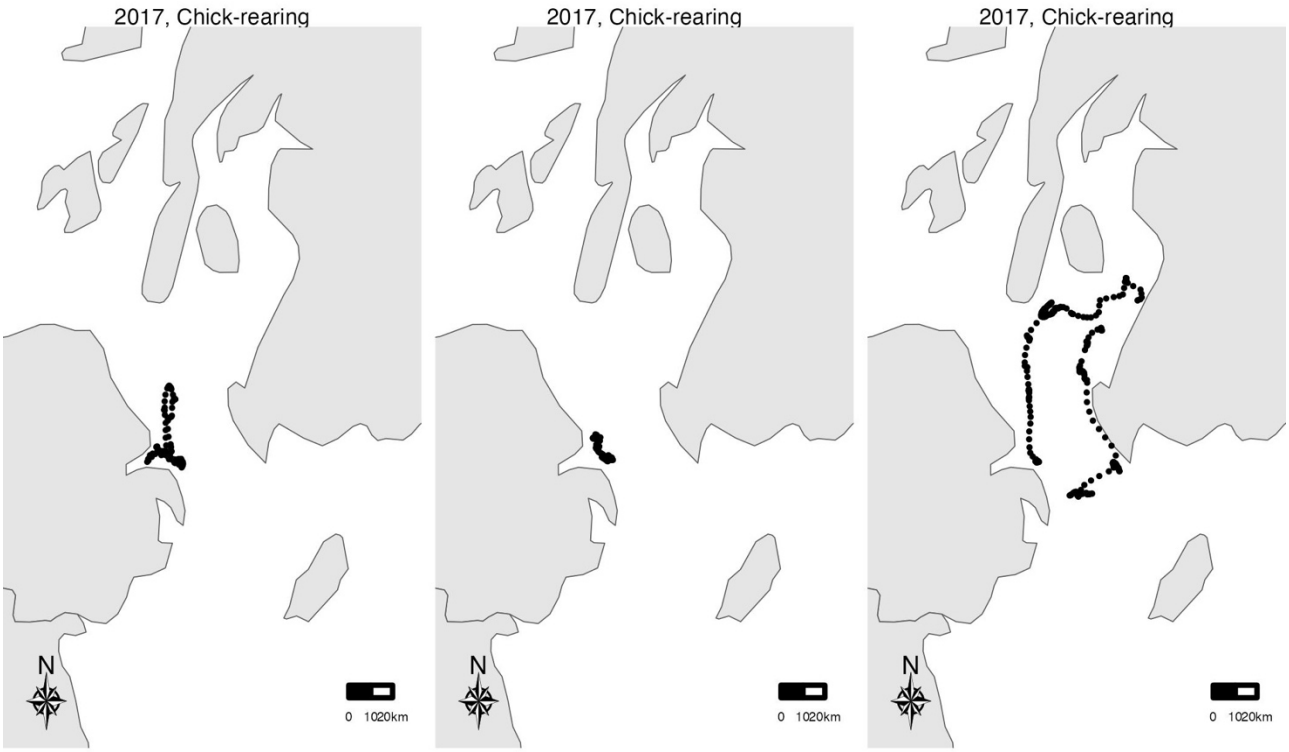
EX61251



EX61781



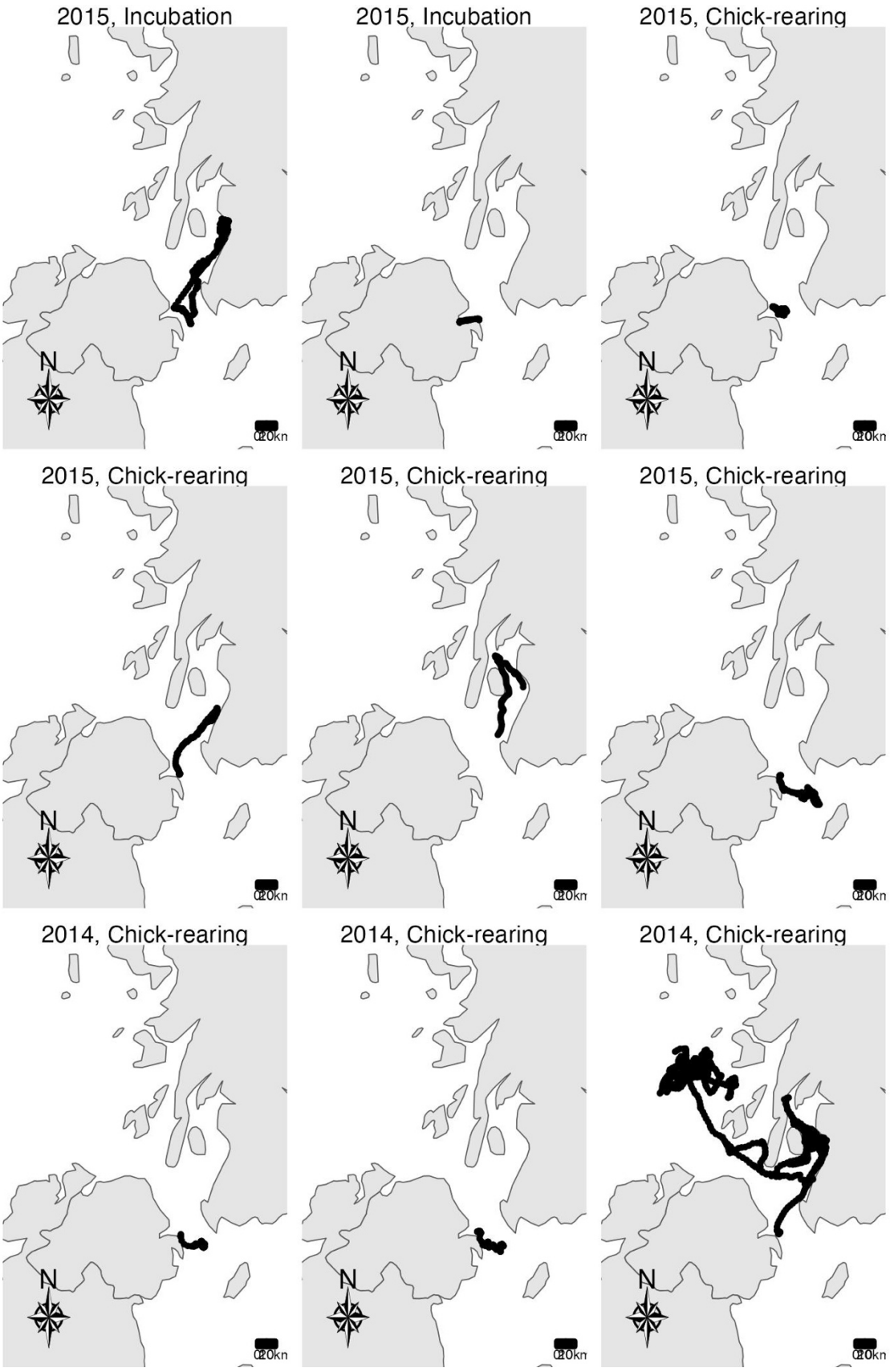
EX63781



