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Feasibility study of large-scale deployment of colour-ringing on Black-legged Kittiwake populations to improve the realism of demographic models assessing the population impacts of offshore wind farms

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Executive Summary

Background

1) Renewable energy developments, including offshore wind farms have been identified as a key component in international efforts to mitigate climate change and its impact on biodiversity. This has led to an increasing number of offshore wind farms around the UK, however, these can have negative impacts on seabird populations.
2) Population Viability Analysis (PVA) is frequently used to quantify these potential negative effects on seabird populations and is a vital part of the consenting process. However, a lack of empirical data on many aspects of seabird demography means that there can be considerable uncertainty in these assessments.
3) Black-legged Kittiwake *Rissa tridactyla* populations are thought to be particularly sensitive to additional mortality caused by collision with offshore wind turbines and are often highlighted as a feature of Special Protection Areas (SPAs). Offshore wind farms, therefore, have been identified as potentially causing an adverse effect on site integrity at some SPAs.
4) Despite being a relatively well-studied species, there is still much uncertainty in our knowledge of Kittiwake demographic rates and meta-population dynamics, which impedes our ability to accurately assess the way populations might respond to additional wind farm-induced mortality.
5) The Offshore Wind Strategic Monitoring and Research Forum (OWSMRF) identified a large-scale colour-ringing programme of Kittiwake colonies across the UK as one potential approach for improving empirical estimates of Kittiwake demographic rates.
6) Therefore, the main aim of this project was to determine the extent to which colour-ringing can be used to obtain reliable baseline estimates of key demographic rates in Kittiwake populations to improve the realism of demographic models assessing the population impacts of offshore wind farms, and thereby reduce uncertainty around these predicted impacts.

Review of demographic rates and their importance

7) We conducted a review of the literature to identify key demographic rates, across the breeding range of Kittiwakes, that can be estimated through mark-recapture approaches, namely ringing, and to highlight which rates are important in reducing uncertainty in PVAs.
8) Estimates of adult survival rates are available for 27 colonies across the Kittiwake's range, but few are recent and regional variation is not well understood.
9) There are very few published estimates of juvenile and immature survival rates and these had high uncertainty, in part due to low detection rates for marked individuals of these age classes.
10) Age at first breeding is relatively well quantified at around 4 years, but explicit data are available for only a small number of colonies.
11) Incidences of non-breeding in adult Kittiwakes are poorly quantified, with data available from very few colonies. Therefore, it is not well understood how this parameter varies spatially and temporally, especially in association with colony status and environmentally induced events, such as local breeding failures.
12) Dispersal by breeding adults is also poorly characterised, both in terms of frequency and dispersal distance, with data from very few colonies. Whilst it is thought to be relatively infrequent, and of limited consequence for population viability compared to other rates, it is known to vary between the sexes.
13) Although natal dispersal is much more frequent (and occurs over greater distances) than breeding dispersal, empirical data are very scarce and from a very small number of

colonies. Therefore, it is unknown to what extent dispersal rates and distances differ between regions.

14) For all demographic rates regional variation, as well as variation between age-classes and sex, is not well understood, especially in relation to variation in population size and regulatory mechanisms as mediated by environmental variation and density dependence.
15) To assess the importance of each of the demographic rates used in PVAs we constructed a Leslie matrix model with plausible parameters for each rate that reproduced the observed population change. The greatest sensitivity was to juvenile and immature survival rates, in part because very little is known about what actual values these might take and a wide range of values had to be considered in order to reflect this uncertainty. Variation in adult survival was also important, but varies less, and breeding success had a lesser influence on population change, so quantifying these is of intermediate importance in assessing PVA outcomes, unless regionally-specific estimates are required. Variation in the age at first breeding and the proportion of adults that bred each year (or, equivalently, the proportion of adults that skipped breeding) had relatively little impact on the PVA outcome.

Assessment of ringing effort required

16) We assessed the level of sampling effort required to obtain estimates of mean apparent juvenile, immature and adult Kittiwake survival rates, and to detect a change in these rates over time, based on a realistic set of scenarios that varied the number of individuals ringed, chick survival, resighting probability by age, and the length of the study, all of which are known to influence the ability to estimate demographic rates. We then determined, based on data from one intensively studied colony (Isle of May), the amount of field effort required to achieve a given level of resighting probability.
17) Because seabird population dynamics are known to be sensitive to the value of adult survival, we followed Horswill *et al.* (2018) and determined the level of effort necessary to achieve a relatively high precision (± 2%) in the estimated rate. Juvenile and immature survival rates are more poorly known, and harder to estimate, so we required a lower level of precision (±10%) for these rates. These values should be taken as indicative of the precision likely to be required rather than as absolute recommendations.
18) We found that:
    (i) **5-year studies are insufficient to provide the chosen level of precision for either adult survival or juvenile /immature survival**, even under the highest levels of ringing effort considered in the scenarios;
    (ii) **studies of 10 years or longer can provide these levels of precision for survival estimates**, with required levels of ringing effort dependent on the age classes of interest; and
    (iii) **only 20-year studies gave sufficient power (>80%) to detect a 4% step change in adult survival.** None of the other levels of effort considered gave greater than 80% power to detect any of the magnitudes of change considered.
19) It would be necessary to maintain marked populations of 100-150 adults to estimate colony-specific adult survival rates. To estimate juvenile/immature survival rates would require several hundred chicks per year to be ringed. This is not feasible on a colony-specific basis, but may be feasible on a, pooled, regional basis, although the power analysis did not address this scenario specifically.
20) Key results from the resighting analysis using Isle of May data showed that (i) increased resighting effort (in terms of number of visits in the same year) led to increased resighting probability, with 10 or more visits estimated to give greater than 90% resighting probability in all subareas surveyed; (ii) misread tags (0-5%) had a negligible impact on resighting probability; and (iii) there was some evidence that resighting levels

varied by area, highlighting that extrapolating these findings to other sites or colonies should be done with caution.

21) The approach taken to assess power was relatively simple and could be extended. In particular, hierarchical Bayesian models to account for between and within-colony spatio-temporal variation would allow assessment of the extent to which information could be pooled across multiple colonies. Moving away from the restrictive assumption of closed populations will require meta-population modelling based on population trends, productivity and distance between colonies. More generally, Integrated Population Models offer a potential mechanism to link survival models from colour-ringing data with models of productivity based on long-term monitoring data into a unified framework, and learn simultaneously about multiple demographic rates via multiple data sources enhancing their certainty and precision.

Review of existing Kittiwake ringing effort in the UK

22) We assessed whether existing ringing effort (largely undertaken by volunteers) approached the levels of effort outlined above and explored the feasibility of increasing colour-ringing effort to identify any opportunities and challenges that might exist.
23) Participants in the BTO's Re-trapping Adults for Survival (RAS) scheme gather data on adult survival. There are seven existing RAS projects, and seven colonies (five RAS and two non-RAS colonies) where colour-rings are currently used, five of which colour-ring adults and two that colour-ring both chicks and adults. There are four colonies in Britain and Ireland where around 100 chicks are ringed annually, and there are clusters of adjacent colonies where it may be achievable to ring c. 500 chicks per year. There are also a small number of additional colonies where a ringed population of around 150 individuals could be maintained, including on the east coast: Isle of May, Dunbar, and Whinnyfold; and on the west coast: Puffin Island (Anglesey) and Canna; thus, some years data are already available for the time-series required.
24) Based on British and Irish ringing recoveries of individuals ringed as chicks (either with only metal rings or also colour-rings) and recovered during or after their fourth summer (i.e. of breeding age), **83% were re-trapped or resighted within 100 km of their natal colony during the breeding season**. Although individuals can disperse further, searching adjacent colonies within this range is likely to characterise the majority of dispersal events. **For individuals ringed as adults, 98% were re-trapped or resighted within 3 km of the colony where they were ringed, suggesting low levels of adult dispersal**.
25) Based on the large number of Kittiwake chicks and adults that would need to be colour-ringed to achieve the stated level of precision in estimates of adult and chick survival, current ringing and resighting effort would need to be expanded to a larger number of colonies, but, given sufficient resource, would be feasible, if ambitious.

Methods for estimating demographic rates

26) To implement a large-scale Kittiwake colour-ringing project that can obtain empirical data to improve estimates of demographic rates, the number of colonies where adults are colour-ringed should be expanded to ensure good geographical coverage, and effort (particularly around resighting) increased at colonies where this already occurs. Colour-ringing of chicks would be more feasible in specific regions based around clusters of colonies to achieve the necessary levels of ringing (several hundred chicks per year per cluster of colonies). Focusing resighting effort in these regions will also increase the likelihood of detecting colour-ringed immatures, and adults, that disperse to surrounding colonies.
27) Given the intensity of effort required to achieve a sufficiently high resighting rate, a coordinator position, and dedicated fieldworkers to resight colour-ringed individuals would be necessary.

28) Many aspects need to be considered when assessing a site for its suitability for a Kittiwake colour-ringing study at the nest/bird level and at the site level within a colony, with safe accessibility for ringing and resighting a key aspect to both. At the site level, it is important to consider whether long-term and sufficient levels of effort are possible, whether there are any constraints to access, and who will be responsible for resighting effort. At the nest/bird level, it is important to consider the number of nests accessible for ringing and visible to resighters.

29) Alternative methods for collating data on Kittiwake demographic rates were reviewed covering technological and molecular alternatives. Most of these approaches are not completely adapted or tested to work in a Kittiwake context, and further feasibility studies would be needed to assess their suitability. Other approaches have been shown to be ineffective for Kittiwakes, despite being successful in other species (e.g. genetic approaches).

Conclusions and recommendations

30) The largest knowledge gap in Kittiwake demography centres on juvenile and immature survival and hence recruitment of individuals into the breeding population. Currently few empirical data exist on this, especially in a UK context, creating great uncertainty in the application of PVA models. Reducing this uncertainty has the potential to more than halve the uncertainty in projected population growth rate.

31) At present the only feasible way to quantify survival rates is through a co-ordinated program of colour-ringing studies.

32) We recommend that, initially at least, colour-ringing of chicks is focused on specific regions of the UK, concentrating on the east coast of Britain. This reflects the importance of the North Sea to the offshore wind farm industry, and the greater feasibility of ringing high levels of chicks in addition to adults along this coastline.

33) While baseline data on adult survival are available, we recommend that the number of colonies where adult Kittiwakes are colour-ringed is increased across the UK to provide empirical data to estimate regionally relevant adult survival rates

34) Due to the delayed maturation of Kittiwakes, colour-ringing studies of longer than 5 years will be required to obtain estimates of juvenile and immature demographic rates.

35) Realistically, at least 10 years of colour-ringing is likely to be needed to generate reliable estimates of demographic rates; however, the data achieved after five years are likely to be helpful in narrowing the frame of uncertainty around some of these rates in the models, particularly juvenile survival.

Contents

1 Background

Seabirds are one of the most threatened groups of birds; they face a range of threats from changing climates to overfishing, both globally (Dias *et al.* 2019) and in the UK (Mitchell *et al.* 2020). Renewable energy developments have been identified as a key component in international efforts to mitigate climate change (IPCC 2011, 2014). This has led to an increasing demand and expansion of marine renewable energy developments, particularly offshore wind farms around the UK (Marques *et al.* 2010; Higgins & Foley 2014; Perveen *et al.* 2014; Scottish Government 2020). However, offshore wind farms can have negative impacts on seabird populations including displacement from foraging habitats, acting as barriers to commuting and migration, and collision mortality from turbines (Garthe & Hüppop 2004; Drewitt & Langston 2006; Masden *et al.* 2009; Furness *et al.* 2013; Searle *et al.* 2014; Dierschke *et al.* 2016).

Quantifying the potential negative effects of offshore wind farms on seabird populations, particularly the cumulative impact of multiple wind farms on collision risk, displacement, and barrier effects, is a vital part of the consenting process. Demographic models, such as Population Viability Analysis (PVAs), are frequently used to quantify the population level consequences of the impacts associated with offshore wind farms on seabirds (Cook *et al.* 2018). However, a lack of empirical data on many aspects of seabird demography means that there can be considerable uncertainty in the assessments of the impact of offshore wind farms on seabirds and therefore in decision making around the consent process.

Various metrics have been used to assess population level consequences of offshore wind farms, however, these can also be sensitive to assumptions and uncertainty around demographic rates and their dependence on density or population levels (Cook & Robinson 2016; Horswill *et al*. 2017). The current recommended approach to assess whether a planned offshore wind farm will likely cause an adverse effect of the integrity of a site is to use ratio metrics (Green *et al.* 2016). This ratio metrics approach compares the population size (or growth rate) of a population in the presence and absence of a wind farm, which provides a relatively easy to interpret statistic to assess the population level impact of offshore wind farms, however, they can be sensitive to misspecification (i.e. using data which may not be accurate or precise). Therefore, without up-to date and accurate data on demographic rates, including heterogeneity among regions and over time, it is not possible to accurately assess the effects of wind farm development on seabird populations. This uncertainty around seabird demographic rates may lead to inaccurate models being used in Environmental Impact Assessments (EIA) as part of the consenting process (Green *et al.* 2016). One common approach to mitigate this is to borrow estimates of key demographic rates such as adult or immature survival that have been measured elsewhere (Horswill *et al*. 2021). However, if there is regional variation in these demographic rates then such an approach can lead to inaccurate population projections. It is also important to understand which demographic rates determine population size, and identify other potential drivers of change in these populations, to predict the extent to which seabird populations may decline as a result of additional mortality from offshore wind farm developments (Ruffino *et al.* 2020).

A major consideration in recent consenting decisions regarding offshore wind farm developments in the UK is the impact that additional mortality of Black-legged Kittiwakes *Rissa tridactyla* (hereafter Kittiwakes), caused by offshore wind farms, will have on their populations (Ruffino *et al.* 2020). Kittiwakes are particularly sensitive to offshore wind farm developments as they have been identified as being at high risk to collision mortality, and because populations are sensitive to further declines due to their dwindling numbers (Furness *et al.* 2013). UK breeding Kittiwake populations declined by 25% between the second (Seabird Colony Register 1985-1988; Lloyd *et al.* 1991) and third (Seabird 2000 1998-2002; Mitchell *et al.* 2004) national seabird censuses, with a decline in the abundance index of 65% in 2018 below the 1986 baseline (JNCC 2020). Kittiwakes are therefore categorized as a red-list species of conservation concern in the UK due to recent breeding population and range declines (Eaton *et al.* 2015). They are also categorized as threatened and vulnerable on the European and global red list, respectively (BirdLife International 2021), with declines in breeding populations observed across Europe (Keller *et al*. 2020). Despite being a relatively well-studied species there is still much uncertainty in our knowledge of Kittiwake demographic rates and meta-population dynamics (Johnston *et al*. 2020), which impedes our ability to accurately assess the way populations might respond to additional wind farm-induced mortality. This is particularly critical currently given the sensitivity of Kittiwake populations to offshore wind developments (Furness *et al*. 2013) and the increased potential for cumulative effects as the area occupied by developments expands, with these developments identified as causing adverse effects to the integrity of SPAs that Kittiwake populations are an interest feature.

Obtaining long-term data on seabird demographic rates, including Kittiwakes, is challenging as most species are long-lived with extended maturation periods as well as being highly pelagic for certain periods of the year (Schreiber & Burger 2002). Many seabird colonies are also located in relatively remote and inaccessible locations, adding further challenges to obtaining data on demographic rates. Thanks to several long-term monitoring programmes at colonies across the UK, including the Seabird Monitoring Programme (JNCC 2020), we do have data on breeding productivity and adult survival for some species and colonies. However, data on adult survival is generally sparse, a critical knowledge gap given the sensitivity of population size to this key demographic rate. Further, data on demography associated with juveniles (fledging year) and immatures (years between fledging and recruitment to the breeding colony), specifically survival, recruitment rates, natal dispersal and age of first breeding are poorly quantified, as are adult dispersal and incidences of nonbreeding, or skipped breeding, by adults.

One potential approach for improving empirical estimates of Kittiwake demographic rates that was identified by the Offshore Wind Strategic Monitoring and Research Forum (OWSMRF) is through large-scale co-ordinated colour-ringing of Kittiwake colonies across the UK (Ruffino *et al.* 2020). Mark-recapture methods are hugely valuable in estimating demographic rates of birds such as adult survival (Lebreton *et al.* 1992; Harris & Tasker 1999; Robinson & Ratcliffe 2010). Data from long-term colour-ringing studies on Kittiwakes have also provided estimates on age of first breeding and recruitment (Porter & Coulson 1987; Porter 1990; Cam *et al.* 2002a); incidences of skipped breeding (Danchin & Monnat 1992) and on adult and natal dispersal (Coulson & Neve De Mevergnies 1992; Danchin & Monnat 1992; Coulson & Coulson 2008). The use of colour-rings is particularly beneficial as it allows individual birds to be identified in the field without them needing to be recaptured or relying on members of the public to find ringed birds dead, making it easier to obtain sufficient data for estimating survival rates, as well as, potentially, dispersal and age of first breeding. Improving empirical estimates of natal and adult dispersal may also improve our understanding of connectivity among Kittiwake colonies, particularly metapopulation dynamics and how these may affect populations of specific Special Protection Areas (SPA) (Black & Ruffino 2020; Ruffino *et al.* 2020).

1.1 Project Aims

This project therefore aims to establish whether carrying out a large-scale colour-ringing project of Kittiwakes across the UK can result in more precise, and up to date, estimates of demographic rates, based on empirical data, that will provide greater realism to demographic models and reduce the current uncertainty in these models, which are used extensively in assessing population impacts of windfarm-induced mortality. The focus of this project is to improve estimates of demographic rates at a large regional or national scale rather than attempting to understand population processes at the individual colony scale. To this aim, this report provides:

i) a review of the literature and of currently existing kittiwake colour-ringing studies to identify the key demographic rates that can be estimated through mark-recapture approaches, highlighting which of these rates are important to reducing uncertainty in PVAs;
ii) a power analysis to quantify the levels of accuracy in the adult and immature survival estimates achieved under various scenarios of colour-ringing efforts;
iii) a scoping exercise informed by
    a. existing ringing effort from the British ringing scheme database
    b. the motivation of people involved in Kittiwake studies/ringing obtained through a ringing questionnaire and two workshops, one focused on Kittiwake ecology and the second on the logistics of ringing and resighting Kittiwakes
    c. an assessment of field effort and resighting rates
    d. considering alternative approaches and technology to colour-ringing; and
iv) recommendations on the feasibility of colour-ringing Black-legged Kittiwake populations to improve the realism of demographic models used to assess the population impacts of offshore wind farms.

2 Review of demographic rates and their importance

2.1 Kittiwake Life History

Black-legged Kittiwakes are small, long-lived, colonial gulls with an average lifespan of 12 years (Robinson 2005). They have a widespread distribution across the Northern Hemisphere and breed in the northern Atlantic and Pacific Oceans, typically in subarctic and arctic regions. Kittiwakes are surface-feeders which prey predominantly on sandeels, but also on gadoids, clupeids and sprats in some areas of the UK (Harris & Wanless 1997; Bull *et al.* 2004; Swann *et al.* 2008; Chivers *et al.* 2012).

Adult Kittiwakes return to the breeding colony during early spring where they typically nest on sheer cliffs, although buildings, bridges, sea walls and oil installations are occasionally used (Coulson 2019). Kittiwakes lay a clutch of 1 – 3 eggs in May, with the majority laying two-egg clutches, which are incubated for 27 days by both members of the pair. Juvenile Kittiwakes fledge after 33 – 54 days, leaving the breeding colony in late-July/August (Coulson & White 1958; Coulson 2019).

During the non-breeding season Kittiwakes are largely oceanic and disperse widely across the North Atlantic with populations from different breeding locations mixing together in the North Atlantic and North Sea during the winter (Frederiksen *et al.* 2012; Bogdanova *et al.* 2017). Juvenile and immature birds disperse further than adults during their first few years and are largely oceanic (Barrett & Bakken 1997). However, immature/pre-breeding Kittiwakes do make occasional prospecting visits to colonies during the breeding season before they recruit to the breeding population (Cadiou 1999), although the frequency with which this happens is hard to quantify. Kittiwakes generally recruit into the breeding population at around four-years old; however, there can be considerable variation, ranging from 2 – 10 years (Wooller & Coulson 1977; Cam *et al.* 2002a; Coulson 2011; McKnight *et al.* 2019).

Natal philopatry, the tendency of an individual to return to breed in the colony where it was born, is relatively low in Kittiwakes, with philopatric recruitment, where it has been quantified, typically accounting for less than 50% of new recruits; with males having higher natal site fidelity than females (Wooller & Coulson 1977; Coulson & Neve De Mevergnies 1992;

Coulson & Coulson 2008). Once individuals have recruited to a breeding colony, adult breeding site fidelity is considered to be very high, however, emigration of breeding birds can occur, especially when colonies are disturbed, for example if they suffer from a high incidence of predation (Danchin & Monnat 1992; Ponchon *et al.* 2015).

2.2 Literature search

To establish what quantitative data on the identified demographic rates of interest are currently available, we conducted a systematic literature review of the peer-reviewed and grey literature to search for demographic rates that can be estimated from colour-ringing individuals globally: age-specific survival, age of first breeding, instances of nonbreeding, age-specific philopatry, and age-specific dispersal rates Table 2.1). Although productivity is also an important demographic rate, we did not include it in this literature review as productivity is not estimated through colour-ringing (Table 2.2).

The following search terms were used in Google Scholar and Web of Science: Kittiwake *Rissa tridactyla*; Kittiwake *Rissa tridactyla* survival; Kittiwake *Rissa tridactyla* dispersal. At least the first 70 search return pages were assessed in case they contained relevant information on Kittiwake demography. We also assessed the references of the literature found during the systematic literature review and in other known sources of Kittiwake demography (Coulson 2011, 2019; Horswill & Robinson 2015). Finally, we also included available estimates of demographic rates from unpublished data of colour-ringing projects.

2.3 Results

2.3.1 Background

The literature review returned 65 reference sources that provided information on Kittiwake demography relating to age-specific survival, age of first breeding, incidences of non-breeding and dispersal. Published studies spanned a time-period from 1954 to the present day and came from 22 colonies / populations across the UK, Brittany, Denmark, Norway, Svalbard, and Alaska (Table 2.1).

From the 17 locations where mark-recapture studies were conducted, two used metal-rings only (Oro & Furness 2002; Lerche-Jørgensen *et al.* 2012), whilst the remaining 15 also used colour-rings, using either a unique combination of coloured rings or a single alpha-numeric engraved colour-ring. Nine of these studies marked adults only and eight marked both chicks and adults. Eight of these studies reported how birds were caught. Using a noose pole was the most common reported method for catching adults, whilst chicks were generally caught by hand, helped at one location with rope access equipment. In Canada, rocket nets were used to catch adults that nested on a gradual slope. In addition, one colony used short-term GPS deployments to obtain data on adult dispersal (Ponchon *et al.* 2014, 2017) while two used colony counts to obtain data on counts of non-breeders in the colony (Coulson & White 1956; Richardson 1985).

Survival rates were generally reported as annual estimates. In cases where multiple values were reported (i.e. by years or sex), we report the mean value as well as a measure of the variability around this value where possible (i.e. standard deviation / range). Age-specific demographic rates refer to juvenile (fledging year), immature (years between fledging and recruitment to the breeding colony) and adult (breeding age bird).

2.3.2 Survival

Adults

Estimates of adult survival were the most frequently reported demographic rate for Kittiwakes across the published literature. Published adult survival estimates were available for 16 colonies, or populations, across the Northern Hemisphere. From the published literature, the majority of colonies were located in the north Atlantic (Figure 2.1) with eight in the UK and one each in Brittany, Denmark, Norway and Svalbard, with a further four in Alaska, in the Pacific Ocean. The duration over which survival rates were estimated varied considerably from 3 years to 31 years. In addition, data on adult survival (or return rates) from unpublished colour-ringing projects were available from an additional five Kittiwake Retrapping Adults for Survival scheme (RAS; a national standardised ringing programme within the BTO Ringing Scheme to estimate adult survival rates, https://www.bto.org/our-science/projects/ringing/surveys/ras) sites in the UK and seven colonies as part of the SEAPOP network in Norway (https://www2.nina.no/seapop/seapophtml/).

The majority of published colony-specific estimates of adult survival in the UK are relatively old, with most data collected pre 2000. However, up to date UK estimates of adult survival are available from Skomer (1978-2018, Wilkie *et al.* 2019) the Isle of May (1986-2017, JNCC) and the five RAS sites (Table 2.1).

Annual survival rates of adult Kittiwakes were variable but generally high, with reported rates of mean adult survival ranging from 0.67 to 0.93 (Table 2.1). Part of the variation in reported survival rate estimates were related to specific circumstances, which have resulted in short-term reductions in adult survival at certain locations. For example, high mortality caused by toxin-producing algal blooms, reduced adult survival considerably in some colonies in northeast England between 1984-1987 and 1997-1998 (Coulson & Strowger 1999). Although some of these survival estimates are associated with short-term high mortality events, it is important to understand these extreme events, as they are predicted to become increasingly important due to climate change (Jenouvrier *et al.* 2015). Furthermore, survival estimates reported in some studies were actually apparent survival, which incorporate both true mortality and permanent emigration from the study colony. These values will likely underestimate true survival given that populations are not necessarily closed, and not all studies searched surrounding colonies for marked individuals.

Other factors that may result in heterogeneity in adult survival rates include the age of individuals, with evidence of a progressive decline in survival rates of older individuals in some studies (Aebischer & Coulson 1990; Cam & Monnat 2000a; Frederiksen *et al.* 2004a). There is little evidence for differences in survival rate between the sexes where separate survival rates for males and females have been reported (Coulson & Wooller 1976; Hatch *et al.* 1993; Cam & Monnat 2000a). However, Aebischer and Coulson (1990) reported consistently lower survival rates of male Kittiwakes relative to females, over a period of 34 years in North Shields (North-east England). Cam and Monnat (2000b) found no evidence for differences in survival rates between first-time breeders and non-breeders, however experienced breeders did have higher survival (0.82 ± SD 0.14) than first-year and non-breeders (0.76 ± 0.16). Adult survival was found to vary slightly dependent on the position of breeding birds within the colony during the long-term study at North Shields with individuals breeding in the colony centre having a slightly higher mean survival rate (0.81) compared to those breeding at the edge (0.79; Aebischer & Coulson 1990), potentially due to peripheral birds typically being first-time or inexperienced breeders.

Knowledge gaps: Estimates of adult survival are available for a number of studies, but several of these no longer operate meaning that survival estimates from these studies are not contemporary, and regional variation is not well understood.

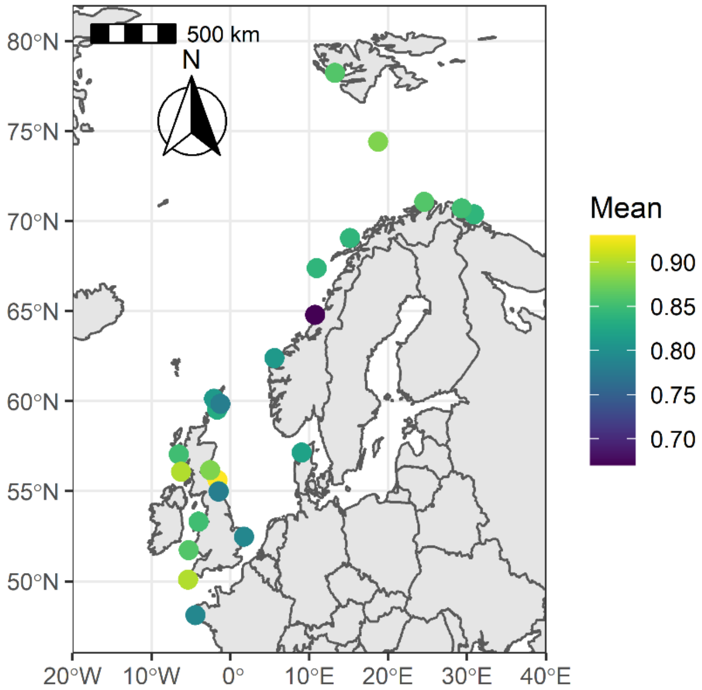


Figure 2.1. Mean survival rates in Kittiwake colonies across Europe for which adult survival estimates were reported from the published literature or unpublished colour-ring projects (range: 0.67– 0.93). Adult survival rates were also reported for four colonies in Alaska (range: 0.86 – 0.93, see Table 2.1).

Juveniles and immatures

Age-specific estimates of survival rates for juveniles (in their first year of life) or immatures (typically individuals aged 2-4 years) are very poorly quantified due to their assumed lower survival and high natal dispersal, resulting in low resighting rates. From a small sample of ring recoveries at North Shields, Coulson and White (1959) estimated first year mortality of 21%, giving a juvenile survival rate of 0.79; although, Coulson (2011) subsequently suggested that juvenile survival was more likely to be around 0.63, after re-calculating estimated first year mortality to take into account that mortality risk is likely to be higher during an individual's first year compared to later years. However, this estimate is unlikely to be very robust due to the small sample sizes and methods involved in its calculation.

In Shoup Bay, Alaska, there was high variation in apparent fledgling survival and recruitment over a 20-year period dependent on the cohort, ranging from 0.81 (95 % CI 0.73–0.87, 1995) to 0.23 (95 % CI 0.10–0.47, 2005) (McKnight *et al.* 2019). However, very few first-year birds were resighted back at the natal colony (i.e. 8 of 5090 individuals), therefore these juvenile survival estimates relate to the cumulative probability of apparent survival over an individual's first two years of life (McKnight *et al.* 2019), implying that average annual survival over these first two years is in the range of 0.48 – 0.90. Part of this variation in apparent survival may be due to emigration as dispersal is thought to have increased over the study period (McKnight *et al.* 2019). Estimates of pre-breeder survival probabilities are also reported by age (0 to ≥5) for Kittiwake cohorts between 1984 and 1994 in Britany, which range between 0.54 and 0.84 (Cam *et al.* 2005).

Due to the difficulties of estimating age-specific survival, survival for age-classes combined, i.e. from fledging to recruitment, has instead been estimated for some colonies: from colour-ringing chicks on Fair Isle, an estimate of 20% survival from fledging to recruitment was reported, derived from empirical adult survival and breeding success data (Rothery *et al.* 2002). Between 1954 and 1984, at North Shields, the 5-year running mean recruitment rate for both males and females varied considerably between 0.22 and 0.45, generally being higher for males than females given their greater natal philopatry (Porter & Coulson 1987).

Although a small proportion of immature Kittiwakes do make prospecting trips to breeding colonies, the detection of immatures at colonies is typically very low, given that they are largely oceanic in their first few years of life, and there are relatively low levels of natal philopatry in Kittiwakes, which can be sex biased (see section 2.3.5; Coulson & Neve De Mevergnies 1992; Cadiou 1999; McKnight *et al.* 2019). This is likely to be further complicated by temporal and spatial variation in the proportion of immature birds that do prospect, given that cohorts of chicks can have different fledging and juvenile survival rates (McKnight *et al.* 2019). The subsequent low resighting probabilities for juvenile and immature Kittiwakes makes it difficult to precisely estimate survival rates for these age-classes from marked individuals.

Understanding juveniles and immature is also important given that they are likely to make up a large proportion of the population (Carneiro *et al.* 2020). Although, Kittiwakes are more oceanic in their early years, immatures may be more susceptible behaviourally to collision risk if they do associate with offshore wind farms.

Knowledge gaps: Juvenile and immature survival rates are poorly quantified and highly uncertain largely because of low detection rates for these age classes and their relatively high natal dispersal (see below). There is also likely to be substantial temporal and spatial variation in these rates although the extent of this is unknown.

2.3.3 Age at first breeding

The mean age of first breeding in Kittiwakes is generally taken to be 4 years, although it can vary considerably from 2 to 10 years, with part of this variation driven by the availability of nest sites (Wooller & Coulson 1977; Cam *et al.* 2002b; Coulson 2011; McKnight *et al.* 2019).

In the eastern North Atlantic, the mean age of first breeding was 4.2 years based on two long-term study populations in North Shields (Coulson & Porter 1985) and Brittany (Cam *et al.* 2002b). There is some evidence that age of first breeding varied by sex, with females recruiting to the breeding colony at a slightly later age than males (Wooller & Coulson 1977; Coulson 2011). In the Pacific, in Prince William Sound, Alaska, the mean age of first breeding was higher, estimated at 7 years, although some individuals were recorded in the colony as pre-breeders after 2 years (McKnight *et al.* 2019). In Brittany, nearly all pre-breeders were thought to attend colonies in the year(s) before they recruited into the breeding population, although first-year birds were seen very rarely (Danchin *et al.* 1998; Cam *et al.* 2002a, 2003). Therefore, when determining the age of first breeding of individuals it is important to establish their breeding status, so as to record age of first breeding rather than simply age of first resighting. In Norway, most Kittiwakes were not resighted at the breeding colony until their third summer (Barrett & Bakken 1997).

As highlighted by Horswill and Robinson (2015), the published data on age of recruitment is relatively old (Porter & Coulson 1987; Cam *et al.* 2002) and comes from a limited number of colonies. If in colonies with declining numbers age of recruitment is lower, this value may not be representative for all colonies, especially given the declines observed in UK Kittiwake populations since these two studies were published. For example, the age of first breeding fell from 5 to 4 years in response to high adult mortality in the early 1970s at North Shields (Coulson & Porter 1987). However, age of recruitment was not found to differ between a declining and increasing colony in Brittany (Danchin & Monnat 1992). Changes in the age at which individuals first breed is likely to be one common way in which density-dependent relationships are manifested (see below).

Knowledge gaps: Age of first breeding is relatively well quantified; however, the estimates are based on relatively old data and from a small number of colonies. As such, regional variation is not well understood, especially in relation to variation in colony size and regulatory mechanisms as mediated by density dependence.

2.3.4 Incidence of non-breeding

There is little quantitative data published on incidences of nonbreeding, or skipped breeding, by adult Kittiwakes. Based on the long-term colour-ringing study in Brittany, Danchin and Monnat (1992) reported annual probabilities of non-breeding for a declining colony (0.208 ± 0.207) and an increasing colony (0.180 ± 0.188). The likelihood of an individual skipping breeding was also related to adult dispersal with the probability that an individual would skip breeding being higher for individuals that had moved to a new part of the colony compared to those that remained in the same patch (Danchin & Monnat 1992). Colony disturbances that result in dispersal may also result in more cases of nonbreeding. Therefore, there may be considerable heterogeneity in instances of non-breeding related to colony status or disturbances to the colony, as well as external environmental factors. For example, following an oil spill off Shetland, 44% of surviving breeding adults did not return to breed at Sumburgh Head in the year following the spill (Walton *et al.* 1997).

Estimates of the proportion of non-breeding individuals present within a colony during the breeding season were reported for North Shields (0.2, Coulson & White 1956) and Shetland (0.167, Richardson 1985) based on ratio of birds to apparently occupied nests (AON), however these studies included immatures and pre-breeders in their counts of non-breeders, rather than focusing on known marked adult breeders.

Knowledge gaps: There is evidence that a moderate number of adult Kittiwakes (c. 20%) do not breed in any given year, but this is poorly quantified with data from very few studies. Therefore, it is not well understood how this parameter varies regionally and over time, especially in association with colony status (i.e. declining or increasing) and local breeding failures.

2.3.5 Philopatry / dispersal

In addition to being sensitive to misspecification, demographic models have a number of major assumptions that also contribute to uncertainty in impact assessments. The first assumption is that seabird populations are closed, due to a lack of empirical data on immigration and emigration rates, and so immigration and emigration are not accounted for. This means that the models do not consider whether populations can be buffered against additional mortality (e.g. caused by wind farms) by immigration, or whether further declines would occur due to emigration, resulting in inaccurate impact assessments. A better understanding of connectivity between different colonies/populations will therefore increase the confidence in model predictions of population responses to predict more reliable and accurate mortality of seabirds to offshore wind developments. For example, natal dispersal is relatively common in some seabird species, creating connectivity between colonies/ populations (Devlin *et al*. 2008; Lebreton *et al*. 2003; Spendelow *et al*. 1995). Models that can incorporate emigration and immigration parameters based on empirical data will therefore improve the realism of PVA approaches (Ruffino *et al.* 2020). Identifying connectivity between populations is also important in assessing the impacts of offshore wind farms to specific populations, especially Special Protection Areas (SPAs), and in identifying source or sink populations (Black & Ruffino 2020; Ruffino *et al.* 2020). As part of the Habitats Regulations Assessment or Appraisal (HRA) developers are legally required to assess whether offshore wind farm developments will have an adverse effect on protected sites, such as SPAs, and their protected features, with demographic models being an important part of these assessments (Cook *et al.* 2019).

Adult dispersal

Once recruited to a breeding colony, site faithfulness, or philopatry, by adult Kittiwakes is generally considered to be strong, with low levels of breeding dispersal (Coulson & Wooller 1976; Coulson & Strowger 1999). However, although there is little published quantitative information on its frequency, several studies have reported that emigration of breeding adults does occur occasionally, particularly linked to breeding failures caused by local disturbances such as predation or ectoparasitism, with dispersal occurring at local (within-colony) and regional (among-colony) spatial scales (Danchin *et al.* 1998; Ponchon *et al.* 2015; Acker *et al.* 2017). On the Isle of May (East Scotland), a decline in resighting probability of colour-ringed birds since time of ringing was also attributed to the dispersal of breeding adults (Frederiksen *et al.* 2004a).

The only reported rates of breeding adult dispersal in the literature were from the long-term colour-ringing data in Brittany, where the mean dispersal rate for breeding adults was lower in an increasing colony (0.012 ± SD 0.018) than a declining colony (0.062 ± 0.045) (Danchin & Monnat 1992), suggesting that dispersal contributes to apparent population change at a site level (although both of these rates are low in a population context). In Brittany, dispersal of breeding adults within a colony was influenced by the reproductive success of surrounding conspecifics as well as their own, with individuals moving from cliff areas of low productivity to those with higher breeding success (Danchin & Cam 2002; Cam *et al.* 2004). Therefore, the extent of dispersal by breeding adults will likely depend on the success of the colony, or sub-colony, with low dispersal on productive breeding cliffs compared to cliffs which experience significant breeding failures (Danchin *et al.* 1998). Furthermore, failed breeders on productive cliffs can remain in the vicinity of their nest during the remainder of the season, whereas failed breeders on unproductive cliffs tended to immediately desert their nest (Cadiou *et al.* 1994). Conversely, in Alaska, breeding Kittiwakes showed a high level of site faithfulness to breeding cliffs/nest sites even after long periods of poor reproductive success (Hatch *et al.* 1993; Suryan & Irons 2001). One reason proposed for this discrepancy is the potential difference in life histories of Kittiwakes between the two oceans, with Pacific Ocean Kittiwakes having higher survival and age of first breeding, but lower breeding success, compared to their Atlantic counterparts, which may have led to a more conservative tendency to disperse (Hatch *et al.* 1993; Golet *et al.* 1998; McKnight *et al.* 2019).

Several studies based on short-term GPS deployments in Eastern Finnmark, Norway also showed that breeders which failed during incubation, whether through natural predation of eggs or experimental manipulation of nest contents, made prospecting visits to other areas of their breeding colony and other colonies within the region at distances of up to 40-50 km (Ponchon *et al.* 2014, 2015, 2017).

For single colony studies, estimates of adult dispersal are likely to be underestimated as individuals that emigrate have a lower probability of being detected, unless the emigration is temporary (Chambert *et al.* 2012). Therefore, survival rate estimates from single colonies, especially colonies which are subject to colony disturbances or have poor breeding success, are likely to be less accurate than those carried out over multiple colonies. This highlights the importance of searching for marked individuals in buffer areas and colonies around the focal study colony, especially if local breeding failures occur within the study site, to improve the accuracy of all demographic parameter estimates, not just dispersal (Ponchon *et al.* 2018).

Local dispersal within the colony can usually be accounted for by searching buffer areas around the focal site, where accessible. However, the likelihood of detecting individuals that disperse away from the colony will depend on the distances searched for marked individuals. This requires an understanding of how far breeding adult Kittiwakes might disperse, which likely varies by colony/region. Within the literature, the effort to find marked individuals away from the study colony varied considerably, as did the distances searched away from the study colony, if at all, for example: 10 km (Goutte *et al.* 2010), 50 km (Danchin & Cam 2002), 150 km (Danchin *et al.* 1998) and 250 km (Coulson & Strowger 1999), although resighting effort at a particular location in these studies is likely to be lower the greater the area covered.

Knowledge gaps: Dispersal by breeding adults is thought generally to be low, but is relatively poorly characterised, both in terms of frequency and the spatial scale over which individuals disperse, and how this may vary between the sexes.

Natal dispersal

In contrast to breeding adult dispersal, natal dispersal is considered to be relatively high in Kittiwakes. However, there is likely to be considerable heterogeneity in this value, both within and between colonies. Coulson and Neve De Mevergnies (1992) reported that 36% of young Kittiwakes were philopatric based on colour-ringing and ringing recoveries. A mean probability of dispersal of 0.89 was reported at North Shields, based on the estimate that around 11% of each cohort recruited to the natal breeding colony (Porter & Coulson 1987). Over a longer timeframe, colour-ringing from two northeast England colonies revealed 23% of recruits to North Shields over 36 years were philopatric compared to 4.2% at Coquet Island over 16 years (Coulson & Coulson 2008). All studies reported a higher proportion of males than females recruiting to their natal colony (Wooller & Coulson 1977; Coulson & Neve De Mevergnies 1992; Coulson & Coulson 2008; Coulson 2011). At the smaller scale of the cliff, or sub-colony level, Boulinier *et al.* (1997) reported that 14.5% of 807 colour-ringed individuals recruited to their natal cliff within the colony.

In terms of how far individuals disperse away from the natal colony, based on UK ringing recoveries and colour-ring resightings, Coulson and Neve De Mevergnies (1992) estimated that the majority (79%) of Kittiwakes recruit to colonies within 100 km of their natal colony, with a second small peak of recoveries between 400-900 km.

Evidence that recruitment is higher in successful colonies, or in the year following high local breeding success, has been observed in Brittany and Prince William Sound, Alaska, with low breeding success resulting in emigration of breeders (Danchin *et al.* 1998; Suryan & Irons 2001). Immigration to successful colonies will likely be driven by a combination of recruitment of new individuals into the breeding population as well as dispersal by breeding adults. In Prince William Sound, increases in the size of colonies with successful breeding productivity and the decline of colonies with poor productivity has been suggested to indicate high natal philopatry (Suryan & Irons 2001).

The natal dispersal of Kittiwakes, in addition to occasional breeding adult dispersal, indicates that Kittiwake colonies are unlikely to be closed populations. Connectivity between Kittiwake populations has also been suggested based on microsatellite markers sampled from 22 colonies across their range. Kittiwake populations had only a weak structure at large spatial scales indicating frequent dispersal between populations (McCoy *et al.* 2005; see section 5.7.2 for more details).

Knowledge gaps: Although natal dispersal is documented to be relatively high, empirical data on dispersal rates and distances are scarce, and only available at a limited number of locations. Therefore, it is uncertain whether these dispersal rates and distances will be similar in other regions across the UK.

2.3.6 Density-dependence

The second major assumption of demographic models used in impact assessments involves density-dependence, which describes how population growth rates are regulated by population density. Such dependence may be compensatory, i.e. at high population levels, the value of the growth rate falls, reducing future population growth, for example, due to increased intra-specific competition for food resources or nest sites. Alternatively dependence can be depensatory, meaning that as the population falls so too do certain demographic rates, such as survival or productivity, exacerbating declines (Horswill *et al.* 2017), for example, increased nest predation due to low nest density, which results in declining population growth rates. Where there is no strong, clear evidence that a population is operating under density-dependent mechanisms a precautionary approach is taken, of using either:

1) density-independent models, with the assumption that birth and death rates within a colony/population are independent of density, or
2) a range of density-dependent structures, including depensation. Density-independent models are considered to give a maximum estimate of mortality from offshore wind farms, and therefore are considered to be more precautionary, however, this assumes compensatory density dependence. If the density dependence is depensatory, then mortality will likely be underestimated. Including a range of density-dependent structures in models is therefore currently the recommended approach in PVAs (Horswill *et al.* 2017). To achieve greater realism to PVA approaches it is important to obtain empirical data to test these assumptions.

Any demographic rate may be density-dependent, that is its value is contingent on the number of individuals present in the population. There is some evidence that compensatory density-dependence processes occurs in Kittiwakes populations related to recruitment, survival and population growth (Horswill & Robinson 2015); with a compensatory response meaning that variation in population density results in reduced population growth at high densities, and increased growth at low densities.

Competition for nest sites has been observed to restrict age of first breeding and therefore recruitment, with higher recruitment rates reported at small colonies (Coulson 1983; Porter & Coulson 1987; Coulson & Coulson 2008). Prior to the mid-1980s, there was also a relationship between colony size and the rate of increase in expanding colonies in Britain, with greater colony growth in small compared to large, dense colonies (Coulson 1983; Porter & Coulson 1987). It should also be noted that both depensatory and compensatory density-dependence processes have been reported in relation to productivity in Kittiwakes (Coulson & White 1958; Coulson 1971). However, all these studies were undertaken when the status of Kittiwake populations was more favourable.

No evidence for density-dependent processes acting on productivity, growth rate or colony size was observed in three regional-scale Kittiwake studies (Frederiksen *et al.* 2005b; Sandvik *et al.* 2014; Carroll *et al.* 2015). Density-dependence is typically a greater issue at the site or colony level than at the national level, for example when assessing the impact of offshore-wing farms on specific SPAs. To fully understand density-dependence mechanisms it is necessary to also understand the underlying environmental drivers, which requires a detailed research programme. Therefore, although understanding density-dependent processes may be important in improving realism of demographic models (Miller *et al.* 2019), given the other larger uncertainties in Kittiwake population processes, we do not consider density-dependence any further. However, empirical data on demographic rates collected from a large-scale colour-ringing project will likely be useful to feed into more detailed research into density-dependent processes in Kittiwakes.

2.3.7 Resighting probabilities

Estimation of survival relies on re-encountering individually marked birds. Birds may be marked with long-lasting metal rings, varying combinations of colour-rings (one of which might be engraved with alpha-numeric characters reducing the number of rings required to identify an individual) or electronic tags. Survival may be estimated from metal rings, either by recapturing marked individuals to examine the ring, or from reports of marked birds found dead, often at some distance from the site of ringing. Colour-marks are usually observed at the colony of marking and, as the individuals do not need to be recaptured, usually benefit from higher re-encounter rates. Survival probabilities estimated from recapture/resighting studies, though, are confounded by emigration, whereas survival estimated from dead recoveries more often approximates ‘true’ survival (Robinson & Ratcliffe 2010).

Adults

To ensure the precise and accurate estimates of demographic rates, particularly survival, re-encounter probabilities need to be as high as possible, ideally close to 1 (Lebreton *et al.* 1992; Martin *et al.* 1995), although studies with lower re-encounter probabilities can yield useful estimates if a sufficient number of individuals are marked (Horswill *et al.* 2018, see also section 3).

The resighting rates reported in the literature and from unpublished mark-recapture studies were variable. In general, those published in the literature were relatively high as most involved colour-ringed individuals, rather than metal-ringed only, and considerable resighting effort as part of formal studies, which resulted in high detection rates. It is notable that all resighting encounters were generated by the project teams, rather than through ‘citizen science’ projects. For sites where a high proportion of nests were accessible and intensively searched, very high resighting probabilities of adults of almost 1 were reported, for example in Brittany (Cam *et al.* 1998, 2002) and Middleton Island, Alaska (Hatch *et al.* 1993). Lower resighting probabilities were reported on the Isle of May (0.90, Harris *et al.* 2000) and at Shoup Bay, Alaska (0.81, McKnight *et al.* 2019). Although these colonies were also relatively intensively monitored, not all areas of the colonies could be easily viewed, and not all nearby colonies were searched for dispersed individuals.

Participants in the BTO’s Re-trapping Adults for Survival (RAS) scheme gather data on adult survival. Resighting probabilities varied across the five RAS sites in the UK (operated mostly by volunteers) where it has been measured. The two RAS sites that recapture metal-ringed only Kittiwakes had recapture probabilities of 0.46 and 0.48. The resighting probabilities of the three RAS sites that resight colour-ring individuals ranged from 0.36 to 0.84. The lower probability of 0.36 is for an island colony where most effort to resight marked individuals is only carried out during (a limited number of) ringing visits. Conversely, the two RAS sites with higher resighting probabilities (0.72–0.84), are mainland colonies that colour-ring both chicks and adults, and where between 5 and 20 additional visits are made to resight individuals on top of ringing visits (see also section 3.4.3 for a more formal consideration of resighting probability in relation to number of visits). The intensity of effort put into resighting marked individuals can therefore have a large impact on resighting probabilities, influenced by the number of visits and people involved, as well as the time of the breeding season searches take place. Furthermore, resighting probabilities can vary individually depending on the age, sex, breeding and social status of individuals, as well as colony characteristics, for example, how much of the colony is visible to observers.

The detection probability of marked individuals varies throughout the breeding season (Harris & Calladine 1993; Chambert *et al.* 2012). In Kittiwakes, pre-laying is the most successful period for resighting marked breeding adults, when settling and building the nest, and their legs are easier to observe. Chick-rearing can also be moderately successful when brooding has stopped, with incubation being the least successful period (Harris & Calladine 1993; Chambert *et al.* 2012). Resighting probability was found to vary in Kittiwakes based on the timing of the breeding season, their own breeding performance and that of their cliff nesting neighbours, with relatively high detection probabilities on successful cliffs, and very low on cliffs where failure was high, as failed breeders no longer attend the colony regularly (Chambert *et al.* 2012; Ponchon *et al.* 2018). This was also evident at the individual level, with lower resighting probabilities reported for failed breeders than successful breeders, which are more likely to be site faithful and have higher nest attendance (Danchin *et al.* 1998; Boulinier *et al.* 2008; Chambert *et al.* 2012).

Individual Kittiwakes may also change nest sites within a breeding colony, moving distances from 30 m up to 2.5 km in large colonies, which may reduce the chances of resighting these individuals (Hatch *et al.* 1993; Danchin & Cam 2002). Searching for marked individuals in buffer areas around the main study-sites and colonies not only improved dispersal estimates but also improved the accuracy of survival estimates closer to true survival compared to single-site designs, and increased the resighting probability by 9% (Ponchon *et al.* 2018). Danchin *et al.* (1998) reported that 84% of non-breeding adults were observed regularly during the breeding season in years they skipped breeding, therefore searching more widely for colour-ringed individuals may also increase the detection rates of non-breeding adults.

Knowledge gaps: Adult resighting probabilities for colonies where intensive searches for marked individuals are undertaken are relatively well characterized. However, the ability to achieve precise and accurate resighting probabilities are influenced by our knowledge of dispersal and incidences of nonbreeding, which will likely show high heterogeneity across regions and time.

Juveniles and Immatures

Estimating resighting probabilities for juveniles and immatures is challenging given that they are largely oceanic during the first few years after fledging, as well as having relatively high level of dispersal to colonies other than their natal colony and higher mortality. However, estimates have been made based on the low number of immatures that do prospect colonies in the years before they recruit. In Brittany, age-specific resighting probabilities have been estimated for Age 1, (0.082 ±0.006 SD), Age 2 (0.687 ±0.011), Age 3 (0.931 ±0.002) and Age 4 plus Kittiwakes (0.965 ±0.001; Cam *et al.* 2005). Whilst, in Shoup Bay, Alaska, McKnight *et al.* (2019) reported resighting probabilities estimates for juveniles (0.09, 95% confidence intervals = 0.08–0.10) and two-year-old breeders (0.27, 95% CI = 0.24–0.29), as well as for prerecruitment adults (0.53 , 95 % CI = 0.47–0.57) and post-recruitment adults (0.81 , 95% CI = 0.77–0.83).

Prospecting of immatures and pre-breeding adults can occur at colonies later in the breeding season (Boulinier *et al.* 1996), therefore searching for marked individuals during chick rearing, for example, may increase the potential for detecting prospecting individuals of younger age classes.

Knowledge gaps: As with survival, juvenile and immature resighting probabilities are poorly quantified and highly uncertain largely due to rarely being detected at the breeding colony in their early years as well as their assumed lower survival and high natal dispersal.

Table 2.1. Summary of the demographic rates extracted from the literature and unpublished Kittiwake ringing studies. For adult survival, where multiple studies reported estimates for the same location and similar time frames, we include the value from the longest-time series.

Colony	Country/ Region	Study period	Mean	SD	Reference
Adult survival					
Chisik-Duck Islands, Lower Cook Inlet	Alaska	1997-2001	0.93	0.03	Piatt 2004
Gull Island, Lower Cook Inlet	Alaska	1997-2001	0.86	0.04	Piatt 2004
Middleton Island	Alaska	1987-1991	0.93		Hatch *et al*.1993
Shoup Bay, Prince William Sound	Alaska	1995-2010	0.86	0.05	McKnight *et al.* 2018
Bulbjerg	Denmark	1992-2010	0.82		Lerche-Jørgensen *et al*. 2012
Brittany	France	1989-2000	0.79	0·02 (SE)	Cam *et al*. 2003
Hjelmsøya	Norway	2005-2017	0.86	9.31	SEAPOP
Hornøya	Norway	1991-2017	0.84	9.96	SEAPOP
Runde	Norway	2011-2017	0.81	0.00	SEAPOP
Anda	Norway	2006-2017	0.84	6.32	SEAPOP
Røst	Norway	2004-2017	0.84	7.63	SEAPOP
Sør-Gjeslingan	Norway	2012-2017	0.67	9.88	SEAPOP
Bjørnøya	Norway	2005	0.88		SEAPOP
Isfjorden	Svalbard	2010-2016	0.86	10.02	SEAPOP
Kongsfjorden	Svalbard	2007-2010	0.85		Goutte *et al.* 2015
Canna	UK	<2002-2019	0.85	0.02	BTO RAS
Colonsay	UK	<2002-2019	0.90	0.02	BTO RAS
Fair Isle	UK	1986-1999	0.83	0.34	Rothery *et al*. 2002
Farne Isles	UK	1956-1958	0.93		Coulson & White 1959
Foula	UK	1987-1997	0.81	0.13	Oro & Furness 2002
Isle of May	UK	1986-2002	0.88	0.09	Frederiksen *et al*. 2004a
Lowestoft	UK	2004-2019	0.79	0.02	BTO RAS
North Shields	UK	1954-1985	0.79	0.08	Aebischer & Coulson 1990
North Shields	UK	1991-1993	0.84	0.07	Fairweather and Coulson 1995
Puffin Island, Anglesey	UK	<2002-2019	0.85	0.01	BTO RAS
River Tyne	UK	1990-1998	0.78	0.11	Coulson & Strowger 1999
Skomer	UK	1978-2018	0.86		Wilkie *et al*. 2019
Sumburgh Head, Shetland	UK	1991-1995	0.78		Walton *et al*.1997
Trewavas Head	UK	2016-2018	0.90	0.03	BTO RAS
Juvenile survival					
Farne Isles	UK	1956-1958	0.79		Coulson & White 1959
Recruitment					
Fair Isle	UK	1986-1999	0.20		Rothery *et al*. 2002
North Shields	UK	1954-1978	10.4		Coulson & Porter 1985
Age of first breeding					
Shoup Bay, Prince William Sound	Alaska	1979, 1988-2008	7.00	1.41	McKnight *et al*. 2019
Brittany	France	1979-1983	3.90	0.83	Danchin & Monnat 1992
Brittany	France	1987-1999	3.96		Cam *et al*. 2002a
North Shields	UK	1955-1974	4.90		Wooller & Coulson 1977
North Shields	UK	1954-1984	4.54	1.46	Porter & Coulson 1987
Incidences of non-breeders					
Shetland	UK	1980-1981	0.17		Richardson 1985
Marsden Bay	UK	1953-1954	0.19		Coulson & White 1956
Incidences of non-breeding adults					
Brittany (increasing colony)	France	1979-1988	0.18	0.19	Danchin & Monnat 1992
Brittany (declining colony)	France	1979-1988	0.21	0.21	Danchin & Monnat 1992
Natal dispersal					
NE England	UK	1923-1987	0.64		Coulson & Neve de Mevergnies 1992
Coquet Island	UK	1991–2006	0.96		Coulson & Coulson 2008
North Shields	UK	1954-1984	0.89		Porter & Coulson 1987
North Shields	UK	1955–1990	0.77		Coulson & Coulson 2008

Adult breeding-patch fidelity					
Brittany	France	1983-1994	0.16		Boulinier *et al*. 1997
Adult dispersal					
Brittany (increasing colony)	France	1979-1988	0.01	0.02	Danchin & Monnat 1992
Brittany (declining colony)	France	1979-1988	0.06	0.05	Danchin & Monnat 1992

Table 2.2. Approaches used to estimate Kittiwake demographic rates as reported in the studies from the literature review.

Demographic rate	Approaches used to obtain estimates
Adult survival	Ringing (metal-only or also colour-rings)
Juvenile / immature survival	Ringing (metal-only or also colour-rings)
Recruitment	Ringing (metal-only or also colour-rings)
Age of first breeding	Colour-ringing
Instances of non-breeding	Colour-ringing Ratio of immatures and adults to AON
Natal dispersal	Colour-ringing Population genetic structures of parasites and hosts
Adult dispersal	Colour-ringing Deployment of short-term GPS devices

2.4 Drivers of Kittiwake population change

The UK Kittiwake population has declined dramatically since the 1986 Seabird Monitoring Programme baseline, with a decline in the abundance index of 65% reported in 2018 (JNCC 2020). As surface feeders, Kittiwakes are sensitive to prey availability in the water column (Furness & Tasker 2000), and recent declines in UK populations have been linked to changes in local prey availability, particularly of sandeels, an important prey item of Kittiwakes (Lewis *et al.* 2001; Bull *et al.* 2004), with breeding success and survival negatively affected by reduced sandeel availability (Oro & Furness 2002; Frederiksen *et al.* 2005a). The large declines in Kittiwake productivity and abundance in the North Sea and Northern Isles were attributed to reduced sandeel availability, driven by over-fishing and climate change, as well as a lack of alternative prey (Hamer *et al.* 1993; Rindorf *et al.* 2000; Heubeck 2002; Frederiksen *et al.* 2004b; Eerkes-Medrano *et al.* 2017; MacDonald *et al.* 2017; Olin *et al.* 2020). There is regional variation in the relationship between sandeel abundance and Kittiwake productivity across the UK, largely driven by the availability of alternative prey in some regions, for example Herring *Clupea harengus* and sprats in the Celtic Sea (Chivers *et al.* 2012; Lauria *et al.* 2012). There is also a contrast in Kittiwake population declines between the east and west coasts of the Britain (Cook *et al.* 2011), attributed to regional differences in climate and diet composition (Lauria *et al.* 2012, 2013).

Although poor foraging conditions largely influences Kittiwake productivity, prey abundance can also affect adult survival through carry over effects of foraging conditions during the breeding season, for example adults with greater body mass following the breeding season had higher survival rates (Oro & Furness 2002).

Predation by a range of predators can directly affect Kittiwake productivity and survival, and therefore influence population size at the local level (Heubeck *et al.* 1997; Votier *et al.* 2004; Collins *et al.* 2014). Adverse weather can also impact both survival and productivity with heavy rainfall and wind resulting in reduced chick growth and higher chick mortality (Turner 2010; Christensen-Dalsgaard *et al*. 2018), especially where storms wash entire nests away (Brown *et al*. 2004; Newell *et al*. 2015). Adverse weather is most likely to affect Kittiwake survival rates during the non-breeding season, especially where it prevents foraging, causing starvation and wrecks of immature and adults (McCartan 1958; Craik 1992; Morley *et al.* 2016). Bycatch associated with gillnet fisheries can also impact adult survival in some locations, such as Norway (Bærum *et al.* 2019).

Wind farms also have the potential to directly affect adult, and immature, survival rates through mortality caused by direct collision with offshore wind turbines, with Kittiwakes classified as being at high collision risk (Furness *et al*. 2013). There appears to be little evidence that Kittiwakes are displaced by offshore wind farms (Furness 2016), although modelling has shown that displacement and barrier effects may negatively affect Kittiwake survival and breeding success at certain colonies (Searle *et al.* 2014).

Reduced breeding success has been identified as a key driver of UK population declines in Kittiwakes (Coulson 2017). However, it can be difficult to establish the impacts of reduced survival rates on Kittiwake abundance / colony status, therefore it cannot be ruled out that survival has also had an important role, especially given that in long-lived seabirds population size is typically more sensitive to variation in survival than productivity (Sæther & Bakke 2000).

2.5 What are the key demographic rates?

In long-lived species, such as Kittiwakes, population growth rate is most sensitive to variation in adult survival rates (Sæther & Bakke 2000; Gressetvold 2013). Further, a major determining factor of population size is the rate of recruitment to a breeding colony, which will be influenced by juvenile and immature survival, natal dispersal and age of first breeding (Clobert *et al.* 1993). Therefore, it is important to obtain more precise estimates of these demographic rates given their importance in determining recruitment to the breeding population. However, these demographic rates may not be the most important factors from a stakeholders perspective, in terms of which result in the greatest uncertainty in current PVAs used to assess the impact of offshore wind farms on Kittiwake populations as part of the consenting process.