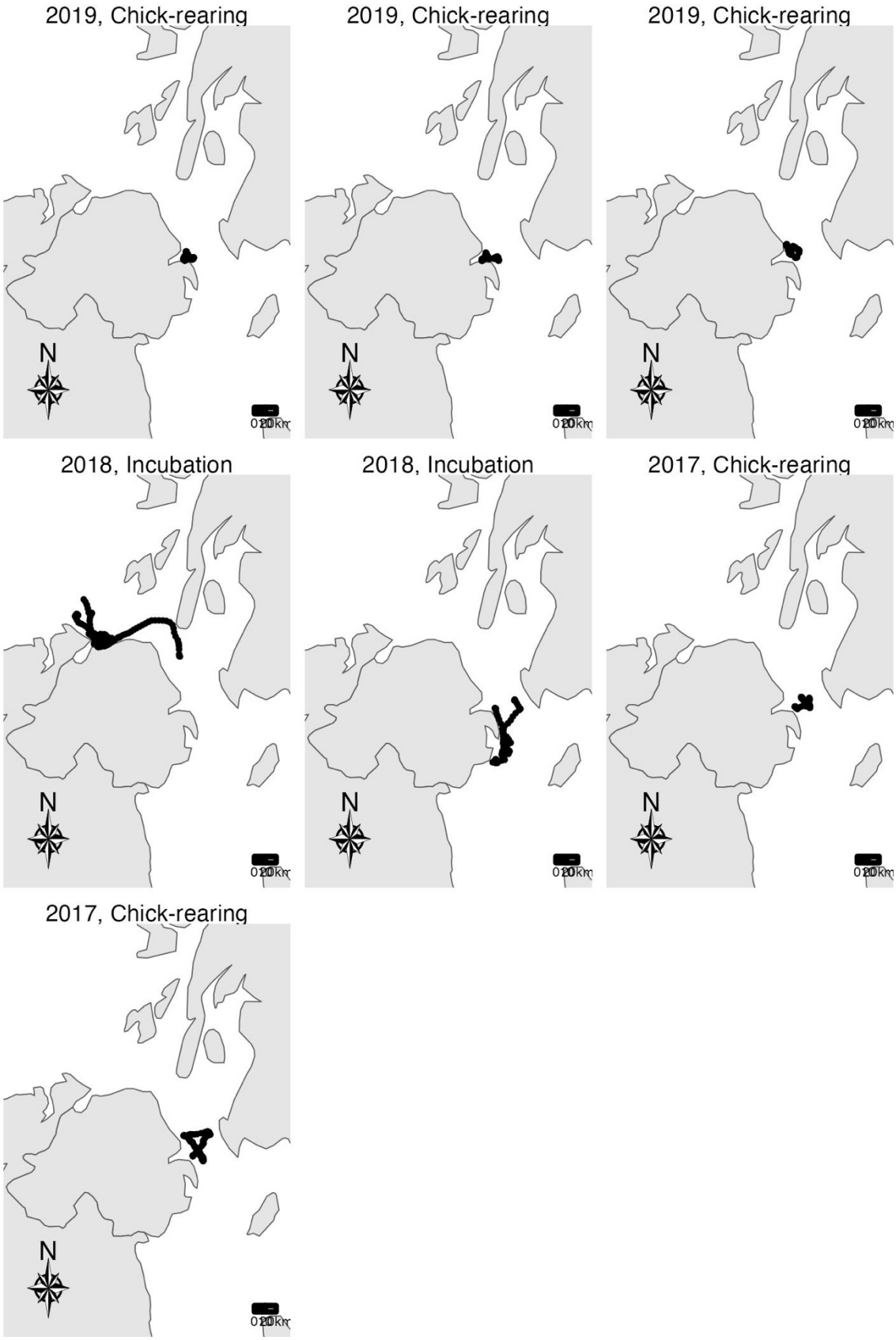
EX97077


2019, Chick-rearing
N
0 10 20km
2019, Chick-rearing
N
0 10 20km
2019, Chick-rearing
N
0 10 20km