The relative importance of different demographic rates to population growth rates can be determined from a matrix-like summary, the projection matrix (Caswell 2000). This specifies the transitions (in terms of fecundity and survival rates) between one age or stage and the next. For birds, age-based (annual) models are most appropriate and these so-called Leslie matrices form the basis of most PVA (Cook & Robinson 2016). The relative importance of demographic rates can be quantified by the sensitivity and elasticity of these matrices. These numbers represent the absolute and relative impact on the population growth rate of small perturbations of each of the demographic rates (Caswell 2000). Populations are most sensitive to the demographic rates with highest elasticity, i.e. the rates for which a small proportional change in value has the greatest effect on overall population growth rate. However, before these quantities can be calculated it is necessary to specify the age-specific demographic rates, which, as we have seen, are poorly known for Kittiwakes.

Summarising the dynamics in a numerical matrix form means the elasticity (or sensitivity) of population growth rates to the different demographic rates is dependent simply on the values of those rates, not the species identity per se, therefore, lessons can be learned from species with similar demographic rates. That is, we would expect most seabird species to exhibit similar patterns when it comes to the extent of influence of demographic rates on population growth. Thus, although we know little about the age-specific demographic rates in Kittiwakes, we can apply insights gained from knowledge of other species to estimate the likely relevance of these rates.

There is limited information in the published literature on the relative contributions of demographic rates to population growth rate in Kittiwakes, in fact there are very few species for which fully age-specific demographic rates are known with any certainty. Among seabirds, the best example comes from a long-term monitored population of marked Southern Fulmars *Fulmarus glacialoides*, a close relative of the Northern Fulmar *Fulmarus glacialis*, and which has fecundity and survival rates similar to Kittiwakes (Jenouvrier *et al.* 2005), so we can use this as a surrogate to make an assessment of the importance of different demographic rates in Kittiwakes. As predicted, the elasticity of adult survival rates was high, but larger temporal variations in the proportion of adults reproducing in a year and their average breeding success meant that these variables had a greater impact on the realised population growth rate, despite their weak elasticities. **Immigration was also observed to have a significant role in the population dynamics of Southern Fulmars** (Jenouvrier & Barbraud 2003; Jenouvrier *et al.* 2005). More generally, across North Atlantic seabirds, it seems that **recruitment into the breeding population (i.e. the combination of fecundity and juvenile/immature survival) has had the greatest impact on population dynamics** (Sandvik *et al.* 2012). However, few environments are actually in an equilibrium state and variability in demographic rates (and covariation between them), both temporally and between individuals, can be equally important (Tuljapurkar *et al.* 2009). Adult survival rates are typically less variable than either immature survival rates or fecundity (Wooller *et al.* 1992; Sæther and Bakke 2000), as in the fulmar example, meaning identifying the rate that is actually the most important in any particular location (rather than that which is theoretically the most important) can be difficult and requires good information about all demographic rates; most of which we currently lack empirical evidence for in Kittiwakes.

Both the ‘true’ biological value of demographic rates, and our knowledge of them, varies. Being able to use representative values in a PVA is clearly critical if realistic projections are to be obtained. To assess the importance of each of the demographic rates we first constructed a Leslie matrix model with plausible parameters for each rate that reproduced the observed Kittiwake population change between the Seabird Colony Register and Seabird 2000 (a 75% decline, equivalent to about a 1.8% per annum change, first row of Table 2.3). It should be noted that the precise values chosen for each are arbitrary; many other combinations of parameters would produce a similar predicted population change. For each parameter in turn we then assessed the population growth rate (λ) that would be expected for a plausible range of values (identified from the literature review, section 2.3). Greater differences ($\Delta\lambda$) in λ between the minimum and maximum values indicate greater sensitivity in the PVA to assumed values and hence greater uncertainty induced by their misspecification.

Table 2.3. Impact of varying key demographic parameters on population growth rate (λ) within plausible ranges. BS: Breeding Success (number of chicks per pair, based on JNCC 2020); pB: proportion of adults breeding (all adults are assumed to breed for simplicity); Age: at first breeding; ϕ_{juv}: apparent survival of first-year birds; ϕ_{imm}: apparent annual survival of immature (between age 2 and first-breeding age) birds; ϕ_{ad}: apparent annual survival of adult birds. Importance in the PVA models is indicated by the difference ($\Delta\lambda$) in values of λ over the plausible range. The first row indicates the reference scenario, see text.

BS	pB	Age	ϕ_{juv}	ϕ_{imm}	ϕ_{ad}	Varying	λ min	λ max	$\Delta\lambda$
0.7	1.0	4	0.35	0.8	0.85	-	0.982		
0.3 – 0.9	1.0	4	0.35	0.8	0.85	BS	0.919	1.008	0.089
0.65	0.7 – 1.0	4	0.35	0.8	0.85	pB	0.952	0.982	0.030
0.7	1.0	3-5	0.35	0.8	0.85	Age	0.999	0.965	0.034
0.65	1.0	4	0.1 - 0.6	0.8	0.85	ϕ_{juv}	0.899	1.041	0.142
0.65	1.0	4	0.35	0.4 - 0.85	0.85	ϕ_{imm}	0.874	1.000	0.126
0.65	1.0	4	0.35	0.8	0.8 - 0.9	ϕ_{ad}	0.947	1.019	0.072

The greatest sensitivity of population growth rate was to juvenile and immature survival rates, in part because very little is known about what actual values these might take, so a wide range of values was considered plausible. It is known that the survival of first-year birds is low, but how low, and what determines variability in this, is largely unknown. An immature survival value of 0.79 is frequently used in PVA analysis (i.e. Searle *et al.* 2020). However, this value is estimated from a very small sample size (84 ring recaptures) using ad hoc methods at a time when Kittiwake population trends were increasing in contrast to recent declines (Coulson & White 1959). Furthermore, Coulson (2011) subsequently suggested that juvenile survival was more likely to be around 0.63, after re-calculating estimated first year mortality to take into account that mortality risk is likely to be higher during an individual's first year compared to later years. Immature survival is almost certainly higher than juvenile survival, and may even approach values for adult survival, but this too is unknown. It should be noted that in multi-colony context, dispersal away from the focal colony is numerically equivalent to a change in apparent survival, so it is also important to quantify these rates if colony-specific changes are of interest. At larger (regional/national) scales, dispersal represents a shifting of individuals rather than overall change in numbers per se so becomes less critical to quantify. Variation in adult survival and breeding success are better quantified, but the former varies relatively little and the latter has less influence, so quantifying these is of intermediate importance in assessing PVA outcomes. Variation in the age at first breeding, and the proportion of adults that bred each year (or, equivalently, the proportion of adults that skipped breeding, 1-pB) had relatively little impact on the PVA outcome.

2.5.1 Key demographic rates to include in the power analysis

To indicate the scale of colour-ringing and resighting effort required to obtain levels of empirical data on Kittiwake demographic rates that would reduce uncertainty in PVAs as part of offshore wind farm impact assessments a power analysis was conducted (section 3). Scenarios used in the power analysis were agreed in advance by the project team.

The power analysis was focused on apparent juvenile, immature and adult survival, given the importance of these demographic rates in maintaining population size at Kittiwake colonies, and their importance in assessing PVA outcomes. Colour-ringing can also provide useful empirical data on age of first breeding and incidences of non-breeding (Table 2.2), however, given that variation in these rates had relatively little impact on the PVA outcome they were not included in the power analysis. Adult dispersal was also not considered given that it occurs infrequently (section 2.3.4). Although variation in natal dispersal does occur more frequently, we have little data on the frequency and distances that could be used in a power analysis.

Accuracy of the power analysis outputs were assessed based on whether survival estimates were within 1 or 2% of true survival for adults as used by Horswill *et al.* (2018), and 10% for juveniles and immatures. We reduced the level of accuracy to 10% of juveniles and immatures given the obtaining 1-2% accuracy for these age classes is challenging given their low resighting rates and due high variability in juvenile and immature survival between years and cohorts (McKnight *et al*. 2019). Furthermore, current survival estimates for these age classes are highly uncertain, based on very limited empirical data, therefore even with this lower level of accuracy juvenile and immature estimates within 10% of true survival will provide more accurate estimates of these rates than what is currently used in PVAs.

To assess the scale of colour-ringing required to reliably estimate true survival rates power analysis scenarios were selected that accounted for variation in the sample size of individuals ringed, the resighting rate and the study duration (Yoccoz *et al.* 2001).

The different levels of adult colour-ringing effort included in the power analysis scenarios were selected based on current levels of Kittiwake ringing effort in the UK, and what level of ringing may be feasible. For the chick-ringing we selected three scenarios within the range of values used by Horswill *et al.* (2018; 50 - 1000 chicks ringed per year). The upper scenario of 500 chicks ringed each year was selected to provide an upper boundary where immature survival estimates within 10% of true survival may be achieved, and as this level of chick ringing could potentially be feasible across clusters of neighbouring colonies.

Variation in colour-ringing resighting probabilities for the power analysis scenarios were taken within the range of values reported in the literature (section 2.3.7) and that were over 0.70 to complement the values used in Horswill *et al.* (2018; where recapture probabilities ranged between 0.05 – 0.60). We also included a scenario which assumed heterogeneous resighting probabilities to account for individuals that show trap-happiness, where individuals are easier to locate after being first encountered, and trap-shyness, where individuals avoid being resighted.

We selected study lengths of 5, 10 and 20 years to include in the scenarios. The 5-year scenario was included given that this timescale is most relevant to the offshore wind industry. However, given the delayed maturity of Kittiwakes (section 2.3.3) scenarios of 10 and 20-years were also included as these timescales are likely required to obtain accurate estimates of survival, especially for juveniles and immatures.

As well as the extent of ringing effort required, it is also important to determine the scale of resighting effort required to obtain high resighting probabilities necessary to accurately estimate apparent survival rates. Occupancy models were used to determine the extent of colour-ringing resighting effort required, in terms of number of visits over the breeding season, to obtain resighting probabilities greater than 90%. To carry out this analysis, 17 years of data on Kittiwake resighting rates from the intensively monitored Isle of May colony were used.

Misreads of colour-rings by observers may also affect resighting probabilities, therefore this was explored by estimating resighting probabilities under three different misread scenarios: 0% probability of a misread (perfect reading of tags), 1% misreads probability and 5% misread probability. This range of scenarios was selected based on values recorded in similar field sighting studies (Tucker *et al*. 2019).

3 Analysis of power to estimate survival rates in a Kittiwake population

3.1 Power analysis conclusions

We assessed the feasibility of large-scale deployment of colour-ringing on Kittiwakes to obtain reliable estimates of key demographic rates of adult and juvenile survival and to detect change over time in these rates.

We also quantified how resighting probability depended on field effort for a specific colony (the Isle of May, east Scotland) to inform the feasibility of achieving a particular level of precision in the demographic rates.

We used a power analysis to investigate apparent adult and juvenile survival and detect variation in these rates over time. Data were simulated from a set of scenarios that varied the number of individuals ringed, juvenile survival, resighting probability by age, and the length of the study. A Cormack-Jolly-Seber method was used to estimate age-specific apparent survival and resighting probabilities from the simulated capture history data. To detect variation over time, changes in survival for adults and juveniles/immatures were introduced.

To understand the effect of misreads on resighting probability, misread probabilities were introduced at levels 0-5% into the analysis.

Key results from the power analysis are:

(1) **5-year studies were unable to provide a precision of 2% for estimates of adult survival or 10% for estimates of juvenile/ immature survival even under the highest levels of ringing effort considered in the scenarios**;

(2) **studies of 10 years or longer can provide these levels of precision, with the required levels of ringing effort dependent on the age classes of interest**; and

(3) **only 20-year studies gave sufficient power (>80%) to detect a 4%-point decrease in adult survival**. None of the other levels of effort considered gave greater than 80% power to detect any of the magnitudes of change considered.

To estimate intra-year resighting probability, full visit histories to the Isle of May between 1992 and 2019 were digitised. The data recorded adult bird presence by area and observer. A single-season occupancy model was fitted to each year of data with area of island as a covariate in the model.

Key results from the resighting analysis using Isle of May data showed that:

(1) Increased resighting effort (in terms of number of visits in the same year) led to increased resighting probability with 10 or more visits estimated to give greater than 90% resighting probability (from one observer);

(2) misread tags (0-5%) had a negligible impact on resighting; and

(3) there was some evidence that resighting levels varied by area, highlighting that extrapolating these findings to other sites or colonies should be done with caution.

Recommendations of how to extend the CJS model are set out at the end of the report, as well as an overview of alternate modelling approaches to address some of the limitations in potential sample size that can be realistically obtained from some kittiwake colonies.

3.2 Introduction

These analyses assess the feasibility of large-scale deployment of colour-ringing to improve estimated demographic rates for Kittiwake populations, in order to improve biological realism of models and result in less precautionary PVAs for offshore wind farms assessments. A key consideration when designing colour-ringing studies is to determine the resources required to collect sufficient data, such as the number of years that a study runs for, number of adults and chicks that need to be ringed in each year, and number of resighting visits to be conducted each year.

Power analysis provides a flexible and widely used analytical framework for informing such decisions (Steidl *et al.* 1997). Power analyses involve considering plausible hypothetical situations and assessing the level and form of sampling effort that would be required to yield acceptable outputs (e.g. accurate/precise estimates of key demographic rates, or power to detect temporal changes in these rates). Stakeholders can then use this information to determine whether realistic levels of resourcing will yield outputs with sufficient power to be of practical use, and to explore trade-offs between resourcing and power.

The general framework that we consider for the power analyses is shown in Figure 3.1. Accuracy, precision and power depend upon sample effort, such as number of years of data collection, number of individuals ringed per year, and annual resighting probability (which is a function of intra-annual field effort), and upon the demographic rates of the population (e.g. survival). The power analyses are divided into two distinct parts: Analysis 1 uses a simulation-based approach to investigate precision obtained for adult and juvenile survival rates under different scenarios of key parameters, and the power required to detect changes over time. Analysis 2 investigates the relationship between field effort and detection probability using data collected from the Isle of May, the site of long-running study with high levels of field effort. We treat these analyses separately because the data-driven approach will be dependent upon the logistics and protocol of the field site such as accessibility and selection, and training of observers, whereas the simulations should be more generalisable between differing populations or colonies.

The demographic rates within the analyses are adult and immature survival, and we consider the possibility that immature survival rates may vary with age. For long-lived species, such as seabirds, adult survival is the demographic rate with the highest elasticity (Sæther & Bakke 2000); however, other studies have also identified recruitment (a combination of fecundity and immature survival) as important in determining the dynamics of seabird populations (Sandvik *et al.* 2012). Adult and immature survival rates are both amenable to quantification through colour-ringing studies and both are potentially important drivers of seabird population viability. We consider apparent survival rather than true survival as paucity of information means that it is beyond the scope of these analyses to estimate age at first breeding and dispersal, emigration and immigration rates. Some of these additional rates, such as age at first breeding, could potentially be estimated from colour-ringing data using the Cormack-Jolly-Seber modelling framework considered here, but this is likely to depend upon the available data and the specific model structure. Theoretical analyses to determine feasibility to estimate these additional parameters (which are sometimes labelled identifiability problems or parameter redundancy) would need to be carried out in order to determine this, and this was beyond the scope of this project (McCrea & Morgan 2015; Cole 2020). Power would need to be considered separately for each of the additional rates that theoretically could be estimated.

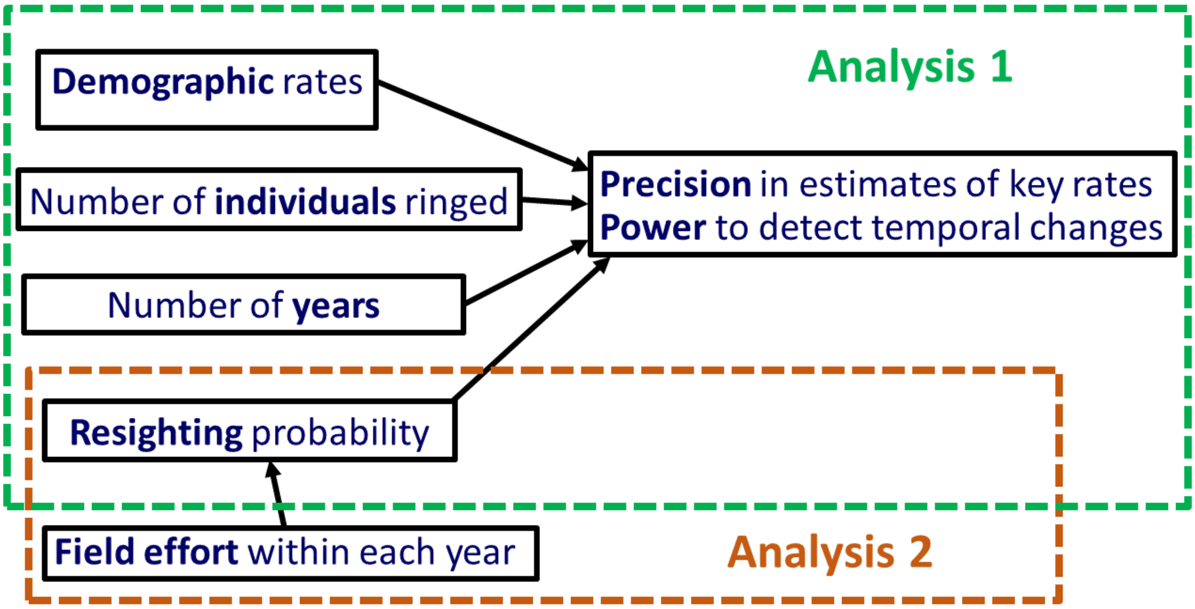


Figure 3.1. Summary of the overall approach to power analysis.

3.3 Methods

3.3.1 Overall approach

Our analysis is split into two main parts: Analysis 1 focuses upon quantifying the impacts of baseline demographic rates (as a proxy for the choice of colony) and factors relating to study design (number of years, resighting probability) upon precision to estimate key demographic rates (Analysis 1a), and the power to detect temporal changes in these rates (Analysis 1b). The overall structure of Analysis 1 is similar to that in Horswill *et al*. (2018), but with the crucial difference that the scenarios considered here, particularly for resighting probability, are selected so as to be plausible for colour-ringed birds (whereas Horswill *et al*. 2018, considered scenarios that were more plausible for mark-recapture studies).

Within this analysis, resighting probability acts as a proxy for field effort. The actual relationship between resighting probability and field effort (e.g. number of site visits per year) is complex and likely to vary substantially between colonies. Sufficient data are not available to estimate how this relationship varies between colonies, and we therefore do not attempt to include field effort (number of visits) within Analysis 1. However, data for one intensively monitored colony, the Isle of May, do allow us to estimate this relationship for one specific colony, and this in turn provides some information that is of wider applicability in selecting the number of visits at other colonies. In Analysis 2 we focus upon quantifying this relationship, using visit-level data for the Isle of May that have been digitized by UKCEH. We use occupancy models (MacKenzie *et al.* 2002) to quantify the resighting probability associated with a single visit and use this probability to show how the annual resighting probability varies with the number of visits, and the uncertainty associated with estimating this.

Misreading of rings is a potential issue as they create false-positive records of individuals, which can bias the estimation of survival rates (Burton 2000; Tucker *et al.* 2019). Within this analysis we explore the impacts of introducing hypothetical misreads at plausible rates upon resulting estimates of the resighting probability.

3.3.2 Analysis 1a - Accuracy of estimated demographic rates

We use a simulation-based approach to our power analyses. This approach is widely used and conceptually straightforward, and follows the approach used in Horswill *et al*. (2018). The approach involves:

i) simulating a large number of datasets;
ii) using each of these datasets to estimate the demographic rates of interest;
iii) summarizing results across the full set of simulations.

Analysis 1a uses this approach to assess accuracy in estimates of adult and juvenile survival by evaluating the proportion of simulations in which the estimated survival rates fall within 1% or 2% of the true value (used when generating simulations; thresholds defined in Horswill *et al.* 2018).

3.3.3 Data simulation

The number of adults and chicks ringed at occasion i are denoted as r_{a_i} and r_{c_i} respectively, where $i = 1, 2, \dots, T$ and T is the duration of the study in years. This gives a ringing schedule for adults which can be written as $\boldsymbol{r_a} = \left(r_{a_1}, r_{a_2}, \dots, r_{a_T}\right)$ and a schedule for chicks of $\boldsymbol{r_c} = \left(r_{c_1}, r_{c_2}, \dots, r_{c_T}\right)$. It was assumed that all ringed adults were ringed at age 4 and all ringed chicks were ringed shortly after hatching.

The three main processes assumed to take place during data simulation are: survival between sampling occasions, dispersal of birds to other colonies between sighting occasions, and resighting during sampling occasions. The assumptions surrounding each of these processes are described below:

1) **Survival**: Data were simulated such that individuals have lower survival as juveniles (the first year after hatching) than over the rest of their life, for which survival was assumed to be constant. Although immature survival rates of Kittiwakes are poorly characterised, McKnight *et al*. (2019) suggest that immature and adult survival rates are not dissimilar, at least for some cohorts. We write the annual juvenile survival probability as ϕ_j (survival of birds ringed as chicks) and the annual survival probability for individuals greater than one year old as ϕ_a.
2) **Resighting:** Individuals alive at a given sampling occasion have a resighting probability that is dependent on their age at that occasion, denoted by p_1 (age 1), p_2 (age 2), p_3 (age 3) and p_{4+} (age 4 or greater), where all individuals of age 4 or higher are assumed be breeding and have equal resighting probability.
3) **Dispersal:** For simplicity we assume that dispersal occurs between ages 3 and 4 (before age 4 resighting) with birds leaving the colony, never to return, with a dispersal probability denoted by d. In reality, dispersal will likely occur between ages 1 and 4, but the there are no data characterising the nature of this.

Capture histories were generated by applying a series of binomial distributions (Figure 3.2) corresponding to the assumptions outlined above and the ringing schedules defined by the scenarios (Table 3.1). This resulted in a matrix of capture histories where the number of rows corresponded to the number of birds ringed and the number of columns to the number of sampling occasions. Capture histories were accompanied by covariate matrices containing information about the age of each ringed animal at each sampling occasion.

We were limited in the number of simulations that could be run in the time available, so chose values within a plausible range (Table 2.1) for each rate as follows. The available information (section 2) shows that adult survival varies over a relatively small range of values, so we chose a mid-range value of 0.85 for all simulations. There is much greater uncertainty in the value of survival for pre-breeding birds. We considered juvenile survival (i.e. that of birds in their first year) to vary over the range of values estimated from the (limited number of) studies that have attempted to quantify this (section 2.3.2). For convenience, and in the absence of firm evidence to the contrary, we assumed that immature survival (i.e. that from 2-4 years of age) is the same as that of breeding birds (0.85). Resighting of colour-rings enables higher re-encounter rates than re-capturing metal-ringed birds (which Horswill *et al*. (2018) considered), so we considered resighting probabilities at the higher end of the range of plausible values to complement that study. To keep the number of simulations manageable, values of resighting probabilities of immature birds were considered to be constant fractions of the adult resighting probability and were informed by those achieved in the Brittany study (Cam *et al.* 2005).

Re-encounter probabilities are rarely truly homogeneous across all individuals, so we additionally considered one plausible scenario in which resighting probabilities differed between individuals based on their previous resighting history (mimicking the effect of trap-dependence, which is commonly encountered in such studies; Pradel & Sanz-Aguilar 2012). The number of individuals ringed was informed by current ringing effort (section 4.3) to indicate the relative value of achievable levels of effort.

All possible parameter combinations for the parameters included in Table 3.1 were considered. This involved considering 3 levels of each of juvenile survival Φj, study length T, chicks ringed per year r_{c_i}, and adults ringed per year r_{a_i}, along with 4 different adult resighting probabilities, p_{4+}. This gave a total of (3*3*3*4 =) 324 parameter combinations. We simulated 1000 datasets for each parameter combination, and we fitted a model to each, as described in the next section.

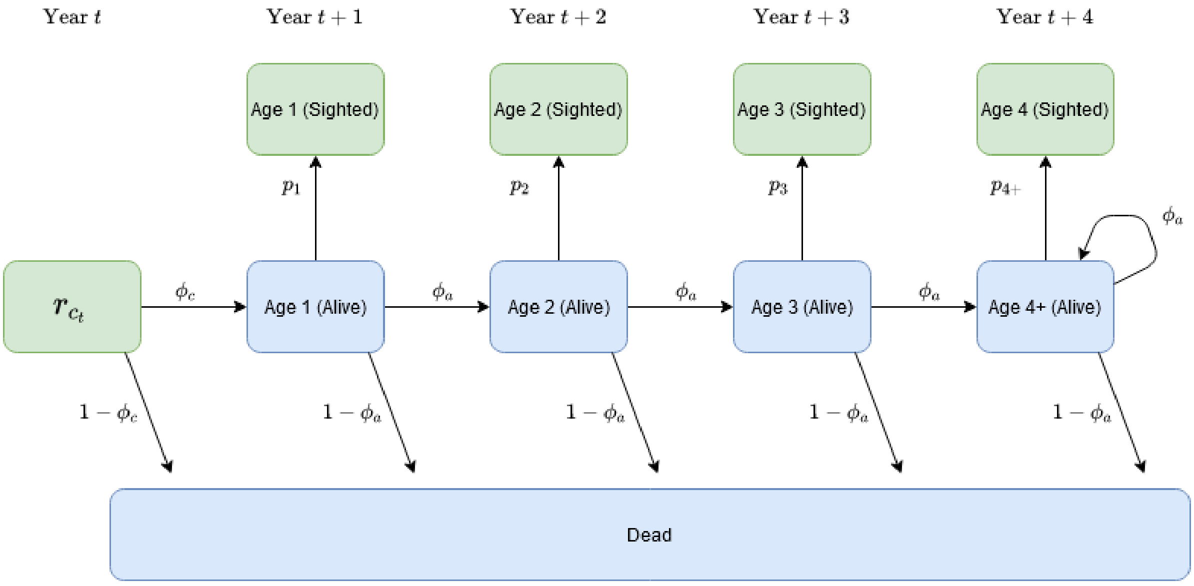


Figure 3.2. A flowchart representing how the capture histories of a cohort of juveniles ringed on year t are simulated. Blue boxes represented unobserved states and green boxes represent observed states.

Table 3.1. Parameters used to simulate data for Analysis 1a.

Parameter	**Value(s)**
Juvenile survival, ϕ_j	0.2, 0.4, 0.6
Adult survival, ϕ_a	0.85
Resighting probability at age 4+, p_{4+}	0.7, 0.8, 0.9, 0.9 and heterogeneous [1]
Resighting probability at age 3, p_3	$0.66p_{4+}$
Resighting probability at age 2, p_2	$0.33p_{4+}$
Resighting probability at age 1, p_1	0.08
Dispersal probability at age 4, d	0.33
Study length in years, y	5, 10, 20
Chicks ringed per year, r_{c_i} for all i	50, 200, 500
Adult ringing schedule, $\boldsymbol{r_a}$	Option A: 50 (year 1), 7 (subsequently) Option B: 75 (year 1), 36 (year 2), 15 (subsequently) Option C: 75 (year 1), 86 (year 2), 23 (subsequently)

[1] In one scenario heterogeneous resighting probabilities were assumed such that each of these probabilities was halved if the animal had not been resighted in the previous year simulating the effects of trap-dependence (Pradel & Sanz-Aguilar 2012).

3.3.4 Model fitting

We used the Cormack-Jolly-Seber (King *et al.* 2010) method to estimate age-specific apparent survival and resighting probabilities from the simulated capture history data using the R package *mra* (McDonald 2018) in R4.0 (R Core Development Team 2020). The fitted models estimate age-specific survival rates for animals aged 0-1 ($\hat{\phi}_j$), 1-2, 2-3, 3-4 and 4+ (all equal to $\hat{\phi}_a$). Likewise, we estimate age-specific resighting rates as $\hat{p}_1$, $\hat{p}_2$, $\hat{p}_3$ and $\hat{p}_{4+}$. The same model was fitted to all simulated datasets under all parameter combinations i.e. the model was not reformulated to capture heterogeneous resighting probabilities when these were included in the simulated dataset. This is appropriate because it allows evaluation of whether heterogeneous resighting probabilities, where present but not recognised, leading to issues in estimating demographic rates if (as would routinely be the case in practice) they are not accounted for within the analysis. The likelihood of the model is given in full in Appendix 1.

For some parameter combinations (particularly those with relatively low numbers of individuals ringed), a proportion of the models failed to robustly estimate all model parameters, returning greatly inflated or missing standard errors. Simplifications of the model were considered to try to obtain reliable estimates across all parameter combinations (e.g. combining survival and/or resighting rate estimates across ages 0-2 due to low survival and resighting probabilities in the first year). This made a small difference to the proportion of unreliable estimates. Even in the extreme case where two pairs of survival and resighting estimates were considered (a single estimate of resighting and survival for individuals younger than age 4 and a single estimate of resighting and survival for individuals older than age 4) model failures were still observed for some parameter combinations and simulated datasets. Given this, we chose to present results fitted to the full model described above alongside *failure rates* for each survival estimate and parameter combination. In doing so, we aim to highlight parameter combinations for which ringing effort may be insufficient to reliably fit a model to the data without making substantial simplifications. This also reflects real situations, where appropriate simplifications in fitting the model may not be known and a more conservative approach is to use a model that avoids making assumptions regarding commonality in survival or resighting rates between different age classes.

Beyond assessing model failure rates, accuracy was assessed by determining whether the estimated apparent survival values occurred within 1 percentage point or 2 percentage points of the true value. It should be noted here that we consider percentage points rather than actual percentage change e.g. if the true survival was 0.50, any estimates in the interval [0.49, 0.51] (inclusive) are within 0.01 of the true probability.

3.3.5 Analysis 1b - Assessment of temporal change

The approach to Analysis 1b was broadly similar to that for Analysis 1a, except that the focus was upon the power to detect change over time in demographic rates, rather than upon the precision involved in estimating time-constant demographic rates. All possible combinations of the parameter values given in Table 3.2 were considered in Analysis 1b.

The ability to detect a temporal change in survival rates was assessed by simulating a step decrease in survival of 0.5%, 1%, 2% or 4% halfway through the study (again we refer to percentage point changes rather than percentages of the original value). In the case of a 5 year study this decrease was placed between years 3 and 4 as the timing of the step change cannot coincide perfectly with the timing of a sample and this placement allows 2 resighting occasions before the change and 2 resighting occasions after. Survival rates were assumed to be static (i.e. neither increasing nor decreasing) across the study period with the exception of the step changes introduced in the simulation.

Table 3.2. Parameters used to simulate data for Analysis 1b.

Parameter	**Value(s)**
Juvenile survival, ϕ_j	0.4
Adult survival, ϕ_a	0.85
Resighting probability at age 4+, p_{4+}	0.7, 0.8, 0.9, 0.9 and heterogeneous[1]
Resighting probability at age 3, p_3	$0.66p_{4+}$
Resighting probability at age 2, p_2	$0.33p_{4+}$
Resighting probability at age 1, p_1	0.08
Dispersal probability at age 4, d	0.33
Study length in years, y	5, 10, 20
Chicks ringed per year, r_{c_i} for all i	200
Adult ringing schedule, $\boldsymbol{r_a}$	Option A: 50 (year 1), 7 (subsequently) Option B: 75 (year 1), 36 (year 2), 15 (subsequently) Option C: 75 (year 1), 86 (year 2), 23 (subsequently)
Juvenile survival step change, δ_j	0.04, 0.08, 0.16
Adult survival step change, δ_a	0.005, 0.01, 0.02, 0.04

[1] In one scenario heterogeneous resighting probabilities were assumed such that each of these probabilities was halved if the animal had not been resighted in the previous year simulating the effects of trap-dependence (Pradel & Sanz-Aguilar 2012).

The models fitted in Analysis 1b were identical to those in Analysis 1a except that additional parameters, representing step changes in survival, were included in the model. Analysis 1b focused upon the power to detect a step change, as in Horswill *et al*. (2018) - i.e. the proportion of simulations in which a significant ($p < 0.05$) step change in survival was detected. Whereas Analysis 1a focused solely upon parameter estimates, Analysis 1b considered p-values, which rely upon the calculation of standard errors for each of the parameters. Due to numerical issues in model fitting resulting in consistently inflated standard errors from the *mra* package, we generated new estimates of the parameter standard errors using a bootstrapping approach as follows:

1) For each simulated dataset we extracted the fitted parameter values;
2) These fitted parameter values were used to simulate *b* new datasets and a model was fitted to each dataset in *mra;*
3) The standard deviation of the estimates of these *b* fitted models (having removed outliers for which the model did not provide reliable estimates) was used as an estimate of the standard error of the parameter values.

The bootstrapping procedure substantially increased computational time and so when estimating power, we simulated 100 datasets for each scenario and performed *b*=100 iterations of the bootstrapping procedure for each.

3.3.6 Analysis 2 - Effect of number of visits on resighting probability

Data on resighting rates (for adults only, empirical p_{4+}) within a season on the Isle of May were provided for 17 years from 1992 to 2019 inclusive. All resightings were of adult birds and recorded by area of the island and observer. The number of resighting attempts for each individual ranged from 1 to 32 per season. A data extraction exercise was undertaken by UKCEH for this project to synthesise full sighting histories at the individual level.

Kittiwake sub-colonies on the Isle of May are visited on multiple occasions each year. An analysis of resighting probability in relation to period of the breeding season demonstrated that the optimal time for resightings is the pre-laying period (Harris & Calladine 1993) and accordingly visits are focussed on that period in up to eight sub-colonies where Kittiwakes are colour-marked each year. In the absence of data from multiple colonies, these subareas provide an indication of the likelihood of variability between areas as a result of, for example, differing topography or accessibility. A full sighting history was available for 1992 only (contributing to the published study), but in subsequent years the field teams synthesised resightings as the number of occasions each individual was resighted in each year, not the dates on which these resightings occurred, because this simpler approach was sufficient for robust estimation of annual survival (e.g. Frederiksen *et al.* 2004a). However, in order to undertake a power analysis of resighting effort, full sighting histories are required including all occasions when individuals were not observed. This required UKCEH staff to revisit the raw data, which was not possible in the years until 2000 (when Dictaphones were used) but was possible thereafter by extracting the information from notebooks which were organised to a high standard and had been, in most cases, archived securely. As such, we were able to add a further 16 years from the period 2001-2019 inclusive to the 1992 data set, giving a 17-year data set of full sighting histories of all marked individuals.

To estimate the visit-level resighting probability we fitted single season occupancy models to each year of data according to the approach of MacKenzie *et al* (2002), using the *unmarked* R package (Fiske & Chandler 2011). The effect of area of the island on the detection probability was considered by its inclusion as a covariate in the model. Comparison of AIC scores suggested that the area affected detection probability in some years but not others. It was decided that area would be included in all models to account for this possible effect. It was not possible to account for any observer effect because there was often only one observer for a given year, making it impossible to separate observer and year effects, although it should be noted all sightings were by experienced observers, so any such effects are likely to be negligible. This approach assumes that there is no mortality or dispersal within a season (e.g. occupancy remains constant within a season). We also assume equal detection probabilities across individuals within a season.

To understand the effects of potential misreads on the resighting probability, we estimated resighting under three different misread scenarios: 0% probability of a misread (perfect reading of tags), 1% misreads probability and 5% misread probability. These values correspond to those seen in other field sighting studies (e.g. Tucker *et al*. 2019) and represent a realistic range of observer experience (the rate of misreads being inversely related to experience). Misreads were simulated in the data by assigning a proportion of sightings (corresponding to the stated misread probability) to other birds which were not sighted on that day but were present in the data. For ease these were assigned at random, but in practice there is likely to be heterogeneity in the likelihood an individual combination is misread depending on either the combination of colours (Burton 2000) or characters used (Tucker *et al*. 2019). For each misread scenario, 50 sets of simulated data were generated, and the model was fitted to each dataset (in the case without misreads no changes were made to the dataset). For each simulated dataset and year, an estimate and 95% CI of the resighting probability was produced. The median of the estimates (and upper and lower limits) across all years and simulated datasets were then calculated to provide an estimate and uncertainty for each combination of area, misread probability and number of visits within a season (ranging from 1 to 15).

3.4 Results

3.4.1 Analysis 1a – Estimating survival rates

Adult survival

The proportion of adult survival estimates within 1% of the true adult survival probability for each of the 324 parameter combinations is shown in Figure 3.3. None of the parameter combinations for a 5-year study results in over 50% of the estimates falling within 1% of the true value. For the 10-year studies, it is possible to achieve 80% of the estimates within 1% (0.01) of the true value, provided that the maximum number of chicks is ringed (500 per year) and that resighting (p_{4+} is 0.8 or 0.9), juvenile survival (ϕj is 0.4 or 0.6) and adult ringing (r_a is B or C) are also sufficiently high. For 20-year studies:

- More than 80% of estimates within 1% of the true value can be achieved at all levels of chick ringing, provided adult ringing (r_a is B or C) in particular is sufficiently intensive.
- More than 90% of estimates within 1% of the true value is achievable when at least 200 chicks per year are ringed (and some other specific conditions are met).
- There are also some parameter combinations where >95% of estimates are predicted to lie within 1% of the true value, most of which involve ringing either the maximum number of adults (yr1=75, yr2=86, yr3+=23) or chicks (500 per year) considered within the scenarios.

Including heterogeneity in capture probabilities, such that animals that were not sighted in a given year are half as likely to be sighted the next year, has a substantial negative impact on our ability to accurately estimate adult survival. This occurs due to two main factors. Firstly, the reduction in resighting probability reduces our ability to estimate the adult survival. Secondly, that heterogeneity is not captured in the model which means that the estimates of adult survival become biased as the resighting probabilities estimated do not reflect reality.

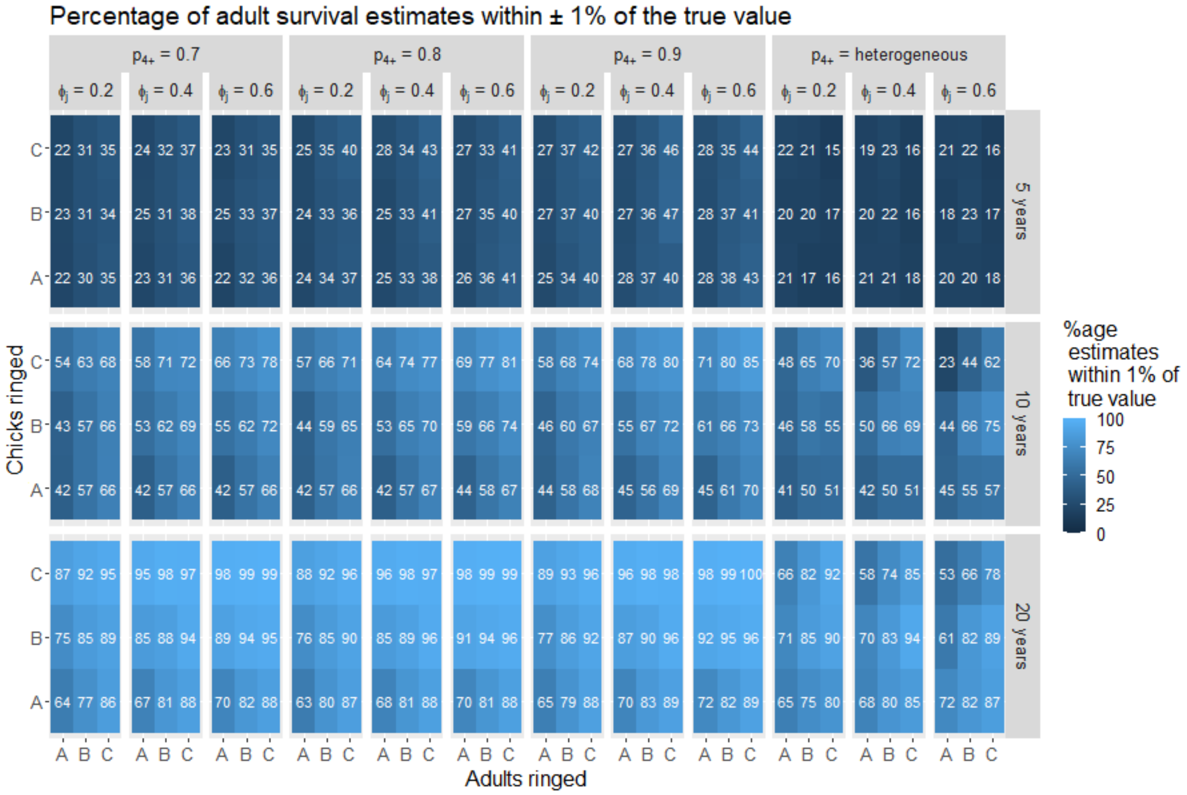


Figure 3.3. The percentage of estimates of adult survival within ± 1% of the true parameter value for all considered parameter combinations is shown, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study (y; 5,10,20 yrs).

If we increase the range of acceptable estimates to those within 2% (0.02) of the true value, as shown in Figure 3.4, we still fail to achieve satisfactory estimates in 5-year studies. However, several combinations for 10-year studies and all for 20-year studies give over 80% of estimates within 2% of the true value. Figure 3.5 shows the proportion of models that completely failed to estimate adult survival (i.e. where there were irresolvable technical problems in estimating model parameters) is notably higher for 5-year studies than for longer studies. Five-5-year studies ringing only 50 chicks per year give failure rates of up to 15%. When the study length is 10-years or longer, model failures are relatively rare for adult survival, though all failures are only avoided when the maximum number (200) of chicks are ringed. For 20-year studies, there are model failures if only the minimum number (50) of chicks are ringed.

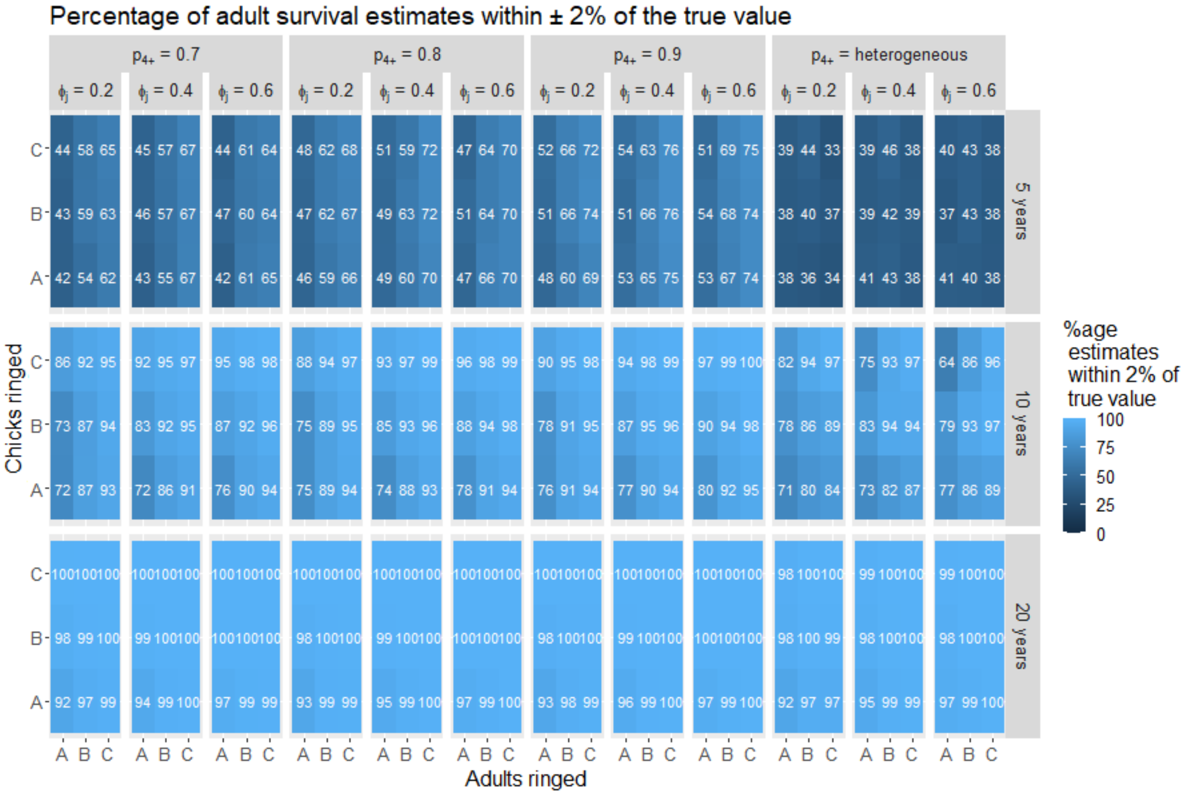


Figure 3.4. The percentage of estimates of adult survival within ± 2% of the true parameter value for all considered parameter combinations, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study (y; 5,10,20 yrs).

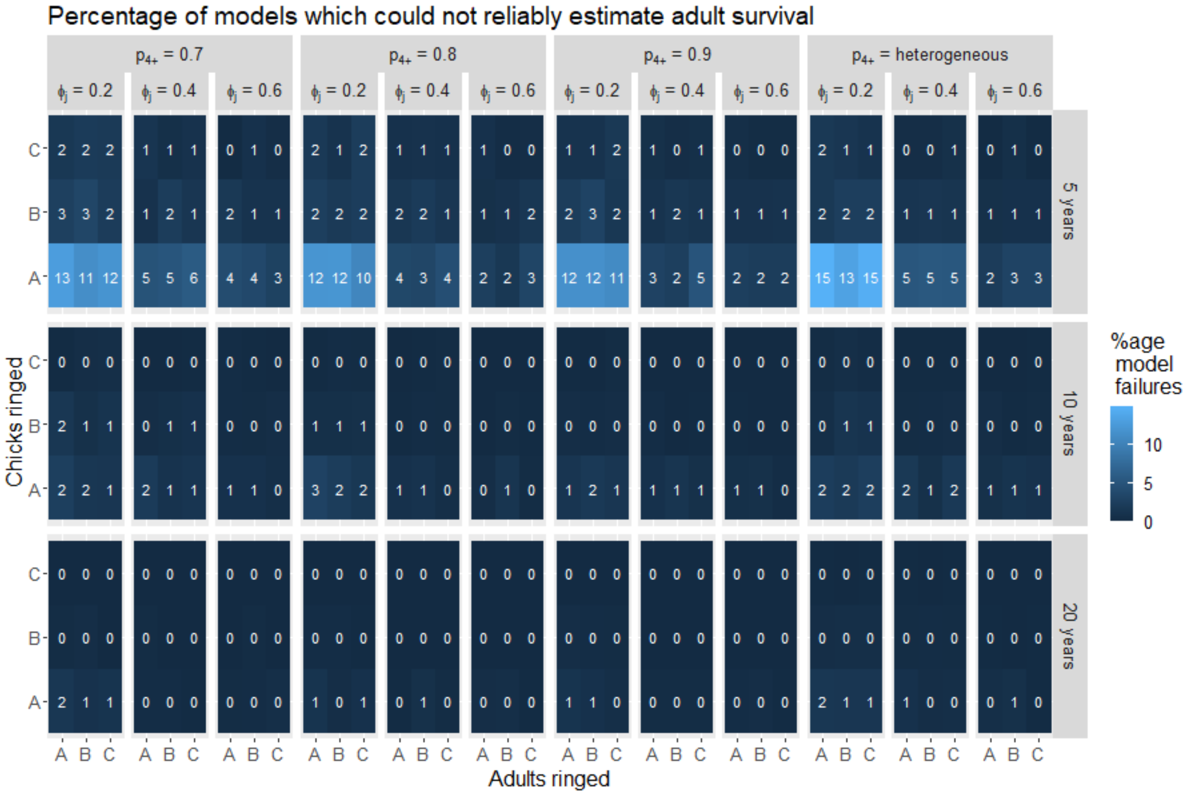


Figure 3.5. The percentage of models which could not reliably estimate adult survival, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study (y; 5,10,20 yrs).

Juvenile survival (age 0 to 1)

The percentage of estimates of juvenile survival, ϕ_j, within 10% of the true value is shown in Figure 3.6 for all considered parameter combinations. The increase to 10% from the 1-2% range considered for adults is appropriate because accurate estimation of juvenile survival is more difficult than adult survival due to low resighting rates, and because juvenile survival shows higher variability than adult survival between years and cohorts (McKnight *et al.* 2019). We exceed 80% of estimates within 10% of the true value in nearly all 20-year studies, in 10-year studies at least 200 chicks per year are ringed, and in 5-year studies that involves ringing 500 chicks per year. A maximum of 500 chicks per year were ringed (with the exception of some heterogenous resighting cases) (Figure 3.6)

The pattern of model failures is very similar when estimating the juvenile survival rate to that observed when estimating adult survival, with the majority of failures occurring when conducting a 5-year study and ringing only 50 chicks per year (Figure 3.7).

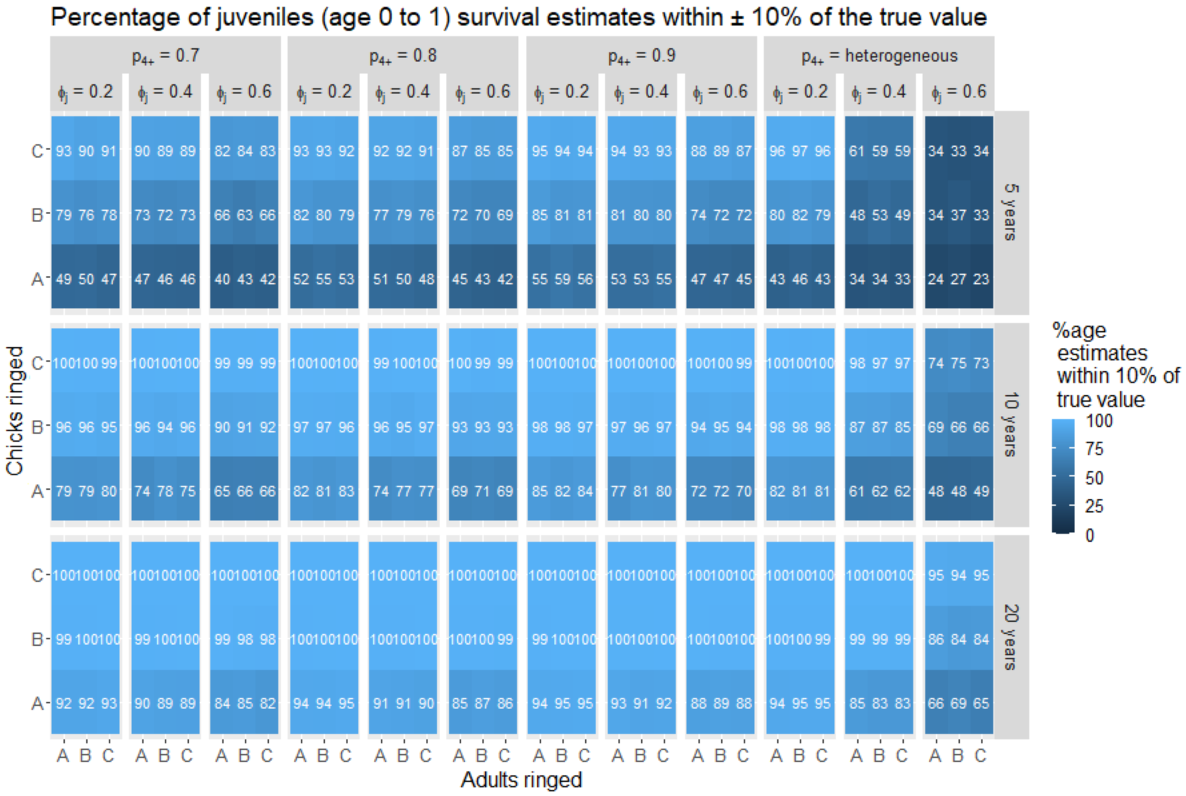


Figure 3.6. The percentage of estimates of juvenile (age 0 to 1) survival within ± 10% of the true parameter value for all considered parameter combinations, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study (y; 5,10,20 yrs).

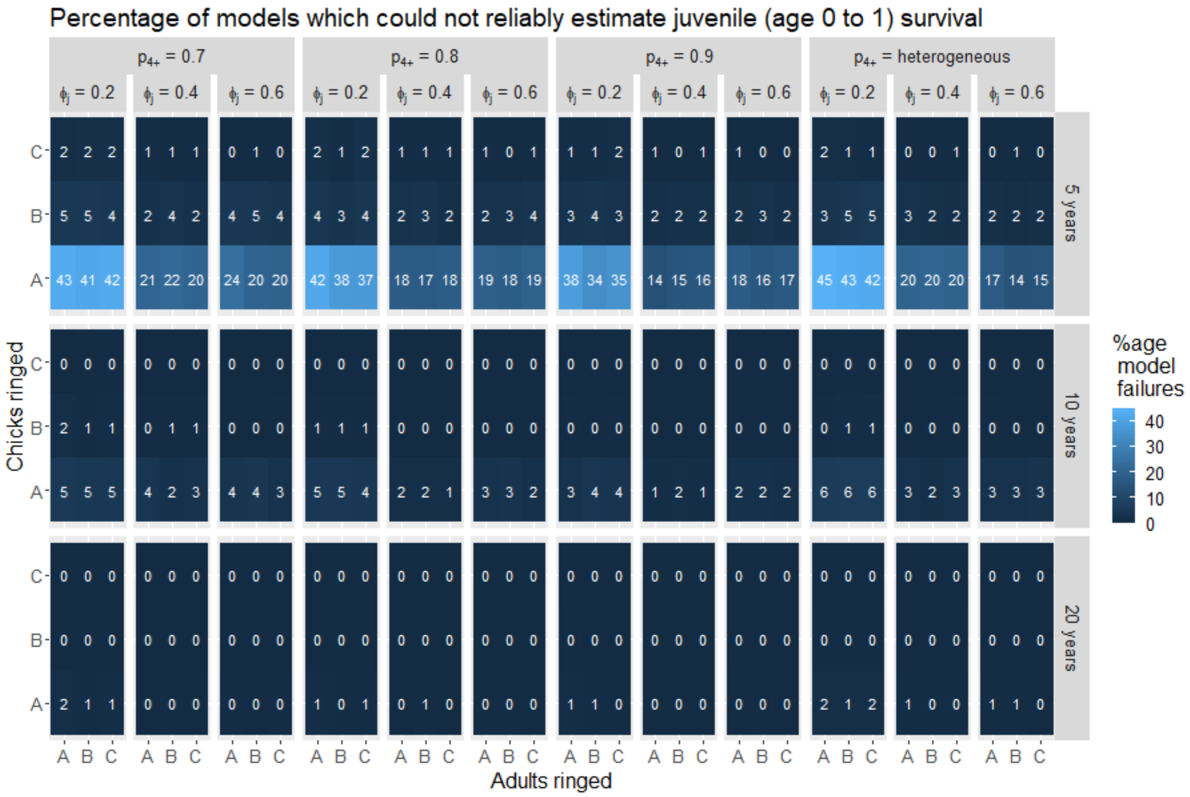


Figure 3.7. The percentage of models which could not reliably estimate juvenile survival, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕj); secondary y-axis is the length of study (y; 5,10,20 yrs).

Age 1 to 2 survival

Survival of birds between the first and second years could be reliably estimated to within 10% of the true value for some 10- and 20-year studies, provided sufficiently high ringing effort and juvenile survival (Figure 3.8). The relative difficulty in producing accurate estimates of age 1 to 2 survival relative to juvenile survival is likely to stem from the relatively low juvenile (age 0 to 1) survival rates (0.2-0.6) and the low resighting of age 2 individuals ($0.33p_{4+}$). These factors combine to result in a low resighting rate of a relatively small population, making inference of survival rates difficult. The difficulty in accurately estimating survival from age 1 to 2 is also reflected in the high proportion of models which could not produce a reliable estimate of this parameter at all (Figure 3.9).

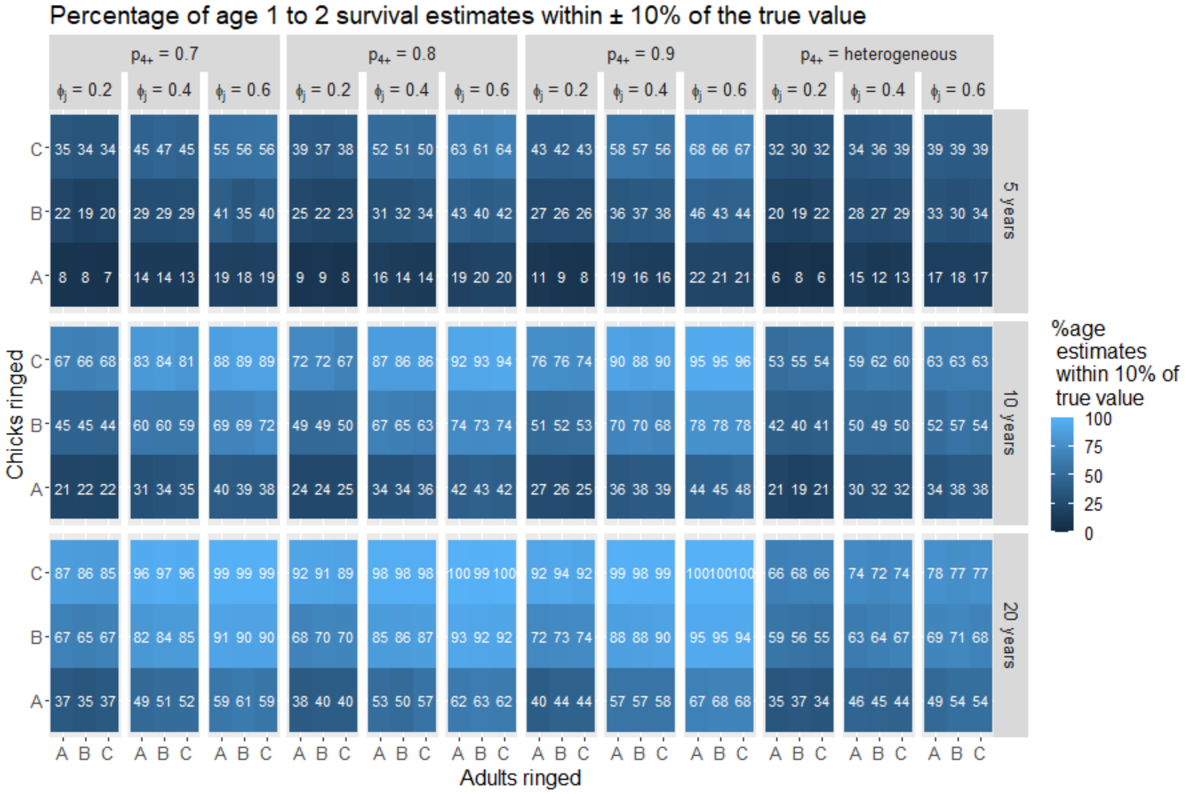


Figure 3.8. The percentage of estimates of age 1 to 2 survival within ± 10% of the true parameter value for all considered parameter combinations, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study (y; 5,10,20 yrs).

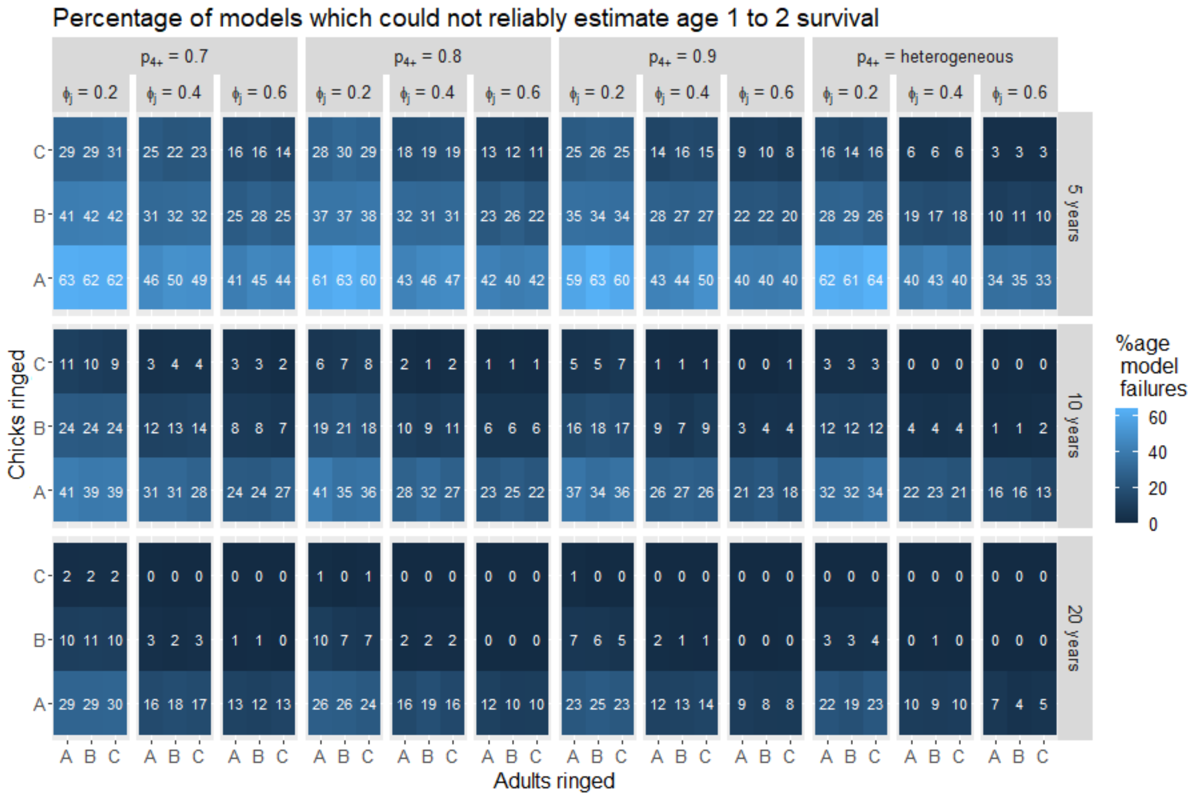


Figure 3.9. The percentage of models which could not reliably estimate age 1 to 2 survival, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study ($y;$ 5,10,20 yrs).