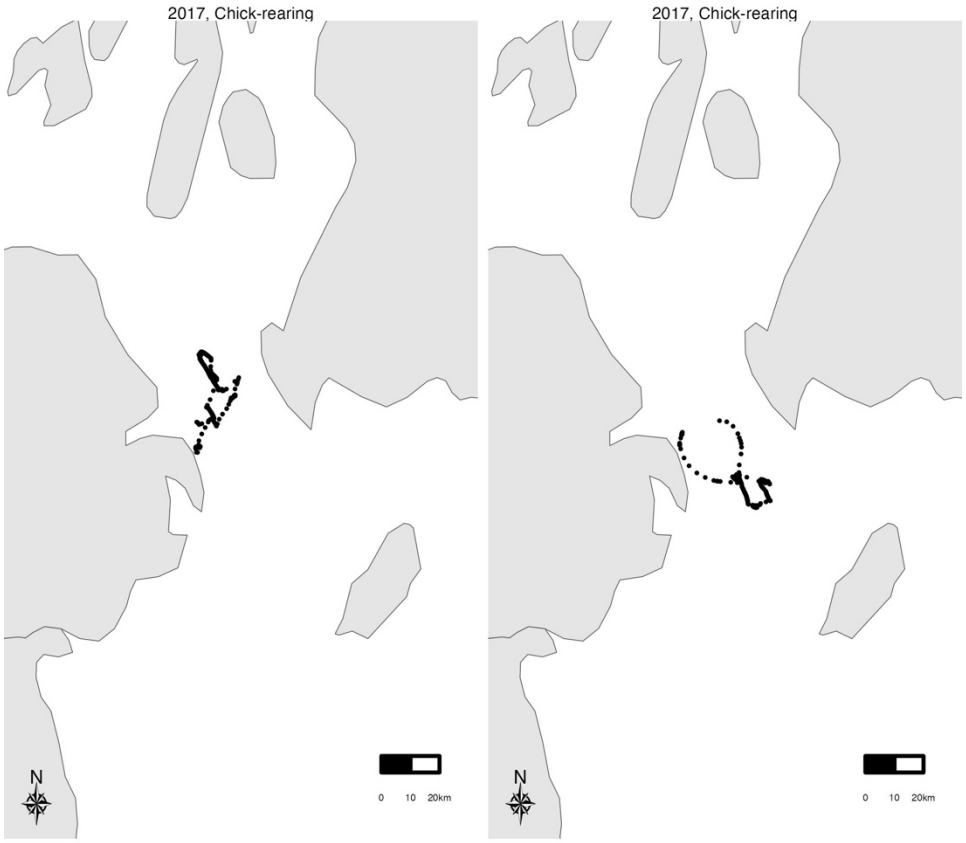
EX97162


2015, Incubation
2015, Incubation
2015, Chick-rearing
2015, Chick-rearing
2015, Chick-rearing
2015, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
2014, Chick-rearing
N