Age 2 to 3 survival

The fitted models estimated age 2 to 3 survival more accurately than age 1 to 2 survival, achieving >80% of estimates within 10% of the true value for 20-year studies with all levels of chick ringing effort, dependent on the other parameter values (Figure 3.10). Greater than 80% of estimates within 10% of the true value was also possible in a number of 10-year scenarios, though not for the lowest ringing effort, but was only possible under the highest juvenile survival, resighting and chick ringing effort for a 5-year study. The failure rates improved slightly from age 1 to 2 but still remained high (Figure 3.11). Any increase in ability to estimate age 2 to 3 survival over age 1 to 2 survival likely stems from the increased resighting probability at age 3.

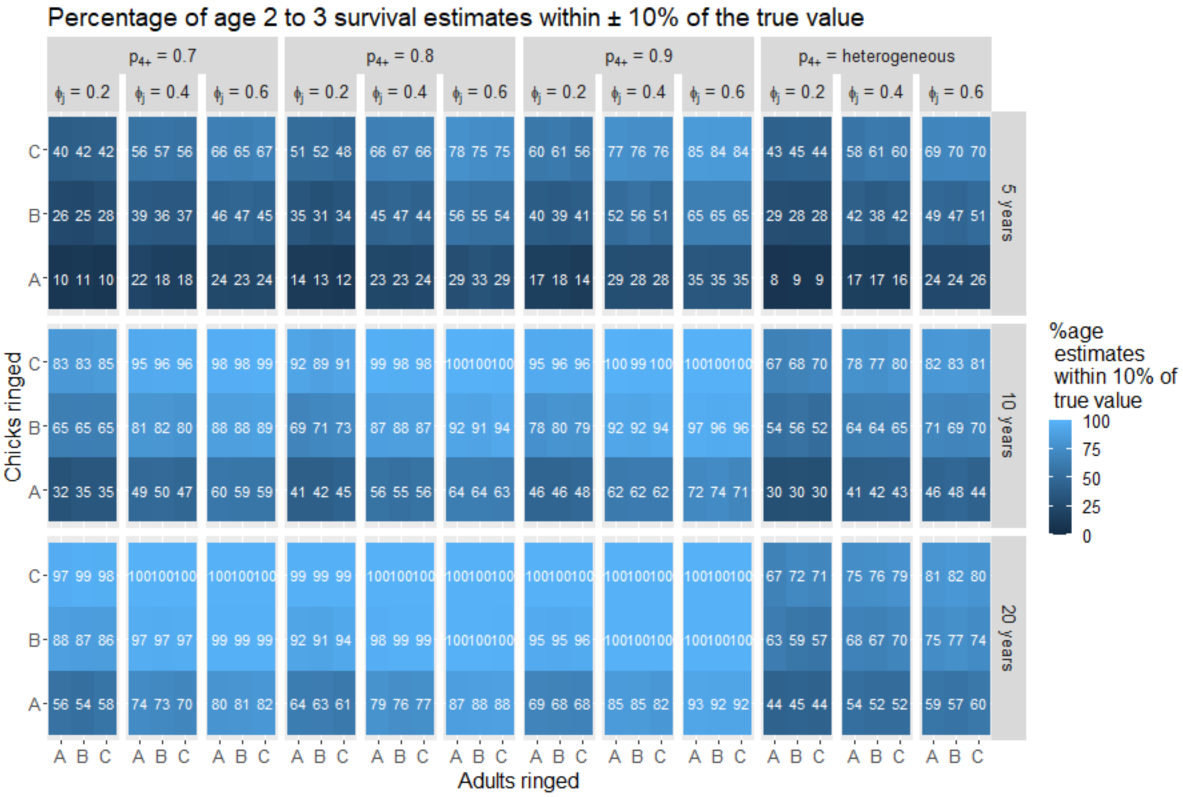


Figure 3.10. The percentage of estimates of age 2 to 3 survival within ± 10% of the true parameter value for all considered parameter combinations, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study (y; 5,10,20 yrs).

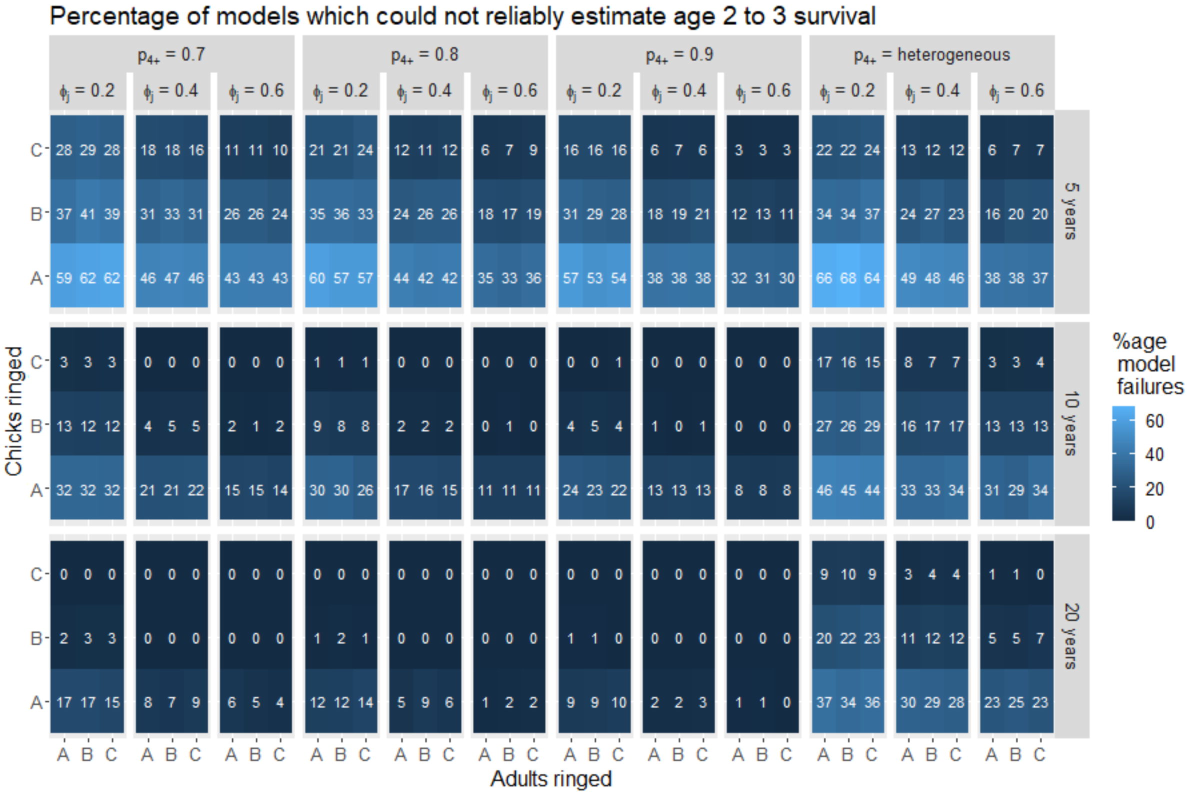


Figure 3.11. The percentage of models which could not reliably estimate age 2 to 3 survival is shown, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study (y; 5,10,20 yrs).

Age 3 to 4 survival

Age 3 to 4 survival rates could be more reliably estimated, with all but one of the parameter combinations for 20-year studies resulting in over 80% of the estimates within 10% of the true value (Figure 3.12). The same was true of 10-year studies where at least 200 chicks were ringed per year and some of the 5-year studies achieved >80% of the estimates with 10% provided the maximum of 500 chicks per year were ringed and the adult resighting probability was sufficiently high. The failure rates also decreased once more to lie between the failure rates of age 0 to 1 survival and adult survival, with most of the failures stemming from 5-year studies with minimal chick ringing (Figure 3.13).

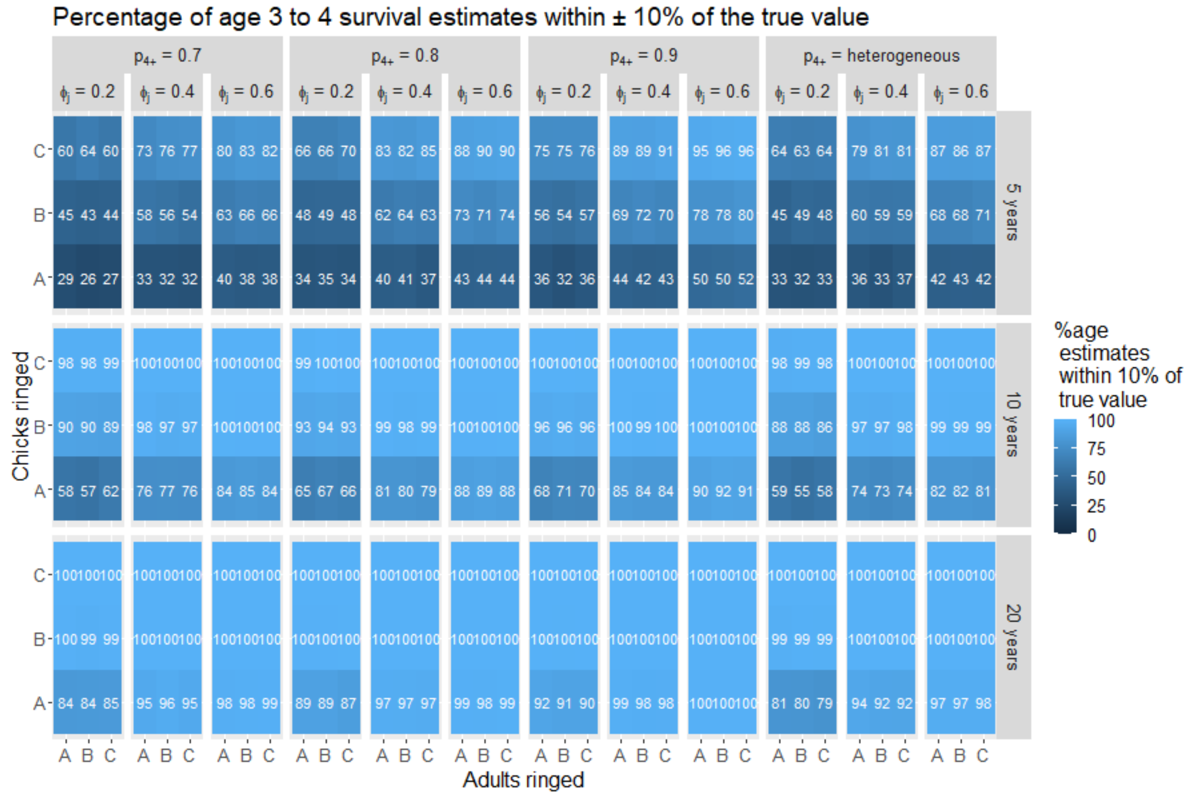


Figure 3.12. The percentage of estimates of age 3 to 4 survival within ± 10% of the true parameter value for all considered parameter combinations, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study (y; 5,10,20 yrs).

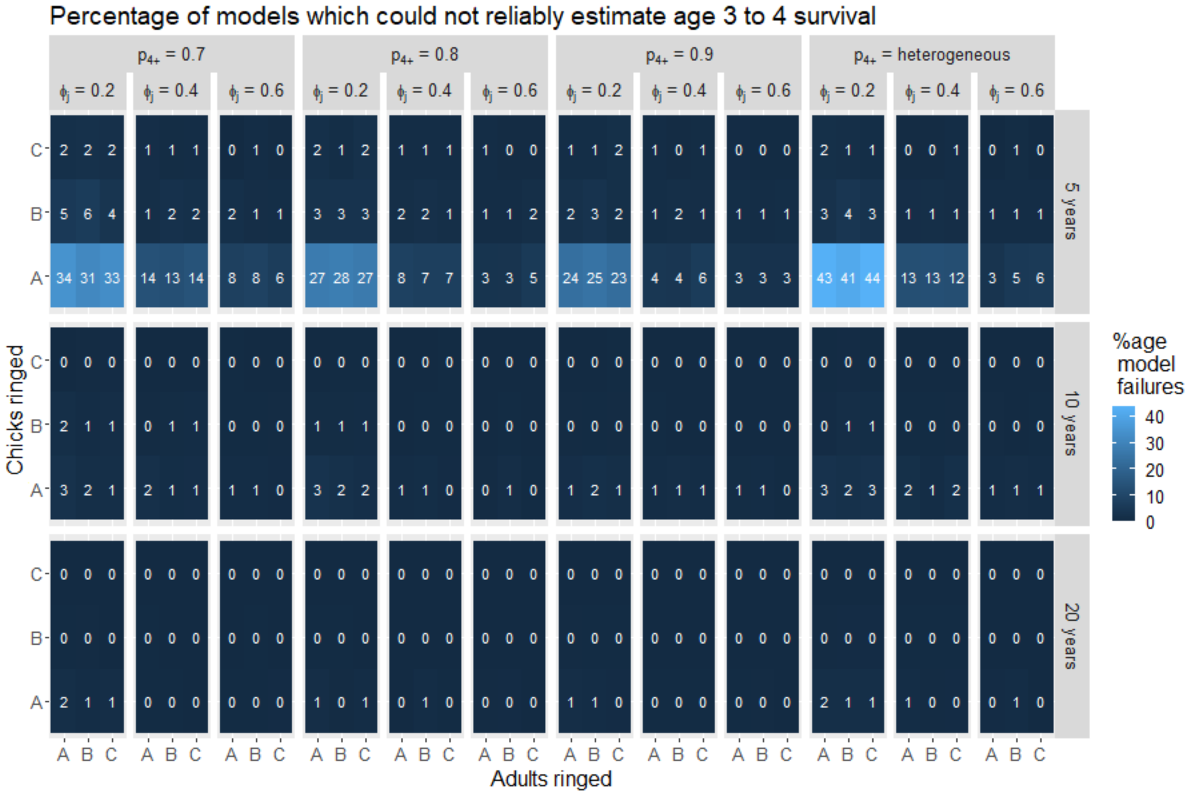
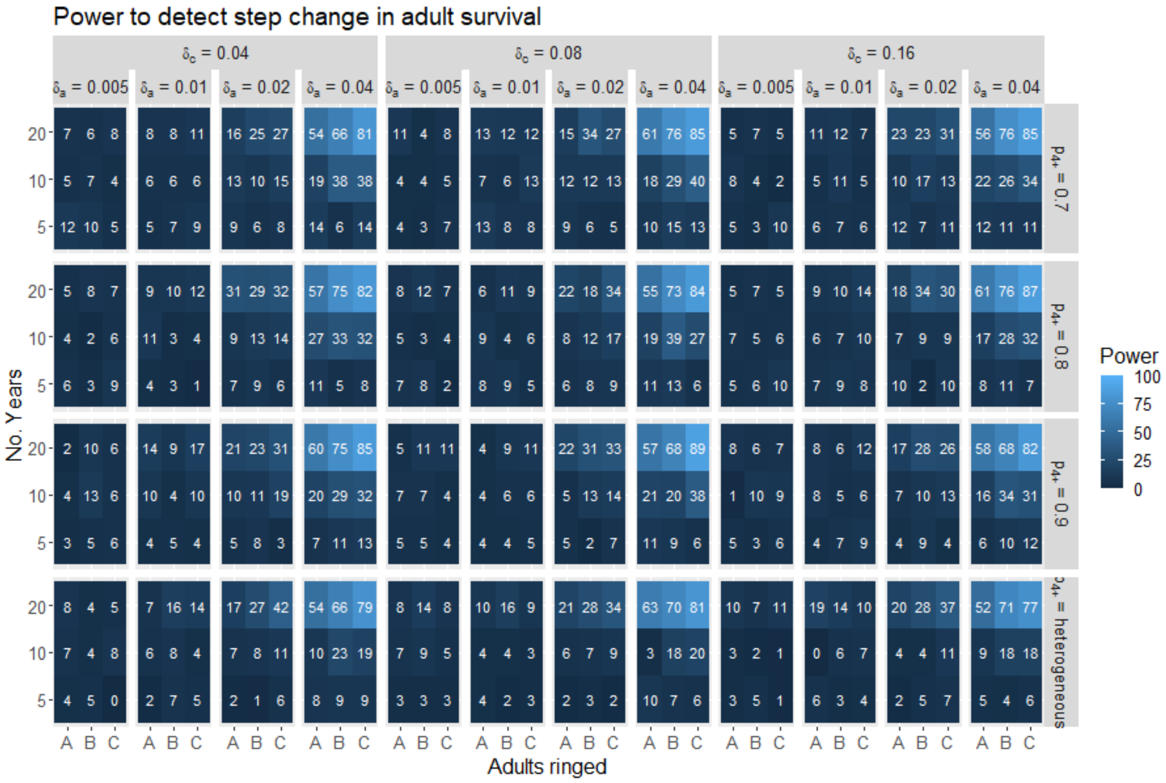


Figure 3.13. The percentage of models which could not reliably estimate age 3 to 4 survival, with the actual percentage annotated in each box. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the number of chicks ringed (r_c) in scenarios A (50) ,B (200), C (500); secondary x-axis: resighting probability for adults (p_{4+}), juvenile survival (ϕ_j); secondary y-axis is the length of study (y; 5,10,20 yrs).

3.4.2 Analysis 1b – Power to detect change in adult and juvenile apparent survival

Adult survival

The power to detect each of the stated step changes in adult survival, δ_a, for each of the parameter combinations is shown in Figure 3.14. There is little power to detect step changes of 0.5%, 1% or 2% across the full range of parameter combinations. A 4% decrease in adult survival could be detected with over 80% power for 20-year studies with the highest levels of adult ringing effort (yr1=75, yr2=86, yr3+=23).



δ_c = 0.04		δ_a = 0.005			δ_a = 0.01			δ_a = 0.02			δ_a = 0.04		
	No. Years	A	B	C	A	B	C	A	B	C	A	B	C
p_{4+} = 0.7	20	7	6	8	8	8	11	16	25	27	54	66	81
	10	5	7	4	6	6	6	13	10	15	19	38	38
	5	12	10	5	5	7	9	9	6	8	14	6	14
p_{4+} = 0.8	20	5	8	7	9	10	12	31	29	32	57	75	82
	10	4	2	6	11	3	4	9	13	14	27	33	32
	5	6	3	9	4	3	1	7	9	6	11	5	8
p_{4+} = 0.9	20	2	10	6	14	9	17	21	23	31	60	75	85
	10	4	13	6	10	4	10	10	11	19	20	29	32
	5	3	5	6	4	5	4	5	8	3	7	11	13
p_{4+} = heterogeneous	20	8	4	5	7	16	14	17	27	42	54	66	79
	10	7	4	8	6	8	4	7	8	11	10	23	19
	5	4	5	0	2	7	5	2	1	6	8	9	9

δ_c = 0.08		δ_a = 0.005			δ_a = 0.01			δ_a = 0.02			δ_a = 0.04		
	No. Years	A	B	C	A	B	C	A	B	C	A	B	C
p_{4+} = 0.7	20	11	4	8	13	12	12	15	34	27	61	76	85
	10	4	4	5	7	6	13	12	12	13	18	29	40
	5	4	3	7	13	8	8	9	6	5	10	15	13
p_{4+} = 0.8	20	8	12	7	6	11	9	22	18	34	55	73	84
	10	5	3	4	9	4	6	8	12	17	19	39	27
	5	7	8	2	8	9	5	6	8	9	11	13	6
p_{4+} = 0.9	20	5	11	11	4	9	11	22	31	33	57	68	89
	10	7	7	4	4	6	6	5	13	14	21	20	38
	5	5	5	4	4	4	5	5	2	7	11	9	6
p_{4+} = heterogeneous	20	8	14	8	10	16	9	21	28	34	63	70	81
	10	7	9	5	4	4	3	6	7	9	3	18	20
	5	3	3	3	4	2	3	2	3	2	10	7	6

δ_c = 0.16		δ_a = 0.005			δ_a = 0.01			δ_a = 0.02			δ_a = 0.04		
	No. Years	A	B	C	A	B	C	A	B	C	A	B	C
p_{4+} = 0.7	20	5	7	5	11	12	7	23	23	31	56	76	85
	10	8	4	2	5	11	5	10	17	13	22	26	34
	5	5	3	10	6	7	6	12	7	11	12	11	11
p_{4+} = 0.8	20	5	7	5	9	10	14	18	34	30	61	76	87
	10	7	5	6	6	7	10	7	9	9	17	28	32
	5	5	6	10	7	9	8	10	2	10	8	11	7
p_{4+} = 0.9	20	8	6	7	8	6	12	17	28	26	58	68	82
	10	1	10	9	8	5	6	7	10	13	16	34	31
	5	5	3	6	4	7	9	4	9	4	6	10	12
p_{4+} = heterogeneous	20	10	7	11	19	14	10	20	28	37	52	71	77
	10	3	2	1	0	6	7	4	4	11	9	18	18
	5	3	5	1	6	3	4	2	5	7	5	4	6

Figure 3.14. Power to detect the stated step changes in adult survival for all parameter combinations. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the length of study (5,10, 20 years); secondary x-axis: step change in juvenile survival over time (δ_j) and step change in adult survival over time (δ_a); secondary y-axis is the resighting probability of adults (p_{4+}).

Juvenile (age 0 to 1) survival

The power to detect step changes in juvenile survival remained low across all parameter combinations (Figure 3.15). For the largest step change considered (16%), the maximum power to detect change was approximately 40-50% for a 20-year study.

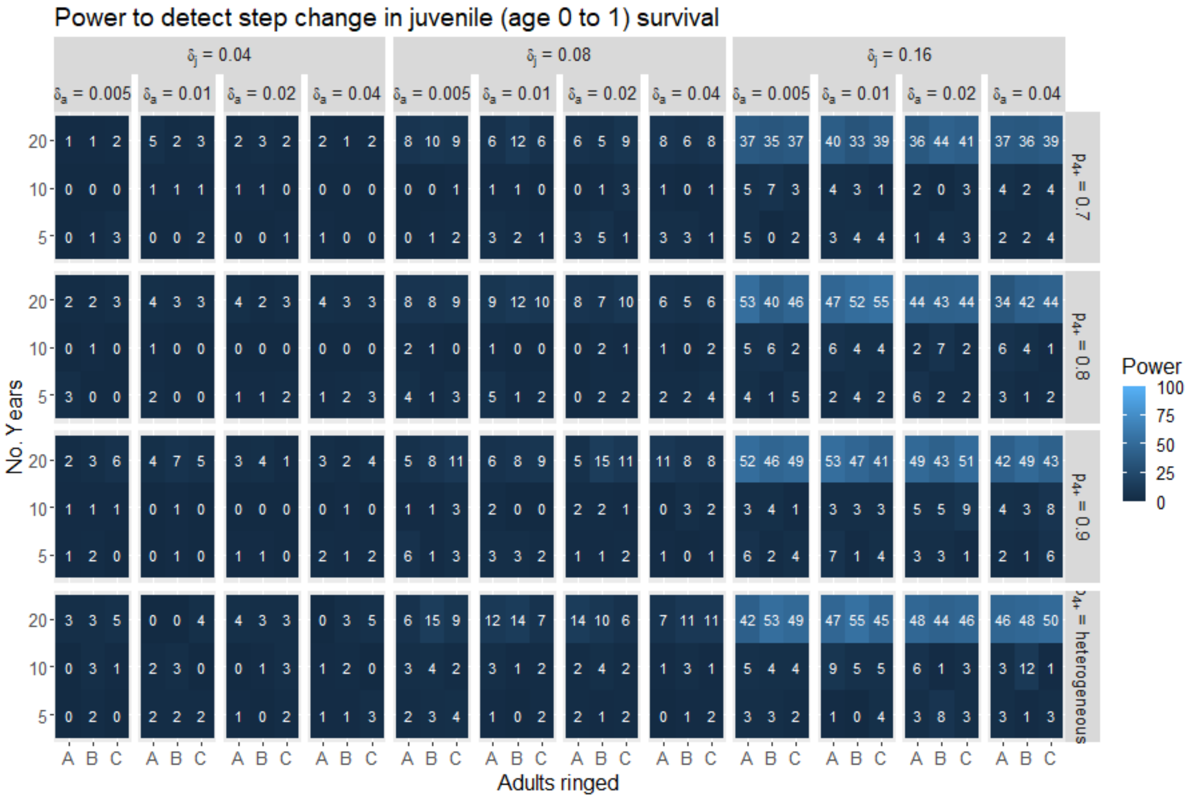


Figure 3.15. Power to detect the stated step changes in juvenile survival for all parameter combinations. Missing values represent combinations of parameters where the model could not be run. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the length of study (5,10, 20 years); secondary x-axis: step change in juvenile survival over time (δ_j) and step change in adult survival over time (δ_a); secondary y-axis is the resighting probability of adults (p_{4+}).

Immature (Ages 1 to 2, 2 to 3 and 3 to 4) survival

It is clear from Figure 3.16 – Figure 3.18 that there is no appreciable power to detect changes in survival of individuals from age 1 to age 4 across any of the parameter combinations considered, due to low juvenile survival rates, relatively low detection probabilities and the added complication of dispersal of individuals between ages 3 and 4.

It should be noted that the marginally higher estimated powers for age 1 to 2 individuals all correspond to the largest decreases in juvenile survival, despite the fact that it is the adult survival rate that acts on age 1 to 2 individuals. Consequently, it seems that this slight increase in estimated power may actually stem from a difficulty in estimating survival separately for each age class due to low resighting probabilities.

It should also be highlighted that it is impossible to detect a change in age 3 to 4 survival in a 5-year study where the change occurs between year 3 and 4 (as is the case here) because there are no individuals of the relevant age ringed before the change occurs, hence estimated power will always be 0 in this case.

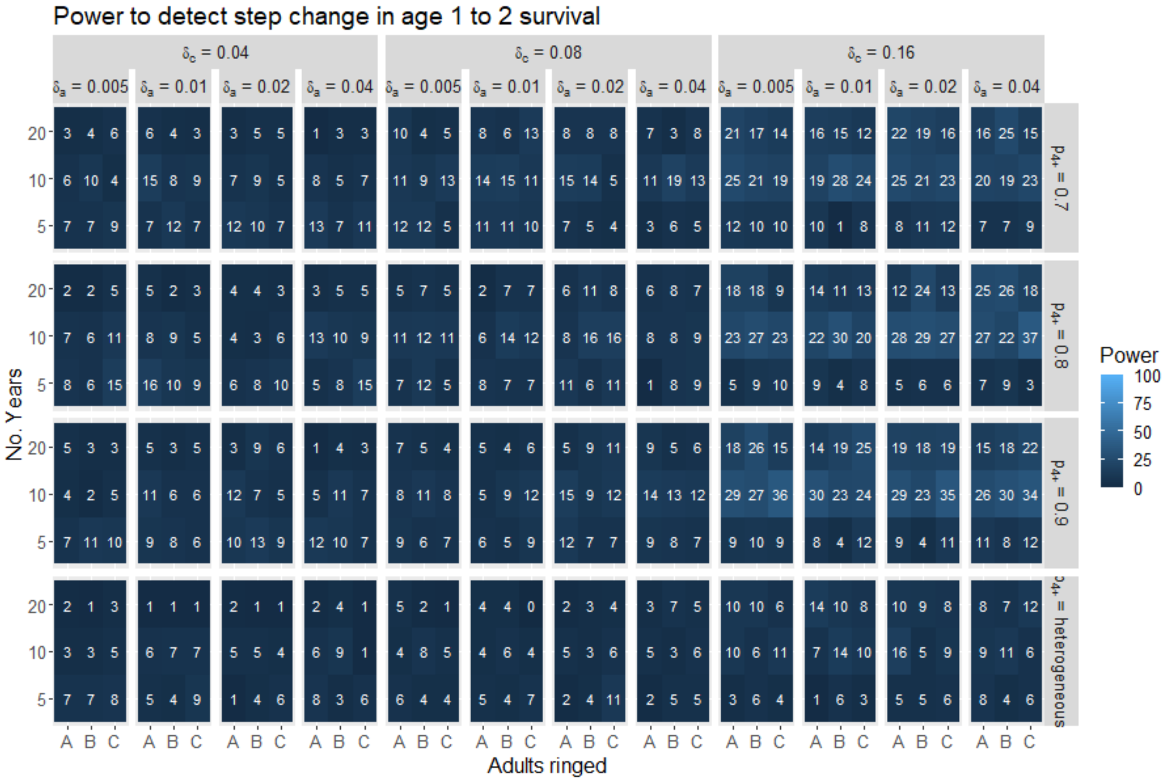


Figure 3.16. Power to detect the stated step changes in age 1 to 2 survival for all parameter combinations. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the length of study (5,10, 20 years); secondary x-axis: step change in juvenile survival over time (δ_j) and step change in adult survival over time (δ_a); secondary y-axis is the resighting probability of adults (p_{4+}).

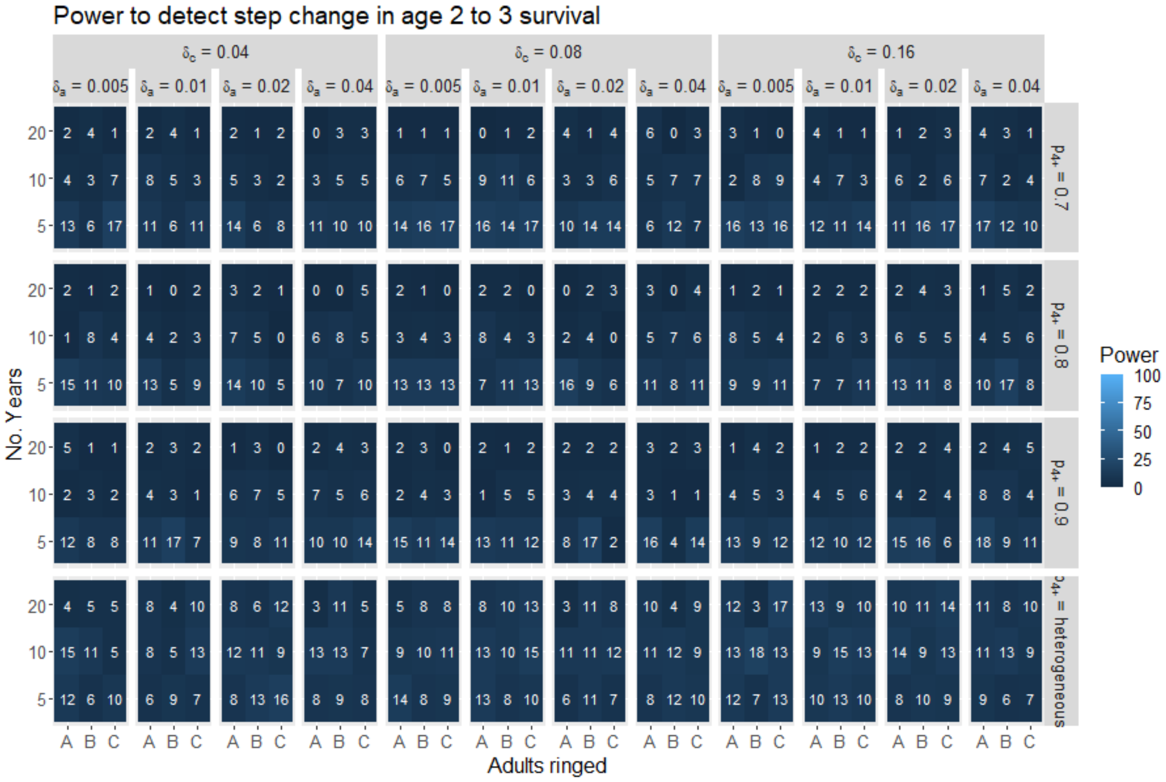


Figure 3.17. Power to detect the stated step changes in age 2 to 3 survival for all parameter combinations. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the length of study (5,10, 20 years); secondary x-axis: step change in juvenile survival over time (δ_j) and step change in adult survival over time (δ_a); secondary y-axis is the resighting probability of adults (p_{4+}).

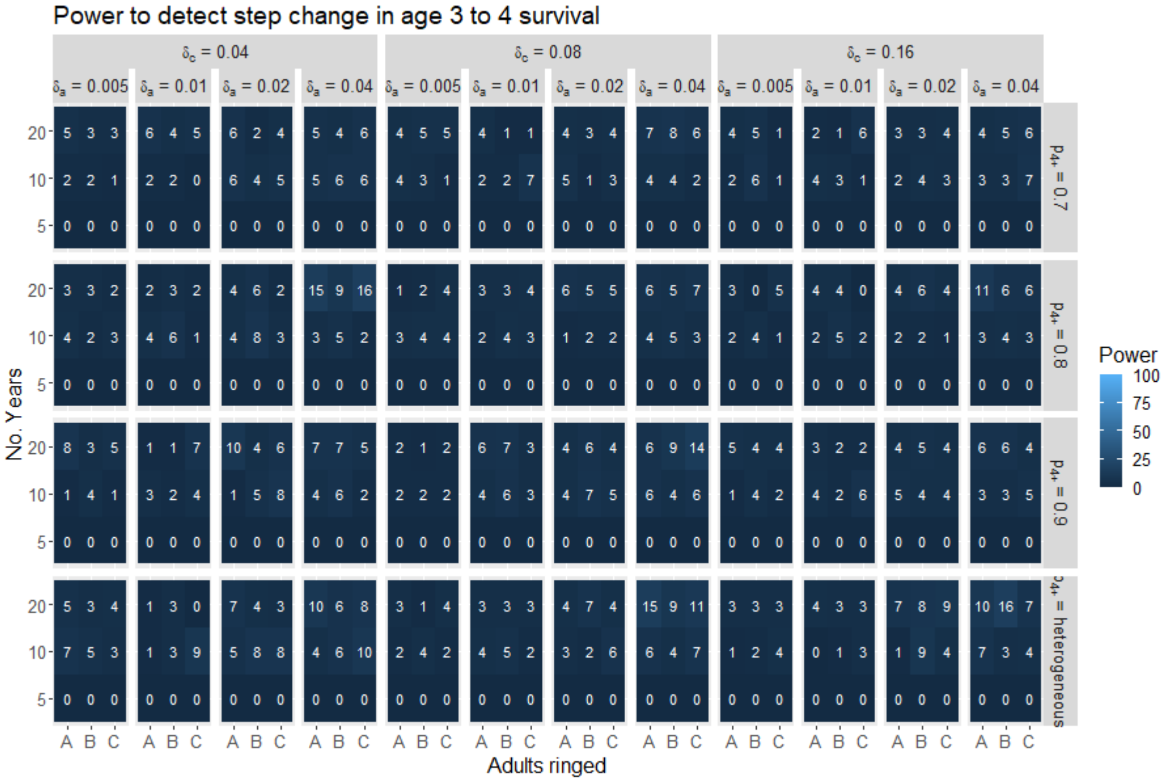


Figure 3.18. Power to detect the stated step changes in age 3 to 4 survival for all parameter combinations. X-axis is the number of adults ringed (r_a) in scenarios A (yr1=50, yr2+=7), B (yr1=75, yr2=36, yr3+=15), C (yr1=75, yr2=86, yr3+=23); y-axis is the length of study (5,10, 20 years); secondary x-axis: step change in juvenile survival over time (δ_j) and step change in adult survival over time (δ_a); secondary y-axis is the resighting probability of adults (p_{4+}).

3.4.3 Analysis 2 – Effect of number of visits on resighting probability

The impact of the number of visits on resighting probability is shown in Figure 3.19. Mean resighting probabilities for a single visit vary from 0.2 to 0.37 depending on area, but uncertainty means it is possible that resighting probabilities per visit for some areas could be as low as 0.12. The results show that the estimated annual detection probability rises rapidly as the number of visits is increased, but that there is considerable variation between areas, and considerable uncertainty within each area. The number of visits required to achieve a mean 90% resighting probability varies between areas but is never greater than ten. However, in order to be confident that a 90% resighting probability will be achieved, a substantially larger number of visits is needed. The lower 95% confidence limit of resighting probability only exceeds 90% at 10 visits or 12 visits for some of the areas, and even with 12 visits it is below 80% for other areas.

Misreading of rings at the levels considered here (1-5%), has a relatively small effect on the estimation of detection probability, and does not change the overall conclusions regarding the annual resighting probability that can be achieved for each number of visits, although it does typically lead to some reduction in the estimated annual resighting probability.

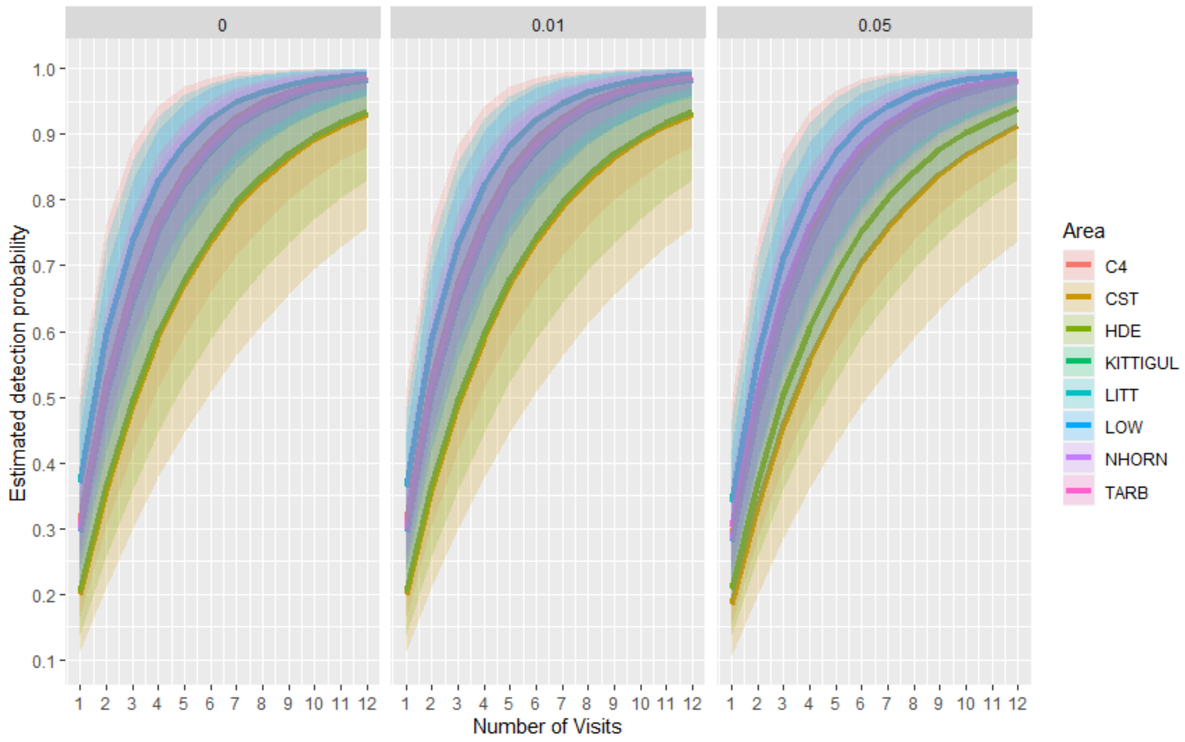


Figure 3.19. The relationship between the number of visits and the estimated detection probability for each area is shown for three different levels of misreads: 0% (i.e. no misreads) on the left, 1% of rings misread in the middle, and 5% of rings misread on the right. The shaded areas show estimated 95% confidence intervals.

3.5 Conclusions

3.5.1 Power analysis - summary and implications

The main power analysis (Analysis 1) focused on our ability to estimate survival rates across the age classes with a specified level of precision (Analysis 1a) and estimated power to detect different magnitudes of step changes in survival rates across the age classes (Analysis 1b). In drawing these comparisons, we considered several levels of ringing and resighting effort.

For adult survival, we observed that reasonably precise estimates (within 2% of the true value) could be achieved for most levels of ringing and resighting effort for studies of 10 or 20 years in length. However, 5-year studies failed to consistently achieve estimation of adult survival rates within 2% of the true value on a consistent basis. In Analysis 1b we observed that it was possible to detect a step change in adult survival of 4% with greater than 80% power, provided the highest level of ringing effort (yr1=75, yr2=86, yr3+=23) was applied over a 20-year study. 80% power could not be achieved for any other sizes of step change, study lengths or levels of ringing effort (see section 3.4.2 for a further discussion of this finding).

For juvenile survival, estimates within 10% of the true value were achieved in the majority of 20-year studies, regardless of ringing effort. In 10-year studies, the lowest level of ringing effort (50 birds per year) generally led to less than 80% of estimates with the desired level of precision, although the two higher levels of effort were sufficient. In 5-year studies, only the highest ringing effort (500 birds per year) consistently provided estimates within 10% of the true value. The power to detect changes in juvenile survival of up to 16% was generally <10%. The only exception was when 500 chicks were ringed per year in a 20-year study, which typically had a power to detect change of 40-50%. It should be remembered that with an age to maturity of 4(+) years, any effective survival estimation study will likely require more than 5 years of operation.

Estimation of survival rates and detection of step changes in survival was much more challenging for ages 1-2, 2-3 and 3-4 due to low survival and resighting rates and dispersal of individuals between ages 3 and 4. Five-year studies failed to achieve a precision of 10% for nearly all levels of ringing effort. Ten- and 20-year studies could achieve these levels of precision dependent on the level of ringing effort and the specific age class considered. There was generally found to be less than 15% power to detect step changes in survival of up to 4%.

Given the stated findings we highlight that:

1. Five-year studies failed to provide a precision of 2% in adult survival or 10% in juvenile/immature survival even under the highest levels of ringing effort considered in the scenarios.
2. Studies of 10 years or longer can potentially provide 2% precision in adult survival and 10% survival in juvenile/immature survival, with the required levels of ringing effort dependent on the age classes of interest; and
3. Only 20-year studies gave sufficient power (>80%) to detect a 4%-point decrease in adult survival. None of the other levels of effort considered gave greater than 80% power to detect any of the magnitudes of change considered.

In Analysis 2, we showed that increased resighting effort (in terms of number of visits) led to increased resighting probability, as expected, with 10 or more visits estimated to give >90% resighting probability in most subareas of the Isle of May. We also found that misread rings at the levels considered (0-5%) had a negligible impact on resighting. There was some evidence that resighting levels varied by area on the Isle of May, potentially due to local geography, highlighting that extrapolating these findings to other sites or colonies should be done with caution.

3.5.2 Power analysis - limitations and caveats

The main power analysis (Analysis 1) necessarily focused upon a highly simplified situation in which a single population is considered. These results may also potentially be applicable to situations in which several colonies within a region are monitored, and the resulting data pooled – however, they will only be directly generalizable in this way in contexts where it is plausible to assume that both survival and resighting rates, for all ages, are common to all of the monitored colonies within the region.

Analysis 1 also assumes that survival and resighting rates are constant over time (except for the step change in survival within Analysis 1b). This approach ignores environmental heterogeneity and baseline trends, and the approach also assumes that field effort, and hence resighting probability, does not vary over time. As the analysis focused on estimating apparent juvenile and adult survival, assumptions necessarily were made in the modelling approach that did not distinguish between dispersal and mortality, or account for the effects of immigration or emigration (as these extra parameters would have increased both the complexity of the approach and the number of scenarios being simulated). The approach also assumes that age at first breeding is fixed and known, and that survival and recapture probabilities are independent of age for breeding adults. Age of first breeding is unlikely to be fixed, and is not known for all regions (see section 2.3.3, Table 2.1), however if we can estimate survival to recruitment for a specific colony or region then it should also be possible estimate age of first breeding.

The data simulations within Analysis 1 assumed that immature survival rates are equal to adult survival rates, and that immature recapture rates are related to adult recapture rates in a specific way. However, the resulting analyses of the simulated datasets do not make these assumptions, and so our power calculations do account for the fact that these assumptions could not typically be relied upon when analysing real data. Conversely, the simulations do allow for the possibility of heterogeneous resighting probabilities, but the resulting analyses of simulated datasets do not allow for this. It would be possible in principle to also allow for heterogeneity in resighting probabilities within this analysis (see section 3.4.3), but this substantially adds to the complexity of the model fitting, and hence was not feasible here. It might be imagined that power would generally be lower, and hence larger sample sizes typically required, when fitting models that include heterogeneity, although this would depend on the specific way in which heterogeneity was modelled. When modelling change over time (Analysis 1b), we assume that the change corresponds to a single step change, halfway through the time series, and assume when analysing the simulated datasets that the timing of the change is known. This model of temporal change is potentially plausible if the change results from the construction of an offshore wind farm (although it does ignore the possibility of habituation, or avoidance (Furness 2016); but would be implausible for capturing the changes in baseline demography that result from climate change and other long-term environmental drivers.

Our auxiliary analysis to look at the relationship between field effort and resighting probability (Analysis 2) uses data from a single colony, the Isle of May, and the results may therefore not be directly relevant for other colonies. In particular, the resighting probability per visit is likely to depend heavily upon the characteristics of the colony (accessibility, visibility), the observer (training, experience) and the study design and management (timing of surveys, quality assurance). Within the Isle of May, the analysis assumes that the resighting probability is the same for all visits within a year, and so ignores the impact of visit timing. The analysis does not account for variations in visit-level resighting probabilities between observers, as confounding between the effects of year, area and observer meant that these effects could not be disentangled. In practice, there may be substantial differences in resighting probabilities between observers.

Within the scenarios that involve misreads we focused upon one specific way in which misreads may occur: the identity of the colour-ring is wrongly attributed to be that of another valid colour-ring, but the selection of the “incorrect” colour-ring is assumed to be random. In practice, the mechanisms by which misreads occur is likely to be substantially more complicated than this (e.g. there are likely to be a very limited set of possible “incorrect” rings, and some colours (Burton 2000) or characters (Tucker *et al*. 2019) are more likely to be confused), so the results of our scenarios that include misreads should be regarded as a basic check on consequences of the failure of the assumption that no misreads occur, and not as a detailed assessment of the relationship between misreads and resighting probability.

3.6 Recommendations for the analysis of colour-ringing data

The purpose of the power analysis is to inform the design of a colour-ringing study. To achieve this, a degree of simplification in the scenarios and analyses were considered. We have focused upon the most standard and straightforward approach to analysis – the use of a CJS model with no covariates (except for Analysis 1b which uses time period), and with separate survival and resighting parameters for juvenile age. We focused upon a single, relatively standard, model because the need to refit this model a very large number of times (in order to consider hundreds of scenarios, and a large number of simulated datasets per scenario) meant that it was computationally and practically infeasible to consider alternative models, or to examine the empirical goodness of fit of each model.

Once the data for a ringing study have been collected, careful attention needs to be paid to the analysis of these data. It is important to ensure that the model used for analysis captures all of the key features of the data and shows adequate goodness-of-fit. For the analysis, it is possible to use a standard CJS model, to extend this model to account for additional complexities in the data, or to use an alternative modelling approach. We consider each of these possibilities separately.

3.6.1 Modelling considerations within a standard CJS model

If a standard CJS model is to be used for the analysis, there are two key modelling decisions that need to be made. The first is the age structure to use within the model: we have assumed here that survival and resighting probabilities are separate for each juvenile age, up to the age at first breeding (4) and for adults are unaffected by age. In practice, the assumption of constant survival probability with age for adult birds may not be realistic: senescence may mean that survival probability may fall with age, whilst survival may increase with age until senescence (Frederiksen *et al.* 2004a). These features may necessitate the inclusion of multiple adult age classes. Conversely, an assumption that juvenile survival and resighting rates are completely separate for each juvenile age may be unnecessarily conservative and could partially explain the low levels of precision and power obtained for estimates of juvenile survival. The CJS model readily allows juvenile age classes to be pooled, for both survival and resighting probabilities, but this should be done with substantial care – exploratory analyses within this project indicate that this pooling has the potential to lead to bias, so parameters should only be pooled across ages if there is a strong biological argument for doing so. Statistical criteria (such as AIC) can also be used in deciding whether or not to pool parameters across age classes: pooling should not be used if it leads to an overall reduction in goodness-of-fit.

The second key modelling decision concerns the inclusion of covariates (explanatory variables), which have the potential to substantially improve goodness-of-fit of the CJS model. Covariates can affect either survival or resighting probabilities, and we may expect different covariates to influence each of these rates. Environmental variables (e.g. climate) may often be useful in explaining variation in survival, whilst resighting probabilities will often depend upon the observer (incorporated as a categorical variable). The choice of appropriate covariates needs to be considered carefully for each dataset and will partly depend upon data availability. Field effort (e.g. the number of visits per year) may be an important covariate to consider in relation to resighting probability, if the field effort varies from year to year.

3.6.2 Extensions of the CJS model

Within the power analysis there are two features of colour-ringing data that we considered: heterogeneous resighting probabilities and misreads of colour-rings. The former arises because some individuals will typically be much easier to resight than others (e.g. because some nest locations are much more visible than others), whilst the latter arises because errors in reading colour-rings can be reduced through training and quality management but cannot be entirely eliminated. In both cases, we considered these features within the data generation scenarios, but not within the resulting analyses of the simulated data. Our approach here has therefore been a form of sensitivity analysis: evaluating how sensitive the results of the power analysis were to a failure of some of the assumptions of the CJS model being used for analysis.

Standard estimation procedures (and hence standard software) for fitting CJS models do not allow either of these features to be accounted for. The model could in principle be extended to consider either or both of these features. Whether this is useful is likely to depend on context. Results here suggest that the relatively low levels of misreads that were considered (between 1% and 5%) are unlikely to have a substantive impact upon the results obtained using a standard CJS model that ignores misreads, but if misreads occur at higher frequency, it may be important to account for them within the analysis. Although extensions of the CJS model to incorporate one or both of these features could not be fitted within standard software, they could be fitted by using more flexible software for Bayesian modelling, such as JAGS (Plummer 2003). In both cases, it would be necessary to decide upon the appropriate assumptions to make in modelling the feature. We assumed in generating simulated datasets that includes heterogeneous resighting, for example, that the resighting probability is halved for individuals that were unobserved in the previous year. However, there are other ways of incorporating heterogeneity (e.g. assuming that there are two groups of individuals, each with a different resighting probability that is constant across time). If extending models to incorporate heterogeneity, it is important to consider which mechanism is the most biologically plausible one to consider, and whether the data contain sufficient information to be able to estimate the additional parameters that are introduced by extending the model.

3.6.3 Alternative modelling approaches

The sample sizes required to reach indicative thresholds of precision (up to ±2% for adults and ±10% for juveniles) for estimates of survival rates, or to reach 80% power to detect changes in these rates, may seem surprisingly high. These sample sizes may also not be achievable for some colonies, even if resources were not a constraint, given the sizes of those colonies and practical and logistical limits on numbers that can be ringed. One reason that power may be lower than expected within the results of our power analysis is because the analysis uses a CJS model. The conceptual framework that underpins this model is one where sampling can be repeated arbitrarily often (i.e. there is an idealised or hypothetical, ‘infinite’ population). Therefore, the CJS model implicitly assumes infinitely repeatable stochastic processes of survival and sighting, and inference is with respect to an arbitrarily large number of birds - a hypothetical population. Perhaps surprisingly, this conceptual framework means that even if all the birds in a colony could be ringed, the desired precision of the parameter estimates may not be achievable. The maximum possible precision that can be achieved for a particular sample size within this conceptual framework can be calculated relatively easily and compared against the levels of precision produced by the CJS model (Appendix C). For example, suppose that the adult survival probability is 0.8 and there are at most 80 birds available for five years in a row, and all 5*80=400 birds are ringed each year and the fate (survival or not) of each bird is known with certainty (detection is 100%), the maximum precision is a standard error of 0.02. More realistically, including a fixed (assumed known) detection probability of 0.60, the maximum precision is a standard error of 0.035.

One potential approach to increasing power would be an alternative analytical approach, based upon finite, rather than infinite, populations. The focus in this case would not be on the probability of survival, per se, but on the fraction of individuals that survive. In this framework, the estimates of this fraction will become very precise once a large proportion of the population has been ringed, and completely precise (with a standard error of zero) if the entire population is ringed. Whether the finite population approach is appropriate and defensible depends upon the primary objective of deploying colour-ringing. In contexts where the deployment is designed to learn solely about the surveyed colony, during the period of surveying, then the finite population approach is a more appropriate and powerful approach. However, in contexts where interest lies in generalizing results to inform understanding to other years or colonies (as in calculating population viability), then the finite sampling approach cannot defensibly be used, and the CJS modelling approach is more appropriate. The finite population approach cannot, therefore, be used to derive generic species-level or regional survival rates that could be applied to multiple SPAs. It could be used in deriving colony-specific survival rates for the SPA at which data are being collected, but only if no extrapolation in time is needed (i.e. if data collection covers the entire period of years, both pre- and, where relevant, post-construction, for which the survival rates need to be calculated). The potential gains in precision from using the finite sampling approach, in situations where it is appropriate, are summarized in Appendix B.

Survival and reproduction parameters for Kittiwakes obviously vary between colonies in the same year, and between years at a single colony. Hierarchical models are one way of modelling such spatial-temporal variation. Such models are sometimes called multi-level or random effects models, and meta-population models for multiple colonies are a specific example. Questions related to hypothesis testing power and precision of parameter estimates become more complex but may more accurately match the conceptual process model of a biologist. Importantly, these models have the potential to allow demographic rates other than survival to be estimated, including, in principle, dispersal, immigration and emigration. In practice, however, the ability to estimate these additional rates depends heavily upon data availability and the structure of the data. An example to demonstrate the potential structure of a hierarchical model is show in Appendix D. Fitting such hierarchical models is more often, and more easily, done within a Bayesian framework, in contrast to the classical likelihood-based approach taken in this report. There are several existing software packages, including JAGS (Plummer 2003) and Nimble (de Valpine *et al.* 2017), which can be accessed via an R interface, to fit hierarchical models.

The ability to estimate juvenile survival, and other demographic rates, solely from colour-ringing data depends heavily upon data availability. The results of our power analysis suggest that very large sample sizes may be needed to obtain precise estimates of juvenile survival rates from colour-ringing data, and the same is likely to be true for demographic rates other than survival (e.g. age at first breeding, dispersal, immigration, emigration). One possible way of improving precision would be through the incorporation of additional data sources. Integrated Population Models (IPMs, Kéry & Schaub 2021) provide a framework for using multiple data sources to learn about the same underlying demographic rates. Freeman *et al.* (2014), for example, assume that adult survival rates can be estimated from mark-recapture or mark-resighting data, and that productivity rates can be estimated from nest monitoring data, and then estimate juvenile survival indirectly using abundance data. This approach relies upon the nest monitoring and abundance datasets both having good coverage (Searle *et al*., in preparation), but does provide a potential way of estimating rates that cannot meaningfully be estimated directly from colour-ringing data.

4 Review of existing Kittiwake ringing effort in the UK

The British and Irish ringing scheme has been operating since 1909, with around 1 million birds currently ringed and 0.25 million re-encounters each year (Walker *et al.* 2018). By individually marking birds and re-encountering them the scheme aims to better quantify and understand the demographic processes (survival, productivity and dispersal) driving changes in Britain’s bird populations (Baillie & Schaub 2009). In support of this aim, the scheme incorporates the Re-trapping Adults for Survival (RAS) protocol, whereby ringers focus their efforts on a particular population or colony of individuals, aiming to ring and re-encounter a high proportion of the breeding birds present to generate more robust estimates of adult survival (Walker *et al.* 2018). Several of these projects operate for seabirds generally and seven active projects focus on Kittiwakes.

In this section, we gathered evidence on the existing availability of ringing data for Kittiwakes and the feasibility of increasing colour-ringing effort to inform the design of a large-scale scheme and to identify any opportunities and challenges that might exist. We did this in three ways:

1. summarizing available records in the scheme database;
2. approaching ringers currently engaged in Kittiwake ringing with a questionnaire asking them to detail their experiences;
3. organising two workshops, the first involving Kittiwake experts from across the species' range, the second those involved with ringing and resighting Kittiwakes in the UK.

4.1 Summary of ringing questionnaire responses

To obtain details on current levels of Kittiwake ringing and resighting effort across the UK, a questionnaire was sent out to 20 people / ringing groups known to ring reasonable numbers of Kittiwakes. Questions also focused on any issues they face in terms of accessibility to birds and logistics. Responses were received from 14 ringers covering 15 colonies.

Ten of these colonies are located on islands, three on mainland cliffs (Flamborough, East Yorkshire; Trewavas Head, Cornwall; Whinnyfold; Grampian) and two on artificial structures on the mainland (Scarborough, North Yorks.; Gateshead, Tyne & Wear). Both chicks and adult are ringed at ten of the colonies, with adults ringed only at four sites (Figure 4.1). Reasons given for not ringing chicks included issues with safe access to nests, concerns over disturbance that might be caused and time limitations. Accessibility also influences adult ringing, with colony areas targeted for ringing not selected at random but based on which nests were easily and safely accessible. The number of apparently occupied nests at each site varied considerably, as did the proportion of nests that are accessible for ringing and resighting (Figure 4.2).

Nine of the 15 studies use metal-rings only, with the remaining six also using colour-rings (40%), the additional cost of, and time to apply, colour-rings were both considerations in choosing not to use colour-rings. Of the colonies that use colour-rings, all involve adults only, except for Trewavas Head where both chicks and adults are colour-ringed. At all colonies, adults are caught using a pole with a noose attached and chicks are caught by hand, generally with the aid of ladders. In Gateshead a cherry picker is used to access nests on the custom-built Kittiwake tower.

The number of ringing visits made to each colony varies, with the majority of colonies visited just once or twice a year, with some of the single visits being 'expedition style' trips to islands to ring multiple species at sites in relatively remote locations (for example, the Treshnish Isles, Argyll, which is visited for a week every June and Sule Skerry, Orkney, which is visited once every 3-5 years).

Resighting is not currently a major focus of activities at most colonies, with most resighting effort undertaken by the ringers during ringing visits. However, specific resighting visits are made at several colonies, including during the early part of the breeding season, pre-incubation, to coincide with the optimal time for resighting colour-ringed adults, with considerable effort undertaken at Flamborough and Skomer, Pembrokeshire. At other colonies, resighting effort occurs later in the year, during chick rearing, where adults can be observed attending the chicks, however, this will likely miss marked individuals that have failed and left the colony before this point. Local birdwatchers and members of the public occasionally report resightings at a couple of the more accessible mainland sites (i.e. Gateshead and Scarborough).

The costs involved in these Kittiwake ringing activities varied considerably from less than £100 (to cover the cost of metal rings and mileage) to over £12,000 (due to the boat costs to Sule Skerry). Excluding Sule Skerry, the average cost of ringing activities was £600 with the main costs being boat transport to islands and accommodation; the cost of rings and catching equipment (ladders, noose poles) made up a small proportion of the costs.

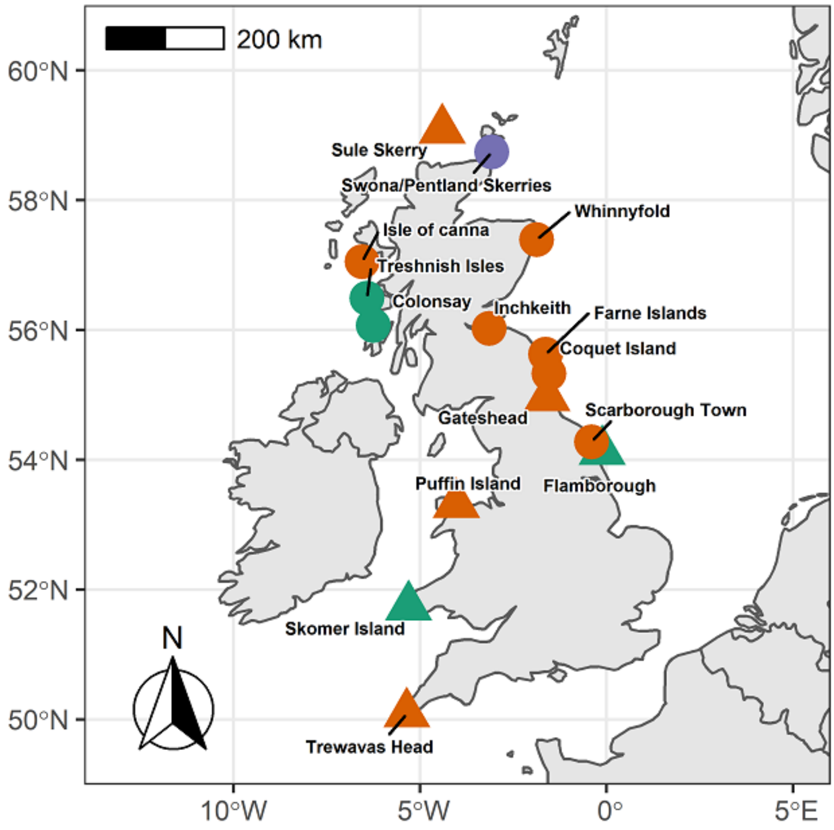


Figure 4.1. Location of Kittiwake colonies where completed ringing questionnaire were received from. The colour of the points relates to whether adults (green), chicks (purple) or both chicks and adults (orange) were ringed. Triangles depict colonies where colour-ringing takes place.