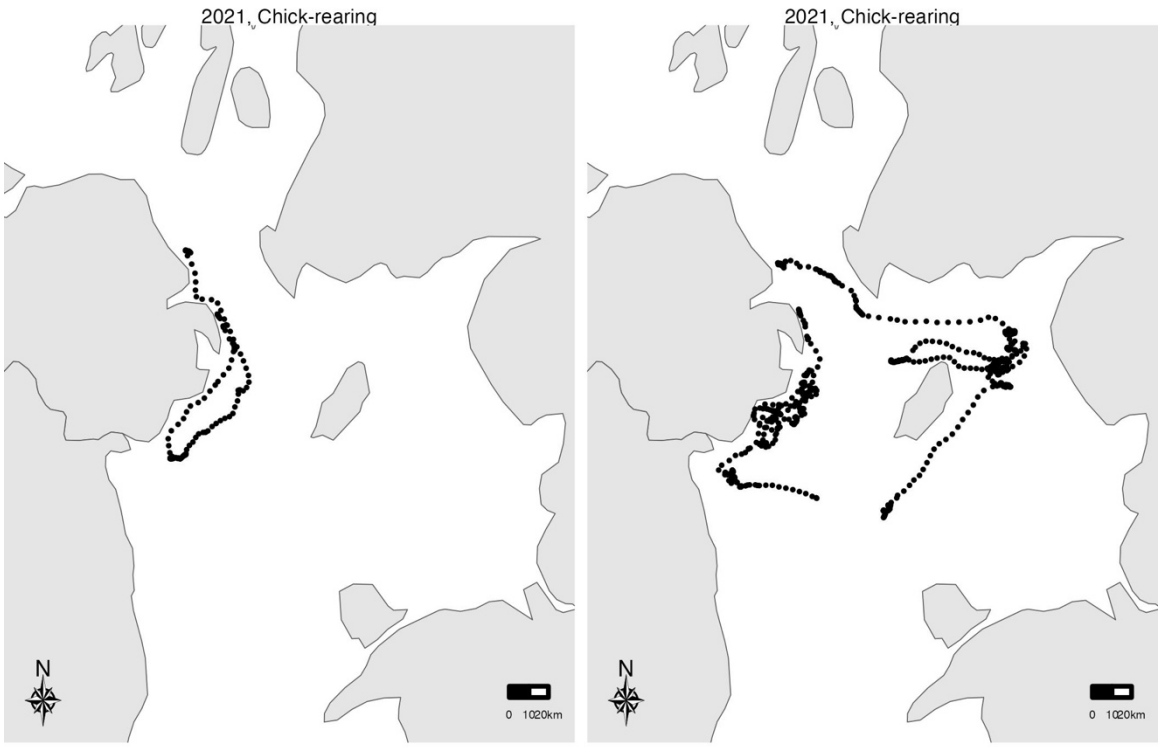
EX97164


2019, Chick-rearing
2019, Chick-rearing
2019, Chick-rearing
2018, Incubation
2018, Incubation
2017, Chick-rearing
2017, Chick-rearing
N
0 20 km

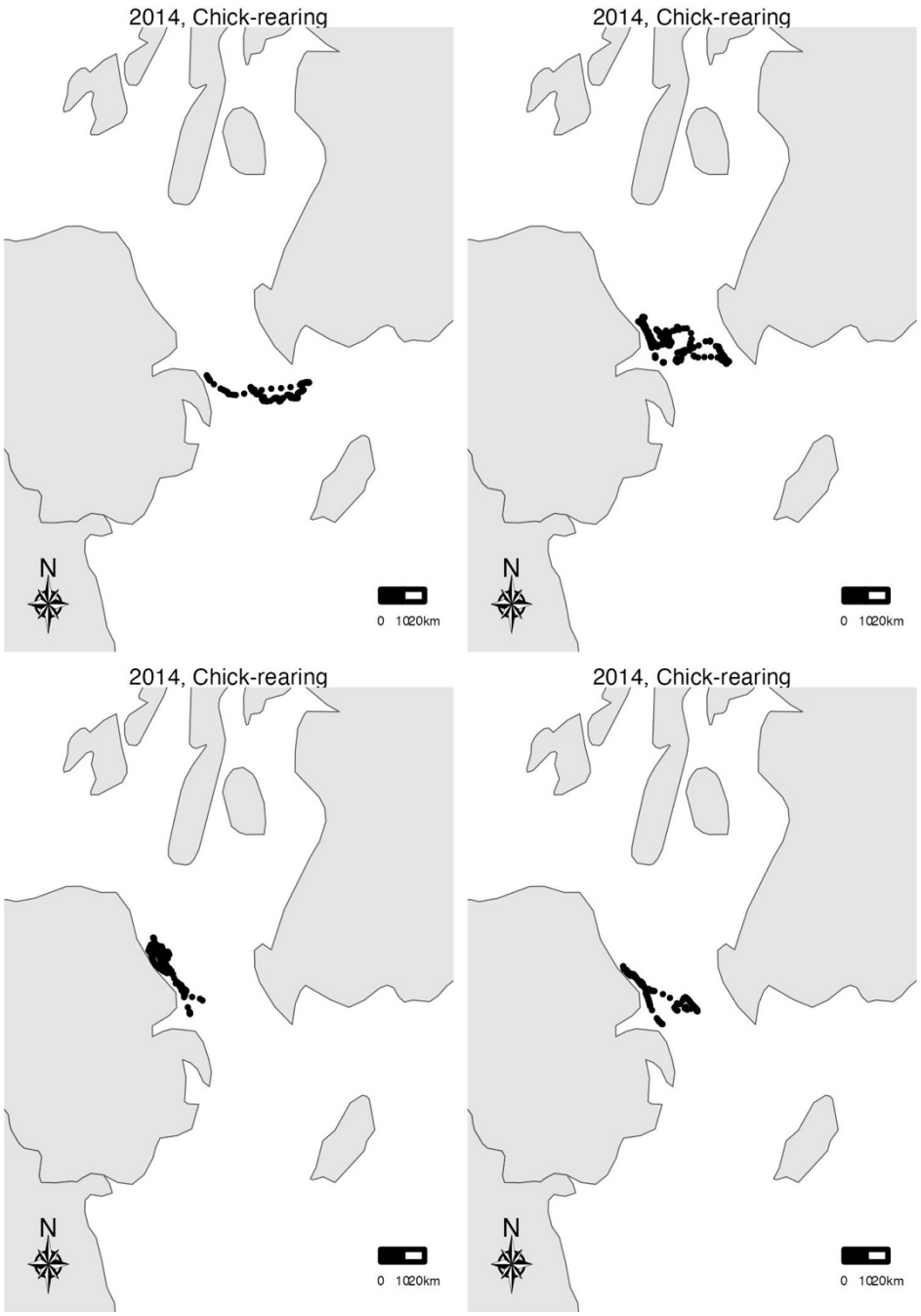
EX97430



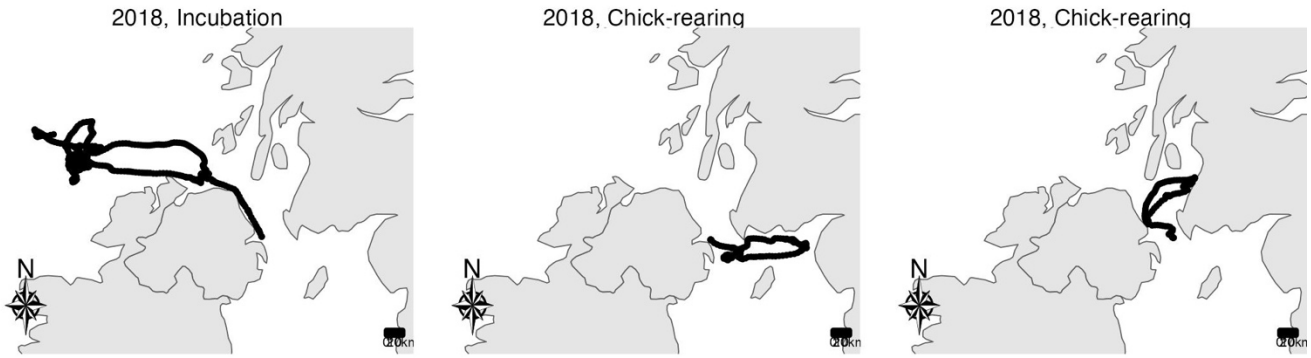
EX97790



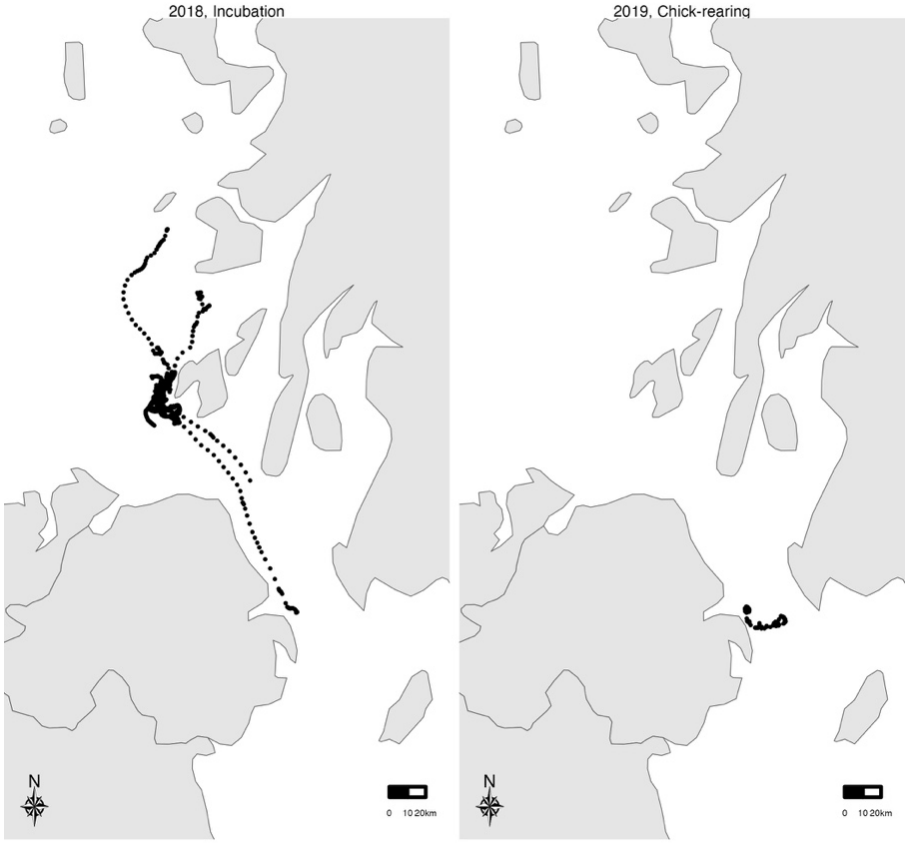
EX97849


2014, Chick-rearing
N
0 1020km
2014, Chick-rearing
N
0 1020km
2014, Chick-rearing
N
0 1020km
2014, Chick-rearing
N
0 1020km