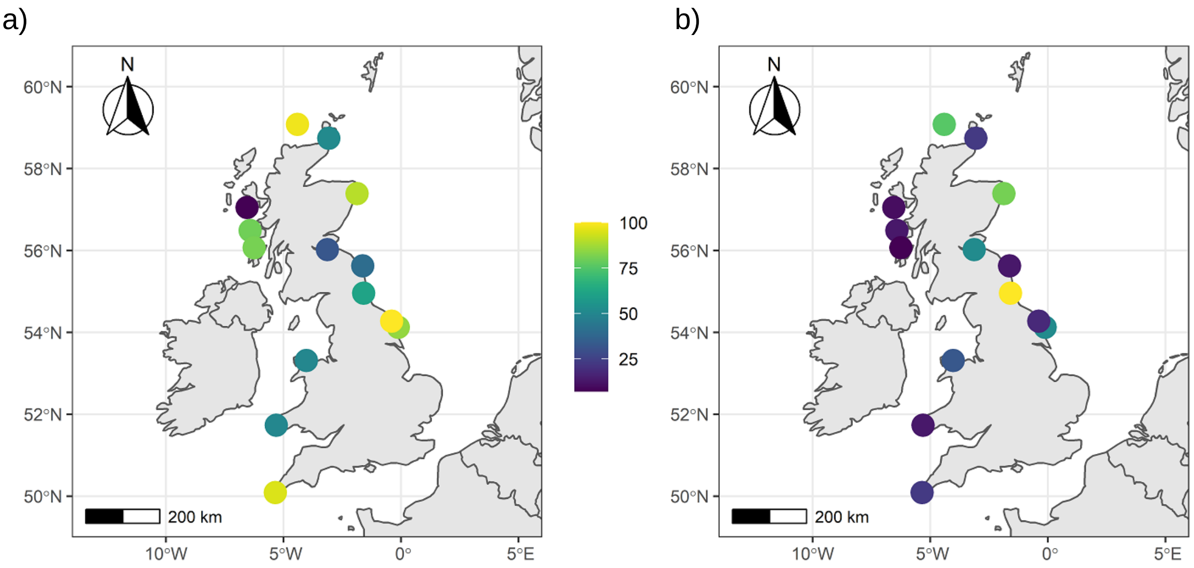


Figure 4.2. Proportion of each colony that is accessible for a) ringing and b) resighting Kittiwakes, from low (blue) to high (yellow).

4.1.1 Ringing questionnaire conclusions

1. At present few ringers focus on colour-ringing to generate resightings therefore encouragement will be required to increase their resighting effort, for example through further highlighting the value of data obtained through colour-ringing resighting. Incentivising additional visits is likely also to be necessary.
2. At present only six of the 15 colonies use colour-rings, with only Trewavas Head colour-ringing chicks.
3. Resighting during ringing activities leads to a mismatch in timings given that the optimal time for resightings is during the pre-laying period – one option to increase resightings is through encouraging ringers to register as a RAS. However, this would require updating the current Kittiwake RAS guidance to allow resighting data to be included pre-April.
4. Individual project costs average £600, although some (notably those using boats to access island colonies, are substantially higher).

4.2 Workshop summaries

To consult a wide range of key experts in Kittiwake demography and ringing we organised two workshops. The aim of the first, ecology-focused, workshop was to discuss the potential of colour-ringing as an approach to obtain more precise and accurate empirical data of Kittiwake demographic rates with key academic experts in Kittiwake demography (Appendix 2). The aim of the second, logistics-focused, workshop was to discuss the logistics of implementing a large-scale colour-ringing project for Kittiwake across the UK with ringers and people who might be involved in resighting colour-ringed individuals (Appendix 3). Below we provide an overview of the key points discussed during both workshops.

4.2.1 Ecology-focused workshop

This workshop brought together one of the largest groups of academics undertaking research on Kittiwakes ever assembled, with representation from the key long-term studies being undertaken in France, Alaska, Norway and the UK. The participants were presented with a short series of talks on the project before breaking into groups to discuss three main topics:

1. The lost years: estimating immature survival, dispersal, recruitment and age at first breeding using colour-ringing
2. Demography of adults: estimating survival, breeding dispersal and non-breeding using colour-ringing
3. Alternative approaches to estimating demographic rates: Motus, GPS and other technologies

A summary of participants' views on these three topics is provided below.

Breakout session 1: The lost years: estimating immature survival, dispersal, recruitment and age at first breeding using colour-ringing

- There are many challenges in measuring these (otherwise they would have been done before!) relating to both the biology of the birds and the availability/motivations of recorders.
- Large-scale colour-ring projects on seabirds can be successful, but colour-ringed Kittiwakes are likely harder to identify (smaller rings, occur in dense colonies) and spend a large portion of the year at sea. Comparison was made with a successful large-scale project on Shags *Phalacrocorax aristotelis*, and it was noted that in this project most of the colour-ringed individuals are re-sighted in the winter, not at breeding colonies.
- Clearly need to ring a large number of chicks (and as close to fledging as possible), but equally if involving citizen scientists they need to be able to expect to record a reasonable of number of birds if their motivation is to be maintained; colony size is likely to be important in this context.
- Important to consider sex, female dispersal is more frequent than males, so return rates are correspondingly (much) lower – this dispersal may be quite distant, necessitating a basin-wide approach to quantify completely.
- Achieving relatively high coverage of multiple colonies within a region (and measuring 'apparent' recruitment) may be better than scattered colonies across multiple areas (with many unobserved 'in between' colonies) which birds might disperse into.
- Increasing the number of colonies covered should increase the number of birds re-sighted (and most of the information resides in the re-sighting events rather than the ringing event), hence increasing precision, but at the likely expense of greater heterogeneity (reflecting individual site characteristics).
- Need to consider the elasticity of the population to different immature rates, if these are low, then relatively imprecise estimates may be sufficient?
- If rates are additive to those of adults, then they may suffice as proxies if the extent of covariation can be quantified.
- Some information is already available – in the form of recoveries of dead ringed birds, and Integrated Population Models offer the ability to combine multiple data sources which can help fill in some of the gaps (and quantify covariation between rates).
- Should evaluate alternative approaches, one suggestion raised to quantify extent of dispersal was the use of genomics, though it was noted that microsatellite studies suggested relatively weak structure, at least within UK colonies, so may be more informative at large scales.

Breakout session 2: Demography of adults: estimating survival, breeding dispersal and non-breeding using colour-ringing

- From a global perspective, and especially a circumpolar one, the UK has one of the best seabird monitoring programmes that it should be proud of. This should be kept in mind when trying to improve our system.

- It is important not to lose sight of the importance of estimating adult survival and ensure the focus of the project doesn’t divert too strongly to investigating juvenile age classes and immigration/emigration. Kittiwakes are relatively long-lived species and one would expect that adult survival is relatively more important, depending on variability and how anthropogenic pressures, such as offshore wind farms, affect different age classes. Adult survival is still restricted geographically and some of it is old (ringing programmes that have ceased).
- Spatial hierarchical models may prove useful in quantifying regional variation.
- Demographic reconstruction is a useful approach (Horswill *et al.* 2021), though there is some concern about how reliable it will be over shorter time scales
- In empirical studies, it is crucial that resighting effort is concentrated in the early part of the season before laying. Important decisions need to be made on colour-rings – colours that minimise misreads, accounting for ring loss, strategies for re-ringing as adults.
- Long-term studies have huge value since models require a robust mean and distribution, and because extreme years are comparatively rare.
- Estimates of non-breeding could potentially be obtained from existing data – for example based on the number and timing of observations of individuals. The rationale is underpinned by differences in colony attendance between breeders and non-breeders. Alternatively, technology could be used (data loggers, cameras).
- Estimates of non-breeding and breeding dispersal can also be obtained by demographic reconstruction.
- It seems clear that any new money spent on the programme would yield more results on adults rather than on immatures. Perhaps investigating immatures will benefit from waiting for new technology to become available.
- The relationship between stress physiology and population processes should be considered when designing the project. Eventually, we will have to face the question - is it food that drives the population processes in kittiwakes or something else, and how does this vary with environmental conditions?
- From the metapopulation perspective, it is important to consider which locations would benefit most from new empirical effort. However, this is challenging to establish without knowing the drivers of inter-population movements.
- A full knowledge gap exercise would help establish where the effort is best spent, which this report serves to address.

Breakout session 3: Alternative approaches to estimating demographic rates: Motus GPS and other technologies

General comments:

- The key knowledge gap is the movement between colonies/metapopulation dynamics and some of these approaches such as genetics/genomics, *etc*. might be able to shed light on the possibility of metapopulation dynamics (given the large differences in population trends/ productivity across North Sea colonies).
- There have been a few studies that have shown that there can be substantial adult dispersal and potential source/sink dynamics linked to breeding success.

Technology:

- Technology (such as VHF/Motus) may have a better chance of achieving reliable estimates due to a less biased “resighting” distribution and a much higher resighting rate (mainly due to a higher resighting probability/resighting effort).
- Might be also worth exploring positioning receivers on ships of opportunity, lighthouses, offshore wind farms and oil rigs to increase resighting rates.

- GPS long-term deployments (e.g. with harnesses) may be able to provide estimates of most of the parameters, in particular those that have additional functionality that estimate timing of mortality (e.g. salinity, altitude). Although others noted concerns around the safety of harnesses on Kittiwakes.

Genetics/Genomics:

- One study using microsatellites did not find a lot of genetic structure in kittiwake populations, but full-genome sequencing might be an option worth investigating.

Ticks/Infectious diseases:

- Ticks might work better than genetics and might provide a key for a complementary study.
- Another complementary approach could be looking for immune responses in birds if there is a spatial structure in the presence of infectious diseases.

Modelling approaches:

- Bayesian meta-population modelling based on population trends, productivity and distance may be available to estimate demographic rates and move away from closed populations, e.g. recent University of Glasgow model for Shetland colonies, but models require empirical data that informs and verifies them.

See section 5.7 for a brief review of alternative approaches to estimate demographic rates.

4.2.2 Logistics-focused workshop

Main discussion on ringing and resighting logistics

- For colonies where single annual visits are made (for example, island expedition-style trips, often aimed at ringing multiple species), the timing of the trip might not be well timed with respect to the optimal time for ringing Kittiwake adults/chicks or, especially, for resighting marked individuals. This is because the timing of such trips is usually fixed to fit in with the volunteers' schedules and not the phenology of the bird's breeding season, which can vary substantially between years and is often not known in advance.
- For some colonies, especially for those on islands, access to the colony may be weather-dependent, which may also result in less optimal timing of visits.
- There may be opportunities at some colonies to ring and/or resight immatures and adults away from the nest, for example, when collecting nest material or at wash and loafing areas, although this will be dependent on local conditions.
- Colour-ringing large numbers of chicks and adults will require a considerable number of colour-ring combinations, which may potentially result in mistakes when reporting colour-rings. One option is to use a colony and/or cohort colour-ring in combination with a unique alpha-numeric engraved colour-ring (i.e. as is used at Flamborough) so at least some information can be obtained even if the ring number cannot be read accurately.
- If this is set up as a national project with clear aims from the start, then people are generally happy to share their ringing data. The success of the project will depend on having someone who can coordinate and motivate disparate groups of people well.

Breakout session 1: How can we achieve high resighting rates of colour-ringed Kittiwakes?

- Resighting colour-ringed Kittiwakes is labour intensive and requires a lot of effort and coordination at the local level, especially when relying on volunteers.
- There is a need to improve the efficiency of submitting colour-ring information, particularly those generating significant quantities of sightings. Ideally, this would feed directly through to the ringing scheme database facilitating rapid feedback of encounter histories to encourage and motivate people to keep searching.
- Need to raise awareness of the project to members of the public to recruit volunteers, however resighting effort and take up will be very site-specific depending on where people live and how well people can be engaged.
- Experience from other species, such as Shags, indicates that typically it is just a small number of dedicated individuals who submit the vast majority of resightings.
- One option to recruit resighting volunteers where there may not be many colour-ringed Kittiwakes is to couple resighting with other colony work such as nest recording to increase recorder engagement (in addition to collecting useful contextual data); this should be linked with the Seabird Monitoring Programme, which might also provide a source for recruiting volunteers.
- One option to encourage colony visits early in the season when resighting colour-ringed adults is optimal (but ringing opportunities may be limited) is to provide an appropriate financial incentive.
- Resighting juveniles and immatures is much more difficult than adults and might require alternative approaches away from the colony such as offshore photography (perhaps involving fishers, boats and/or offshore installations).
- Other technologies may help, i.e. VHF for automated mark-recapture however there are still issues with re-encountering juveniles and immatures given that they spend little time at the colony.
- May need to consider survival at the scale of fledging to recruitment rather than for specific juveniles and immatures age classes.

Breakout session 2: Is it feasible to carry out large-scale chick ringing to obtain information on recruitment and immature survival?

- Due to the life history of Kittiwakes, with the average age of first breeding being four years, means that we need to consider a long-term project of at least 5 – 10 years.
- Ringing chicks on artificial structures or at the edge of colonies on natural cliffs may introduce biases compared to ringing chicks from high-quality nests in natural colonies, or at the centre of a colony if there is variation in chick or parental condition related to nest location.
- Given that natal dispersal is relatively high, it may be better to focus chick ringing, and subsequent resighting, effort on several adjacent colonies rather than several more widely separated colonies spread out across the UK.
- If ringing effort is focused on one region in the UK then one option is the east coast of Britain where colonies are generally easier to access and where there is a larger pool of potential volunteers or citizen scientists that could be recruited to resight colour-ringed Kittiwakes - in comparison, for example, to northwest Scotland, where populations densities are lower, geography more complex and sites, on average, less accessible. However, there is a critical need to consider that one region may not be representative of all others, especially where there are differences in Kittiwake population status.
- Ideally we should be colour-ringing every Kittiwake ringed to increase the likelihood of it being resighted – however, this is not necessarily straightforward as managing colour-ring combinations and providing feedback to people on submitted resighting is

time-consuming and ideally needs a coordinator to manage these aspects of the project which can require substantial effort.
- At some colonies there are few or no chicks accessible to ring.

4.3 Analysis of existing ringing data

Data from the British and Irish Ringing Scheme were explored for two purposes:

1. to establish how many chick and adult Kittiwakes were ringed at the main ringing colonies across Britain and Ireland between 2002 and 2019;
2. to establish the dispersal distances of immature and adult Kittiwakes using recovery data of ringed individuals.

Data on the number of Kittiwake chicks and adults ringed in British and Irish colonies between 2002 and 2019 were extracted from the British and Irish Ringing Scheme for sites where at least 50 adult or chick Kittiwakes (in total) had been ringed during this period. We also extracted all recovery records of Kittiwakes that were ringed as chicks or adults and were subsequently recovered between 1st April and 31st July, and therefore are likely recovered at (or near) a breeding colony. This includes individuals ringed in Britain and Ireland and recovered abroad, and those ringed outside Britain and Ireland that have been recovered here. Recoveries were grouped into three categories based on their finding condition: 1) dead (including records where the bird was reported sick, or the reporting circumstances were unknown), 2) re-trapped, or 3) resighted. Recovery finding conditions were classified into these categories to help determine whether a recovered individual was associated with a breeding colony when estimating dispersal rates and distances. Most re-trapped individuals during the breeding season are likely to have been recaptured at the colony during ringing activities. Resighted individuals are also likely to be reported at the colony, but they may also be resighted away from the colony by members of the public, for example, at loafing sites. Although dead birds may be found near the colony, they have a greater chance of being found away from the colony, especially by members of the public. Given that dead birds, especially those that died at sea, may wash up at varying distances from a colony it is more challenging to draw conclusions on dispersal rates and distances from these data.

4.3.1 Current numbers of chick and adult Kittiwakes ringed in the UK

Focusing on the colonies where the majority of Kittiwake ringing has occurred across Britain and Ireland between 2002 and 2019, 18,110 chicks and 6,693 adult Kittiwakes were ringed from 22 colonies (chicks: range 0 – 2605; adults: range 0 – 1691, Table 4.1, Figure 4.3). Of these colonies, nearly half have consistently ringed Kittiwakes in 16 or more of these 18 years.

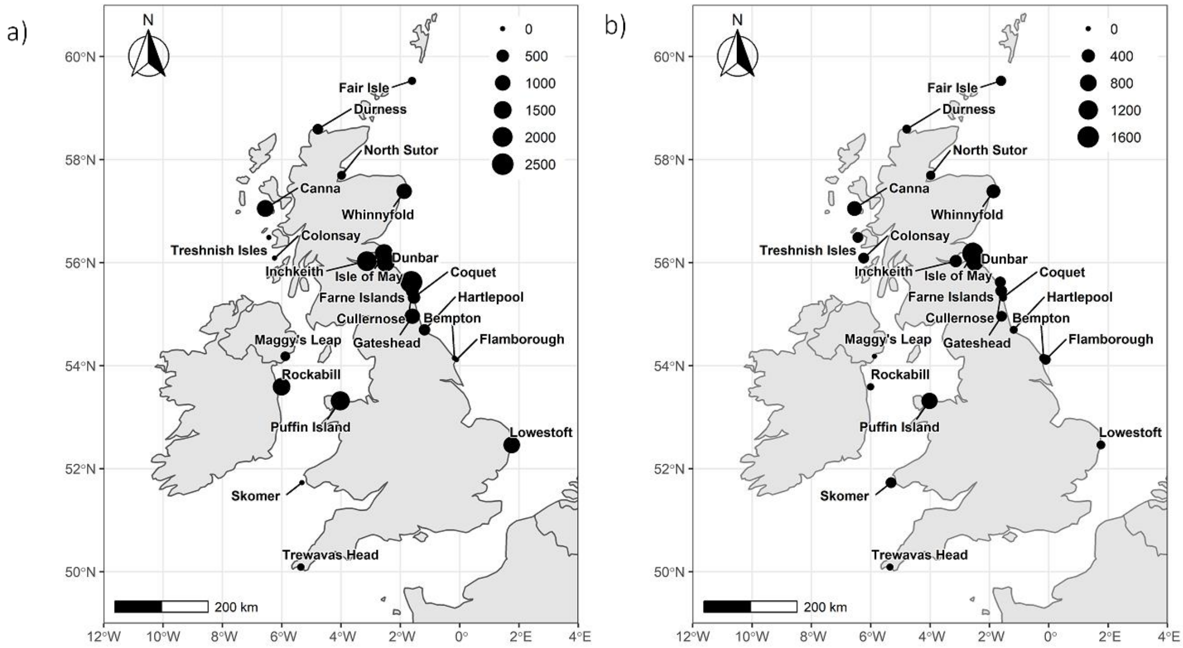


Figure 4.3. Location of colonies with the highest levels of a) chick and b) adult ringing across Britain and Ireland between 2002 and 2019.

Table 4.1. Colonies in Britain and Ireland where the highest number of chicks and adults have been ringed between 2002 and 2019. Colonies are ordered anti-clockwise around Britain and Ireland, starting from Trewavas Head, Cornwall. See Figure 4.3 for locations.

	Chicks		Adults		Recaptures		Resightings	
Colony	Mean ringed per year	Number of years	Mean ringed per year	Number of years	Mean per year	Number of years	Mean per year	Number of years
Trewavas Head	18	3	7	3	2	2	25	4
Skomer Island	0	–	13	16	3	6	62	11
Puffin Island, Anglesey	102	18	42	18	30	18	57	15
Rockabill	85	17	7	4	2	2	–	–
Maggy's Leap, Newcastle	18	11	0	–	0	–	–	–
Colonsay	0	–	13	16	5	13	12	10
Treshnish Isles	0	–	13	16	8	12	–	–
Isle of Canna	72	18	31	18	30	17	–	–
Faraid Head, Durness	21	13	7	13	5	12	–	–
Fair Isle [1]	12	7	14	11	7	9	2	1
North Sutor	8	16	7	16	2	10	–	–
Whinnyfold	57	17	27	17	13	16	–	–
Isle of May	99	17	94	18	57	16	1	3
Inchkeith, Firth of Forth	139	14	22	14	10	14	–	–
Dunbar	87	17	44	18	16	13	6	1
Farne Islands	193	16	23	13	9	12	3	4
Coquet Island	46	11	11	5	8	3	–	–
Cullernose, Howick	52	11	38	7	8	6	–	–
Gateshead	70	14	16	12	7	4	8	2
Bempton, Bridlington	0	–	11	6	11	5	–	–
Hartlepool	36	10	6	8	2	7	–	–
Flamborough Head	0	–	29	5	14	2	–	–

[1] No Kittiwake adults or chicks have been ringed since 2016 due to large populations declines across the island.

4.3.2 Dispersal distances of immatures from their natal colony

Data were available for 3,715 recoveries of 1,833 chicks, which were ringed between 1929 and 2018 and recovered between 1931 and 2019. Based on the duration, in days, between ringing and recovery dates, we split the data into juveniles and immatures (individuals recovered before or during their third summer) and adults (individuals recovered during or after their fourth summer, and which were therefore likely to have recruited into the breeding population).

To map the recovery locations, we split the recovery data further to separate individuals ringed prior or during 1997 from those ringed during or after 1998 to determine whether there were any difference in the geographical extent of recoveries in more recent years compared to historic recoveries. We selected 1998 as there was an increase in the number of recaptures of Kittiwake chicks ringed during and post 1998, and because1998 was the first year of the UK national Seabird 2000 census, with declines observed in the UK Kittiwake population since this census (JNCC 2020).

We identified 2,476 recapture events, involving 1,231 individuals that were ringed as chicks and subsequently recovered during or after their fourth summer during the breeding season (April-July). We also identified 1,239 recaptures of 688 individuals that were subsequently recovered before or during their third summer during the breeding season (April-July), which were likely pre-breeding birds making prospecting trips to breeding colonies.

For individuals that were recaptured during or after their fourth summer, and therefore may have recruited into the breeding population, the majority of re-trapped and resighted individuals, 73% and 66% respectively, were recaptured within 3 km of their natal colony (Table 4.2). However, there is a potential binomial pattern of dispersal, as shown by Coulson and Neve De Mevergnies (1992), with a small peak of individuals re-encountered between 200 and 1000 km from the site of ringing, with the maximum distance being 1,293 km from the natal colony, or 3,673 km for dead individuals (Figures 4.4-6). It should be noted that marked individuals may be more likely to be recovered at their natal colony than surrounding colonies, especially if there is low resighting effort away from the natal colony.

For immature birds recovered dead before or during their third summer, locations covered a broad geographic scale with 46% of recoveries found over 500 km from the natal ringing colony, including in Greenland and North America (Table 4.3, Figure 4.4). Immature Kittiwakes are known to disperse more widely than adults, especially in their first few years (Barrett & Bakken 1997). The recovery locations of these Kittiwakes are not necessarily breeding colonies, and dead birds may have travelled unknown distances before being found, however these recoveries do indicate the scale over which young birds may disperse in their early years. Although the number of dead recoveries involved was smaller after 1998, the distances between the natal colony and where birds were found were shorter than before 1998, as can also be seen for the re-trapped immatures (Figure 4.5). The smaller number of recoveries involved may be due to the fewer number of years and therefore Kittiwakes ringed in more recent times, as well as being associated with a general decline in ring reporting rates (Robinson *et al.* 2009). However, this could also potentially indicate that immatures dispersed less widely in more recent years than historically.

From the chick recovery data, there were only eleven instances of an individual being re-trapped or resighted at a breeding colony during or after their fourth year and then subsequently recovered at a different colony, indicating very few instances of breeding adult dispersal.

Table 4.2. Dispersal distances of individuals from their natal colony (where they were ringed) to where they were recovered during or after their fourth summer during the breeding season (April – July).

Distance recovered from ringing location (km)	Number of recapture events (%) by finding condition[*]		
	Dead N = 327 (327 individuals)	Resighted N = 305 (270 individuals)	Re-trapped N = 637 (634 individuals)
≤ 3	107 (0.33)	201 (0.66)	467 (0.73)
3 > & ≤ 10	28 (0.09)	0 (0.00)	10 (0.02)
10 > & ≤ 50	63 (0.19)	10 (0.03)	58 (0.09)
50 > & ≤ 100	34 (0.10)	7 (0.02)	27 (0.04)
100 > & ≤ 200	23 (0.07)	16 (0.05)	4 (0.01)
200 > & ≤ 500	31 (0.09)	37 (0.12)	24 (0.04)
500 > & ≤ 1000	31 (0.09)	30 (0.10)	45 (0.07)
> 1000	10 (0.03)	4 (0.01)	2 (0.00)
Mean distance (km) ± SD	193 ± 1014	128 ± 243	78 ± 215
Maximum distance (km)	3673	1293	1221

[*] Multiple recoveries of individuals at the same locations were removed.

Table 4.3. Dispersal distances of individuals from their natal colony (where they were ringed) to where they were recaptured before or during their third summer during the breeding season (April – July).

Distance recaptured from ringing location (km)	Number of recapture events (%) by finding condition[*]		
	Dead N = 292 (292 individuals)	Resighted N = 404 (320 individuals)	Re-trapped N = 76 (76 individuals)
≤ 3	46 (0.16)	379 (0.94)	38 (0.50)
3 > & ≤ 10	1 (0.00)	0 (0.00)	0 (0.00)
10 > & ≤ 50	18 (0.06)	7 (0.02)	4 (0.05)
50 > & ≤ 100	14 (0.05)	0 (0.00)	4 (0.05)
100 > & ≤ 200	23 (0.08)	3 (0.01)	7 (0.09)
200 > & ≤ 500	58 (0.20)	7 (0.02)	6 (0.08)
500 > & ≤ 1000	75 (0.26)	8 (0.02)	11 (0.14)
> 1000	57 (0.20)	0 (0.00)	6 (0.08)
Mean distance (km) ± SD	774 ±1014	23 ± 118	321 ± 628
Maximum distance (km)	4483	3131	961

[*] Multiple recoveries of individuals at the same locations were removed.

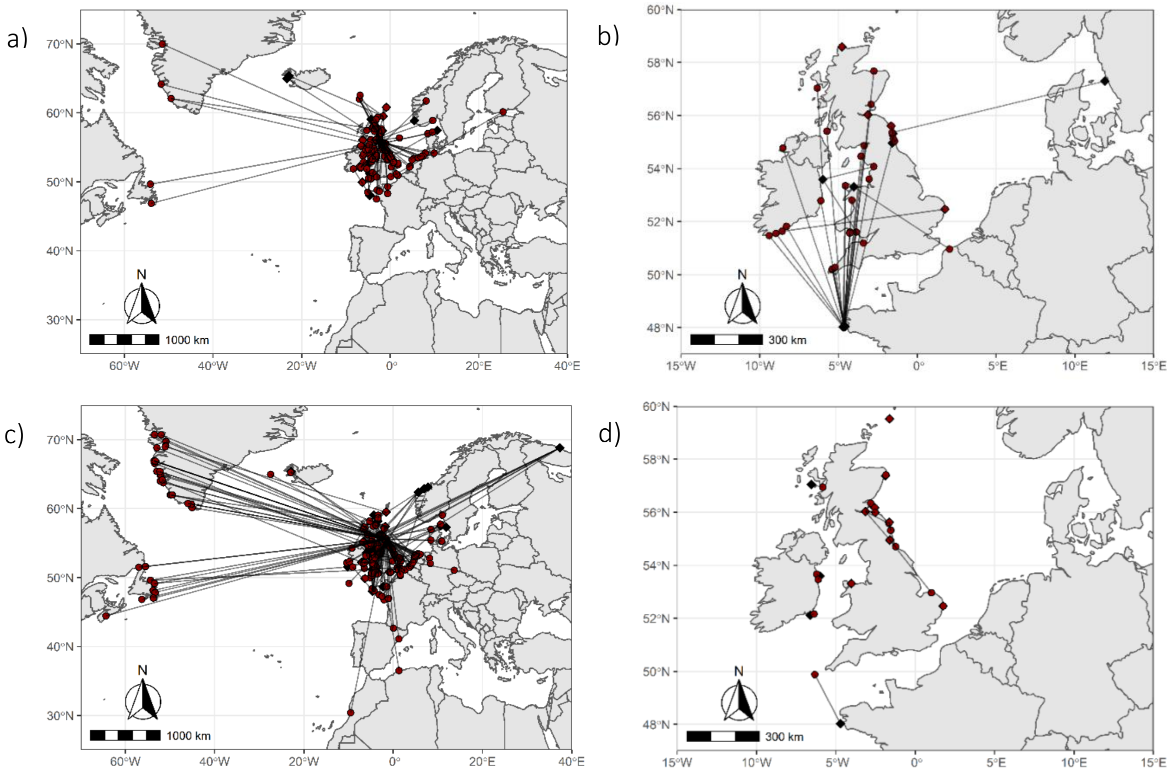


Figure 4.4. The ringing recoveries of Kittiwakes ringed as chicks found dead and involving individuals that were a) ≤ 3 years after ringing and recovered before 1998; b) ≤ 3 years and recovered after 1997, c) more than 4 years after ringing and recovered before 1998 and d) more than 4 years after ringing and recovered after 1997.