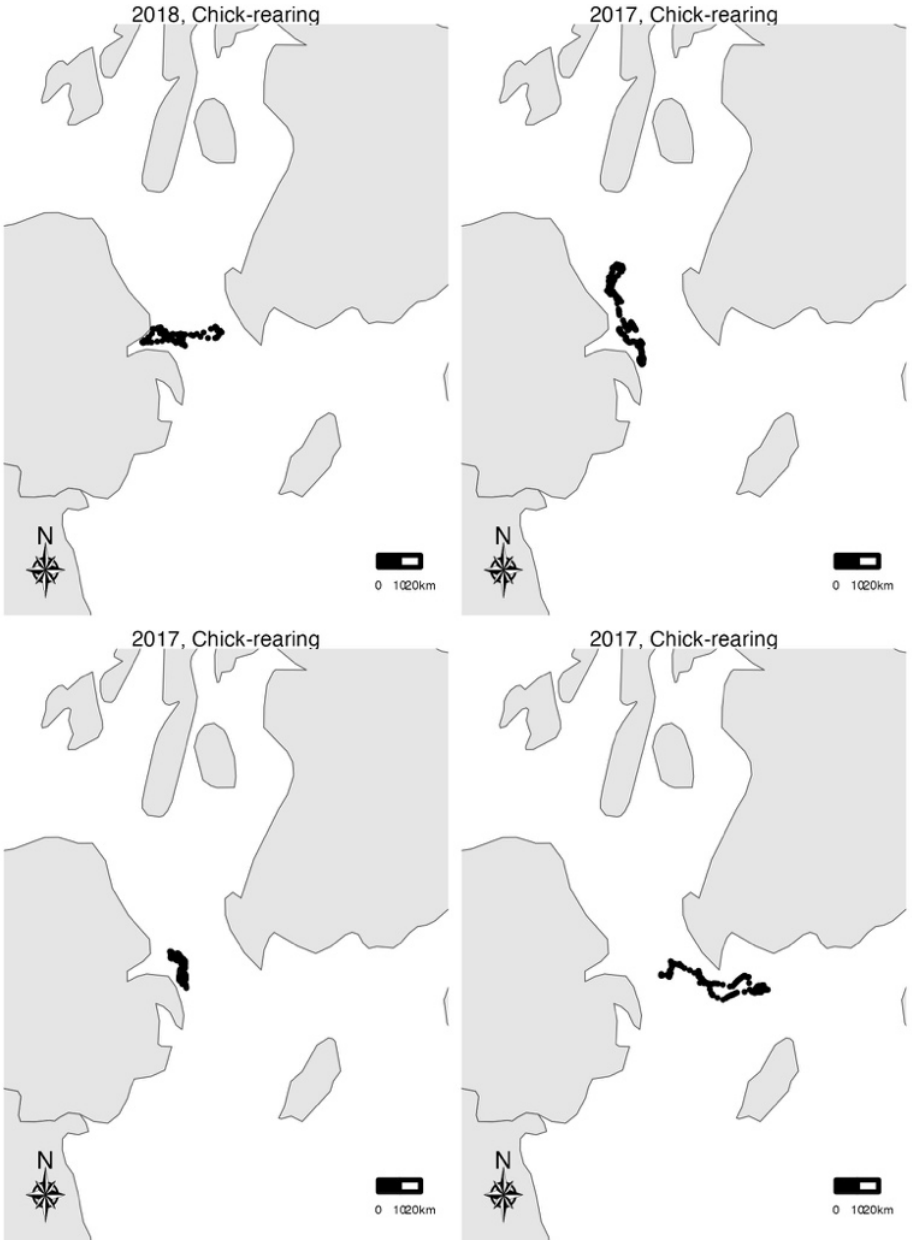
EX98997



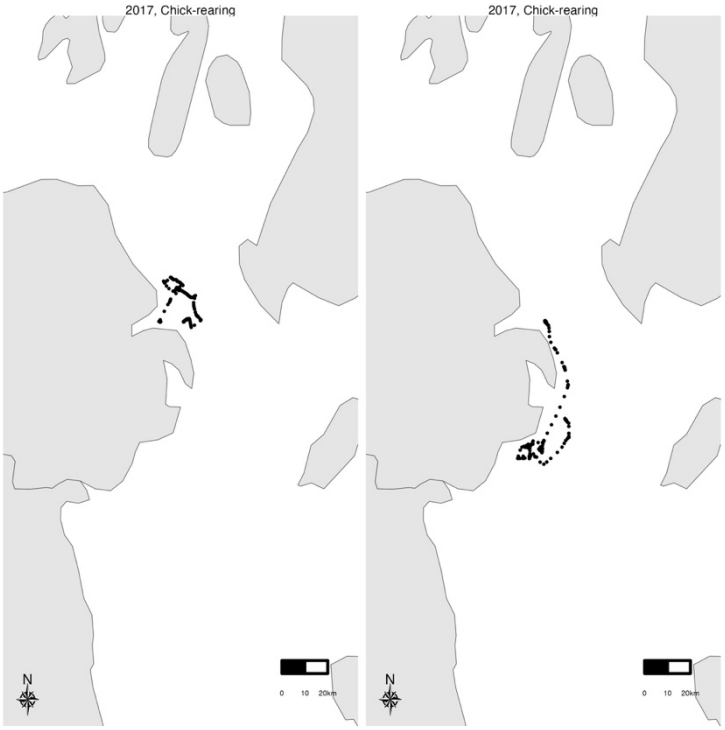
EX99102



EX99469


2018, Chick-rearing
2017, Chick-rearing
2017, Chick-rearing
2017, Chick-rearing
N
0 1020km

EX99470



B – Similarity indices per individual for incubation

(i) Between-year comparisons

Ring	Mean	SE
EJ95535	0.41376667	0.00758963
ES11008	0.66733333	0.00636134
Mean	0.54055	
n	2	

(ii) Within-year comparisons

Ring	Mean	SE
EG47299	0.1568	0.00445424
EL68487	0.52726667	0.00733252
EL91759	0.47333333	0.00528069
EL92310	0.34353333	0.00757804
EN40728	0.06153333	0.00267264
ES11008	0.319	0.01024899
ET00935	0.51196667	0.00793114
ET01125	0.36343333	0.00776129
ET013165	0.4378	0.00892286
EW82682	0.44143333	0.00595332
EX97162	0.6161	0.0069143
EX97164	0.71296667	0.00316029
Mean	0.41376389	
Upper	0.71296667	
Lower	0.06153333	
n	12	

C – Inter-annual variability in IFSF

Estimates per year for within-year randomisation comparisons, for (i) the combined dataset and (ii) chick-rearing only; variation in mean SI per individual by year is shown in (iii).

(i)

Year	Est	p
2009	1.3541996	0.519206
2010	1.1409841	0.048136
2011	1.38107	0.641151
2013	1.7388412	0.193721
2014	1.5513757	0.327209
2015	1.424868	0.979037
2016	1.422556	0.973608
2017	1.4522932	0.879232
2018	1.4668084	0.780908
2019	1.3343696	0.459185

(ii)

Year	Est	p
2009	1.183916	0.38907
2010	0.938595	0.013454
2011	1.217018	0.520133
2013	1.444868	0.480761
2014	1.434983	0.196972
2015	1.529838	0.192098
2016	0.174645	6.46E-06
2017	1.320481	0.778326
2018	1.199426	0.518067
2019	1.174824	0.392399

(iii)