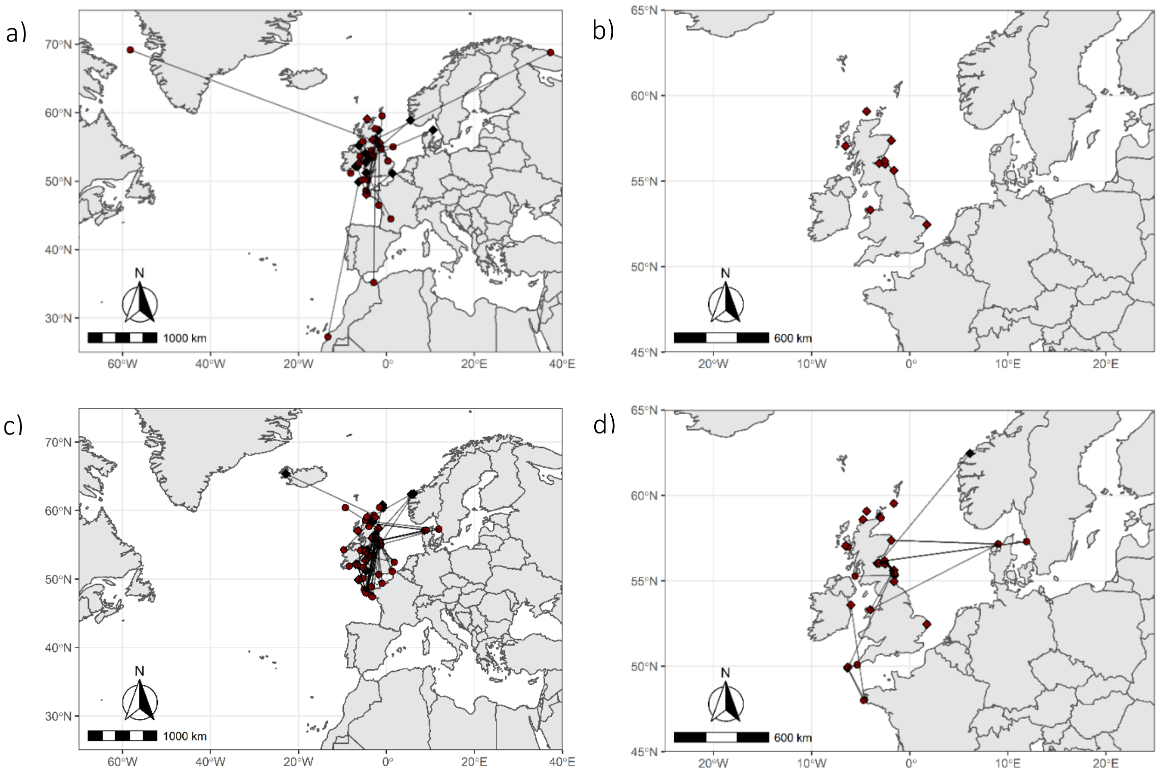


Figure 4.5. The ringing recoveries of Kittiwakes ringed as chicks with a finding condition of re-trapped and involving individuals that were a) ≤ 3 years after ringing and recovered before 1998; b) ≤ 3 years and recovered after 1997, c) more than 4 years after ringing and recovered before 1998 and d) more than 4 years after ringing and recovered after 1997.

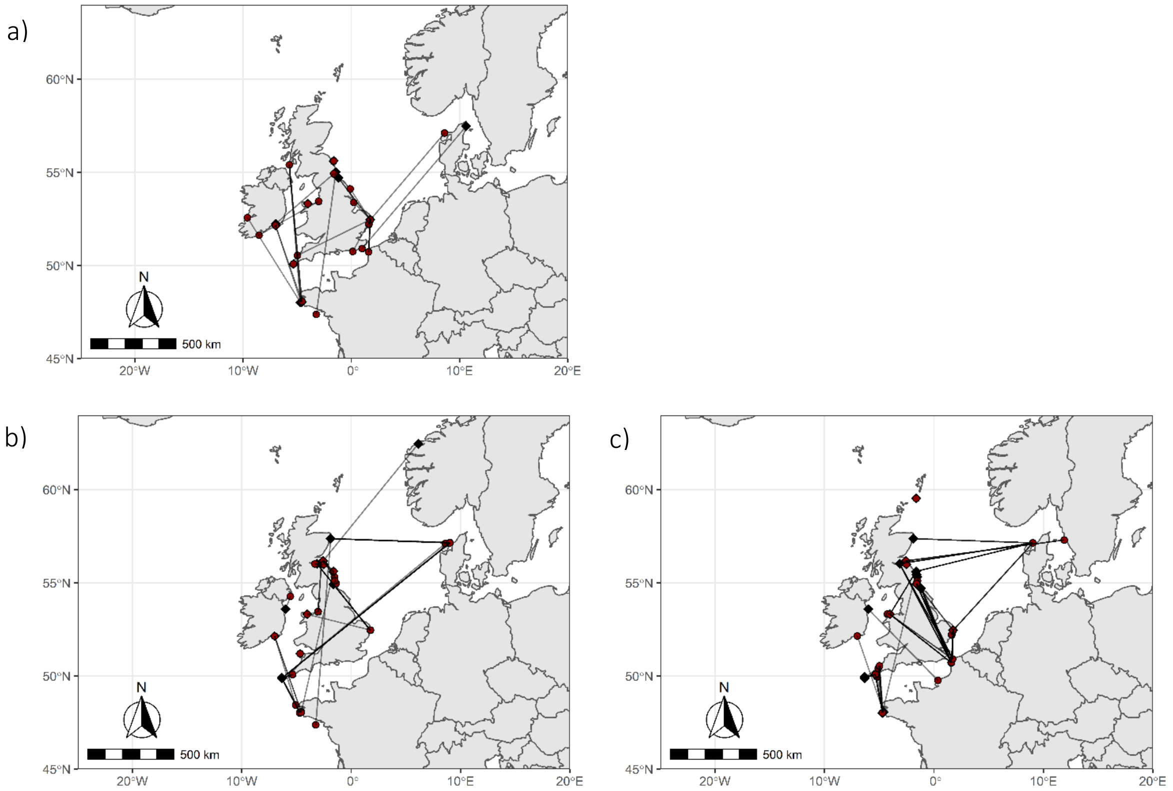


Figure 4.6. The ringing recoveries of Kittiwakes ringed as chicks with a finding condition of resighted and involving individuals that were a) ≤ 3 years after ringing, includes all recoveries as only 8 were recovered before 1998; b) more than 4 years after ringing and recovered before 1998 and c) more than 4 years after ringing and recovered after 1997.

4.3.3 Adult breeding dispersal

From the British and Irish Ringing Scheme, we identified 7,441 recoveries involving 2,815 individuals that were ringed as adults between 1938 and 2018 and were subsequently recovered during the breeding season (1 April – 31 July), between 1940 and 2019.

In contrast to the distances moved from the natal colony by individuals ringed as chicks, the mean distances moved by individuals ringed as adults were very short (Table 4.4, Figures 4.7 and 4.8). Over 99% of adults were re-trapped or recaptured within 3 km of the colony where they were ringed. As has been suggested in the literature (see section 2), the ringing data also indicates that adult dispersal is infrequent. However, as with natal dispersal, individuals have a greater chance of being detected in the colony where they were ringed due to biased resighting effort. The adult recoveries data revealed a small number of long-distance movements away from the ringing colony, however these involved resighted individuals. Therefore, it cannot be assumed that these individuals were breeding when they were resighted as these recoveries may involve prospecting failed breeders (Figure 4.8).

Table 4.4. Dispersal distances of adults from the colony where they were first ringed to where they were recaptured, during the breeding season (April – July).

Distance recaptured from ringing location (km)	Number of recovery events (%) by finding condition*		
	Dead N = 198 (197 individuals)	Resighted N = 746 (716 individuals)	Re-trapped N = 1912 (1907 individuals)
≤ 3	71 (0.36)	725 (0.97)	1885 (0.99)
3 > & ≤ 10	17 (0.09)	0 (0.00)	15 (0.01)
10 > & ≤ 50	48 (0.24)	9 (0.01)	7 (0.00)
50 > & ≤ 100	22 (0.11)	2 (0.00)	2 (0.00)
100 > & ≤ 200	14 (0.07)	2 (0.00)	3 (0.00)
200 > & ≤ 500	10 (0.05)	5 (0.01)	0 (0.00)
500 > & ≤ 1000	9 (0.05)	2 (0.00)	0 (0.00)
> 1000	7 (0.04)	1 (0.00)	0 (0.00)
Mean distance (km) ± SD	154 ± 505	10 ± 113	0.5 ± 7
Maximum distance (km)	4136	2658	176

*Multiple recoveries of individuals at the same locations were removed.

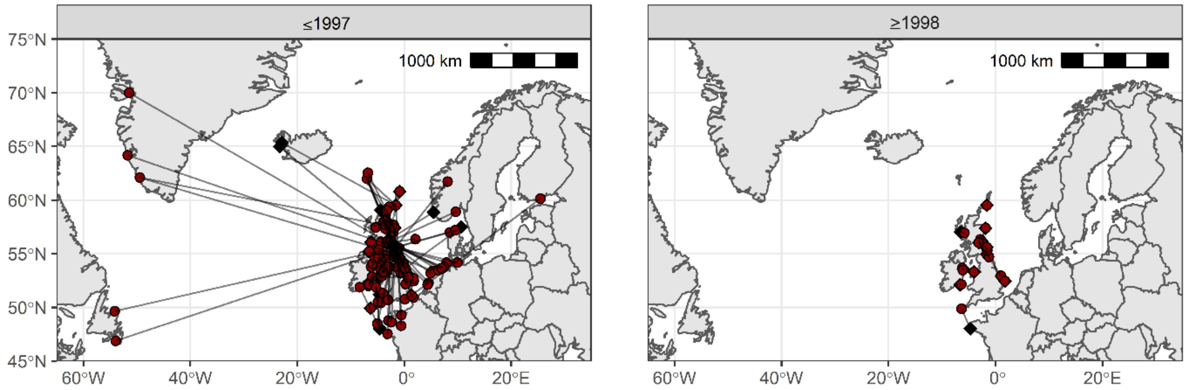


Figure 4.7. The ringing recoveries of Kittiwakes ringed as adults with a finding condition of dead and were recovered a) before 1998, and b) after 1997.

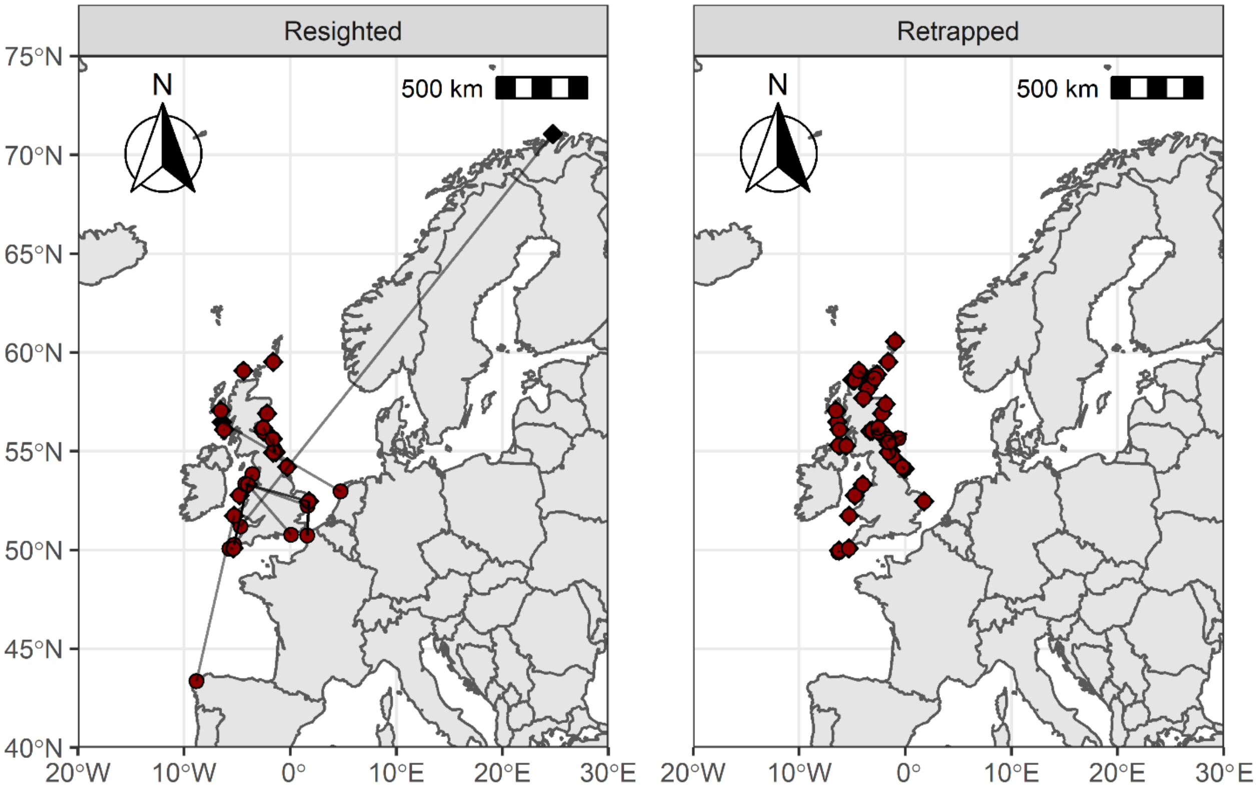


Figure 4.8. The ringing recoveries of all Kittiwakes ringed as adults with a finding condition of a) resighted and b) re-trapped.

4.3.4 Ringing data conclusions

1. There are few colonies across Britain and Ireland that currently ring over 100 chicks annually, however there are clusters of adjacent colonies where it may be achievable to ring large number of chicks: for example, Isle of May, Inchkeith and Dunbar around the Firth of Forth, and the Farne Islands, Coquet and Cullernose in Northumberland.
2. There are a small number of colonies that have ringed adult Kittiwakes since 2002 that likely maintain a ringed population of around 150 individuals, including: Isle of May; Dunbar; Puffin Island, Anglesey; Isle of Canna and Whinnyfold, Grampian, although not all adults are colour-ringed at these colonies.
3. Based on British and Irish ringing recoveries of individuals ringed as chicks and recovered during or after their fourth summer, during the breeding season, 83% were re-trapped or resighted within 100 km of their natal colony. Although some individuals do disperse further, searching adjacent colonies within at least 100 km from the natal colony is required to try and locate dispersed individuals, as also indicated by (Coulson & Neve De Mevergnies 1992).
4. For individuals ringed as adults, 98% were re-trapped or resighted within 3 km of the colony where they were ringed, suggesting low levels of adult dispersal.

5 Feasibility of implementing a large-scale Kittiwake colour-ringing project

In this section we discuss the logistical feasibility of implementing a large-scale Kittiwake colour-ringing project in terms of:

1. considerations required when selecting suitable sites to undertake ringing and resighting effort;
2. a colour-ringing protocol to ensure a well-planned and delivered project; and
3. how a large-scale ringing project could be achieved in terms of survey design, site selection and associated costs.

We then briefly review alternative approaches to colour-ringing that have the potential to provide empirical data on Kittiwake demographic rates.

5.1 Site suitability assessment

Across Britain and Ireland, there are several colonies where ringing of Kittiwake adults and chicks currently takes place (section 4.3), including seven Re-trapping Adults for Survival (RAS) sites and seven colonies that use colour-rings on adults and/or chicks. However, given the results of the power analysis (section 3), and the recommended number of colour-ringed Kittiwake adults and chicks required to improve our current knowledge of Kittiwake demographic rates, ringing, and resighting, effort will need to be expanded to a larger number of colonies, and effort at some existing colonies will need to be increased.

When deciding on a location for a long-term colour-ringing study, numerous aspects regarding their suitability for ringing and resighting must be considered. Most of these aspects can be divided into site-level and nest/bird-level considerations, with a primary focus around the safe accessibility for both ringing and resighting activities (Figure 5.1). Overarching qualities such as the ease of access (e.g. remote islands vs. mainland colonies) and the colony size and population trajectory (e.g. not starting a study at a rapidly declining colony where numbers will soon be too low to maintain an adequate sample size) will inform the suitability assessment.

In the following paragraphs, we will outline the necessary considerations to assess the suitability of a site for a Kittiwake adult and chick colour-ringing study. We consider (a) core aspects (Level 1); (b) essential aspects (Level 2) which are important to consider but can mostly be optimised by changes to the protocols; and (c) mostly logistic aspects (Level 3) that need to be considered but usually by themselves would not deem a site unsuitable. We did not divide these by activities (ringing or resighting), as aspects related to both activities need to be considered together to set-up a successful and effective colour-ringing study.

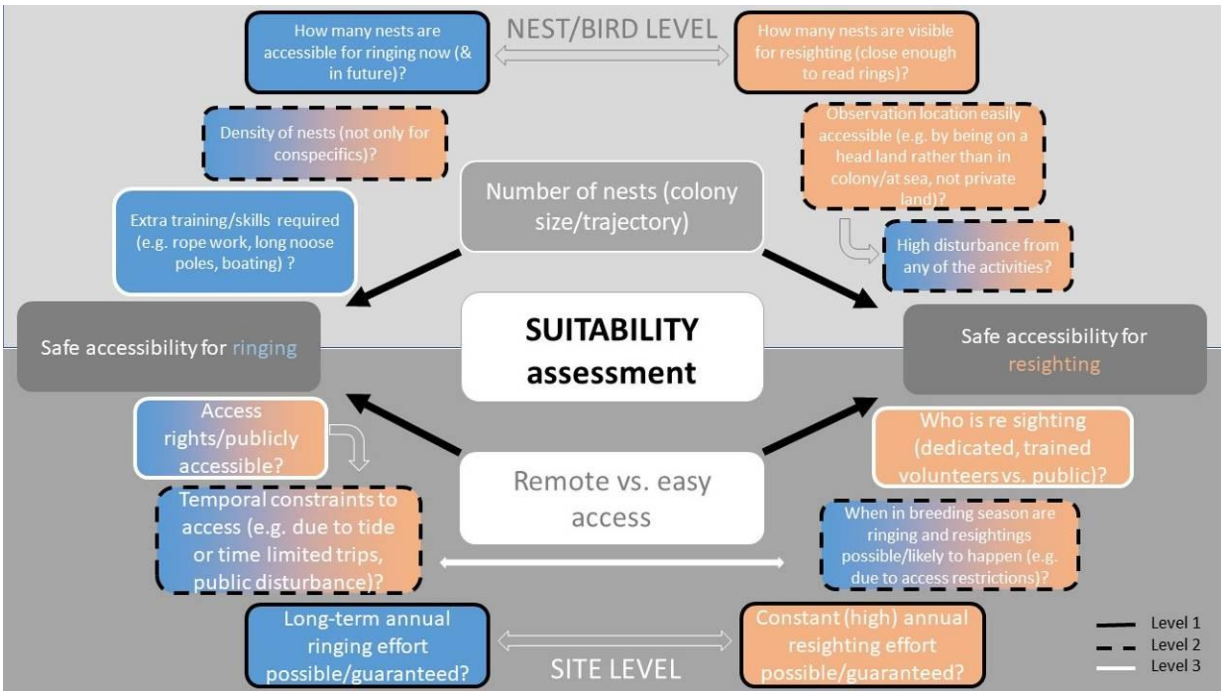


Figure 5.1. Overview of all aspects that need to be considered when assessing a site for their suitability for a Kittiwake colour-ringing study. Outlines of boxes assign aspects to different levels. Level 1= core aspects. Level 2 = essential aspects. Level 3= logistic aspects.

5.2 Level 1 aspects

5.2.1 Site Level

Is long-term annual ringing effort AND a constant (high) annual resighting effort guaranteed or even possible?

This should be one of the first considerations when looking at a potential site. If there is no mechanism for sustaining annual ringing and/or resighting effort (e.g. access to a remote site is not guaranteed every year at the right time), the site should not be considered further. It must be noted that for ringing, the initial ringing effort during the first 1-3 years will usually need to be substantially higher to reach the target number of colour-ringed birds. Once this is reached, it is possible to reduce the ringing effort to only “topping-up” the number of ringed birds.

For chick colour-ringing, it is also important to consider potential resighting effort across the whole colony (not only the ringing site) and even at adjacent colonies, due to dispersal from natal sites (section 4.3).

5.2.2 Nest/Bird Level

How many nests are accessible for ringing now and in the future, AND how many of these nests are visible for resightings (i.e. close enough to read rings)?

This consideration goes hand-in-hand with the effort considerations made at the site level. The ringing target refers to the confirmed number of birds (chicks or adults) colour-ringed at the colony in any given season. For adults, with the exception of the first year where this sample will only consist of newly-ringed birds, it will include resighted birds and birds that were newly ringed to top up the sample to the target number. Even if long-term annual ringing effort and resighting effort is possible, it does not necessarily mean either can be done due to the accessibility of nests for one or both of the activities. The power analysis (section 3) indicated that a colour-ringed population of 100-150 adults would be necessary, so this number of nests should be safely accessible for ringing, and visible for resighting. The number of nests may be reduced if both members of a pair are ringed, but allowance should be made for potential variability in occupancy across years and in catchability between birds, and nest failures during a season. For a chick colour-ringing study, substantially more nests than the chick colour-ringing target should be accessible for ringing to again account for variability in occupancy and success across years and nest failures during a season (we recommend ~1.5 times as many as the ringing target). Note also that chick accessibility is more challenging than adult accessibility. Adults can be caught from above at nests sites with a drop below because they are noosed off the nest. This is generally not safe to undertake with chicks which ideally require accessing from below.

5.3 Level 2 aspects

5.3.1 Site level

Are there any temporal constraints to accessing the site for either of the activities (e.g. due to tide, time-limited trips and/or early morning work due to public disturbance)?

Reasons for temporal access constraints can vary greatly but are important as they can limit the ringing or resighting effort possible in a given year. For adult colour-ringing this is particularly important for the first 1-2 years when large numbers of birds need to be ringed to reach the target number compared to later on when numbers only have to be topped up. For resightings and chick colour-ringing studies this is equally important all the time as a reasonably large effort needs to be possible every year.

When in the breeding season is ringing and resighting possible or likely to happen (e.g. due to access restrictions)?

Possibly even more important than how much time is available for either of the activities, is when in the breeding season it is possible to ring or resight birds, as this will govern the feasibility of, and amount of effort required for, each of the activities. Adult colour-ringing can happen from incubation to mid-chick rearing, but the late chick-rearing period should be avoided because chicks are mobile. The optimal period for chick colour-ringing is more time-constrained. There is a balance to be struck between chicks being large enough for ringing and them being too mobile which means they are unlikely to resettle after handling and the possibility of premature fledging is high.

The time of resightings mainly affects the effort required to achieve good resighting probability. Pre-laying/nest building is the best time for resighting as a) colony attendance is high across breeders (often both adults of a pair) and non-breeders (which includes birds taking sabbaticals (adult colour-ringing) but also immature birds (chick colour-ringing)) and b) birds are likely to be standing making reading leg rings easier (Harris & Calladine 1993; Chambert *et al.* 2012). Resighting is hardest during incubation as change-over rates between adults are low and birds in attendance are likely to sit tight, not showing their legs. It improves again over the chick rearing period (but only for breeding birds whose nests have not failed) before dropping again towards the end of the season when adult nest attendance is lower.

Overall, optimal timings for each of the activities are different and trying to achieve both at the same time (e.g. resighting during chick rearing at the same time as when birds are ringed) will result in a lower resighting probability. Therefore, we recommend that ringing and resighting activities are carried out at different times (though they may share personnel at individual sites).

5.3.2 Nest/Bird Level

What is the density of nests (not only for conspecifics)?

The density of nests at the site also needs to be considered and a medium density is most favourable. A low density of nests spread across a large area will result in a larger ringing and resighting effort needed as ringers and observers need to move between ringing and observation locations. A high density of nests (con- and allo-specific) might result in higher levels of disturbance, which is undesirable both for ethical reasons (disturbance has fitness consequences), and also because it might jeopardize ringing efforts by decreasing catchability of birds. High nest density may also affect resighting effort if it’s harder to get a clear view of individual birds due to other birds being in the way.

While these effects are particularly pronounced in adult colour-ringing studies, chick resighting will have to be spread across a larger area by default, so the disturbance considerations for a high density of nests apply to both types of studies.

Is the observation location easily accessible?

There is likely to be a lower resighting effort and consequently a lower resighting probability if the observation location is not easily accessible and viewable from land (e.g. on a headland opposite the cliff face where the colour-ringed nests are concentrated) and logistical considerations need to be made if resighting requires boating or access to private land. If resightings are only possible within the colony or from sea close to the colony, disturbance to the colony has to be considered again.

Compared to adult-colour-ringing, where nest locations will be largely consistent (and known) from year to year, for chick-colour-ringing studies, having a good selection of vantage points overlooking large parts of the whole colony (and adjacent colonies) is necessary since birds may recruit to any point in the colony.

Will ringing and resighting activity cause disturbance to birds?

While a certain level of short-term disturbance during ringing activities can be expected (even when minimised), having a site where the processing of the birds occurs very close or close to the nests (e.g. due to space limitations) might not be ideal. Similarly, regularly accessing the colony (e.g. being in the same location as from where the birds are caught) to conduct resightings can cause substantial levels of disturbance, all reducing resighting probabilities and nest reoccupation rates, and potentially increasing nest failure.

The same can be true for a headland observation location that is too close to the nests.

The ideal site therefore has enough space to process birds a short distance away from where they are caught, and a resighting observation point a moderate distance away (far enough away to avoid disturbance, close enough to be able to read colour-rings with a telescope).

5.4 Level 3 aspects

5.4.1 Site level

What are the access rights to the site and is the site accessible by the public?

Restricted access rights (e.g. due to private land ownership) and public accessibility of the sites can both limit the time period during which ringing and resighting activities are possible (e.g. at a public site it might be advisable to concentrate ringing activities in the early morning hours before the public arrives). On the other hand, public access might facilitate public involvement in resighting effort and can lead to higher resighting probability.

Who is resighting the birds (e.g. dedicated observers, trained volunteers or the public)?

This is a question that should be answered early in the planning process, balancing expected/targeted resighting effort, possibly costs and resighting probability/data quality (correct ring readings). Each observer group comes with benefits and disadvantages. Dedicated (paid) observers will usually provide the highest (targeted) effort and best data quality, while trained volunteers (e.g. members of ringing groups and bird observatories) might provide equally good data quality, but less consistent effort. The public can seem to be the easy choice but also generally entails the least reliable effort and data quality. One should also consider the time it takes to educate and motivate people to take part in such studies and coordinate their ring resightings. A hybrid system where multiple observer groups (e.g. resighting effort lead by dedicated observers which are supported by trained volunteers and the public) are involved can often be a good alternative.

5.4.2 Nest/Bird Level

Are there any extra skills and/or training required (e.g. rope work, long noose poles experience, boating license)?

This is another key logistical consideration that might have knock-on effects on other aspects of the suitability assessment and that can create challenges due to staffing requirements and/or costs related to it. The fewer extra skills and training that are required to access individuals, the better.

5.5 Colour-ringing protocol

Colour-ringing adult birds and chicks can be a powerful way to assess numerous demographic parameters such as survival rates and dispersal, but studies have to be well planned (including a thorough assessment of the suitability of the site) and delivered with constant (high) ringing and resighting effort for numerous years.

In the following, we will briefly summarise a generic annual protocol for a Kittiwake adult and chick colour-ringing study, but it has to be noted that there might be adjustments that need to be made due to study-specific logistic restraints (e.g. accessibility of sites, see “Site suitability assessment”). Any ringing activity (capture, handling and ringing) can only be undertaken by highly trained individuals with the necessary BTO ringing licenses.

More information on guidelines for BTO RAS (Retrapping Adults for Survival) sites or (colour) ringing in general can be found at (www.bto.org/ras) and we will only discuss important and mostly Kittiwake-specific aspects of the protocol.

5.5.1 Ringing

Ring choice

Before the start of a study, one has to decide which type of colour-ring to use within the limitations of maximum ring length and diameter set by the BTO. This is in most cases a one-off decision and has to be well thought through. In general, the choice is between using multiple single-colour-rings to code individual birds with colour combinations (usually two on one leg and one above the metal ring on the other) or to use a single engraved colour-ring with a unique alpha-numeric code-colour combination (Figure 5.2). Both approaches have advantages and disadvantages and a decision should be governed by individual study parameters (e.g. adult vs. chick colour-ringing; focus on survival rates vs. dispersal; trained observers vs. public).

Like any marking technique, colour-rings can very occasionally cause problems, such as leg injuries, for birds (e.g. Calvo and Furness 1992; Griesser *et al.* 2012), and good application techniques (e.g. sealing colour-rings) should always be used to minimise the likelihood of such problems occurring. Only a very small number of studies on a limited range of species have tested whether colour-rings affect bird survival rates. The limited evidence available suggests that colour-rings do not significantly affect survival (Bart *et al.* 2001, Cresswell *et al.* 2007), but it is nonetheless important to weigh up the small risk of welfare impacts of colour-ringing as part of planning any study.

Colour combinations

Overall colour combinations are easier to read and dependent on the distance to the bird might not require more advanced optics such as spotting scopes. This makes them particularly suitable for studies where resightings will be undertaken by a varying observer group that also includes less experienced observers such as members of the public. Compared to engraved colour-rings, there is also a reasonable chance to be able to read the rings when the bird is not perfectly standing upright in the cliff (e.g. when the bird is in flight).

However, colours can change over time, rings can fall off and accurate recording/reporting of which colours were on which leg can be challenging for inexperienced observers, all leading to inaccurate ring readings (although the effect of such misreads may be limited (section 3.4) The big disadvantage is the limitation of combinations that will limit the number of birds that can be individually marked. While this will be less of a concern in a colony-specific adult colour-ringing study to assess adult survival for which relatively few birds are ringed annually and birds are expected to return to their ringing/resighting site every year, it would be a concern for a larger-scale multi-site study that aims to ring a large number of birds each year (e.g. a study looking at chick dispersal).

Dependent on the study aim, one could individually mark groups of birds (e.g. chicks ringed at one site in a given year) rather than individual birds to mitigate the problem. This can provide some information on dispersal but complicates deriving quantifiable estimates of dispersal or survival rates since individuals cannot be reliably separated.

Engraved colour-rings

While engraved colour-rings have less of a limitation in regard to the number of individual-specific combinations, resighting will require spotting scopes or high-quality cameras and good resighting conditions, as in most cases accurate reading from a distance can be difficult. There is also a trade-off between having a simple alpha-numeric code to make ring reading easier by minimising the number of characters, and the number of individual-specific combinations available, however standard character sets designed to minimise such problems are available (Clark *et al.* 2005).

The other issue to consider is the base colour of ring and writing for engraved colour-rings as they can influence legibility but maximising the contrast between both (e.g. black/white, yellow/black) can help. It is also advisable to choose a colour that stands out, so even if rings cannot be read from a distance, colour-ringed birds can be located in the cliff. This is particularly important for chick colour-ringing studies as juveniles/immatures are likely to disperse to varying degrees, which then means they have to be located in other colonies or in other parts of their natal colony. In practice, multiple background/letter colour combinations will be needed to cover all colonies/studies, and resighting probability may vary between them. It is critical to consider which colour combinations have been used in other colonies/studies to avoid duplication, as movement of birds is likely across the North Sea basin, and even further afield (section 4.3). Colour-ring combinations should be appropriately registered with country ringing schemes and via the European Colour-ring Birding network coordinator for Kittiwake to avoid overlap with other schemes. Using different colours compared to nearby colonies will make it easier for observers to identify if a bird from another colony is present, for example when scanning through the colony at the start of a resighting session, and potentially prioritise reading that ring first if multiple colour-ringed birds are present.

Hybrid approaches

Using unique engraved colour-rings on one leg and a single plain colour-ring (varying between cohorts) above the metal ring on the other can be a great approach in some situations. Marking in this way allows individual identification (through the engraved colour-ring) but also enables us to gain some information about the bird even when the alpha-numeric code cannot be read (through the plain colour-ring). This could be information about the age of the bird (if year cohorts are marked with a different plain colour-ring per year), or about dispersal (if colony cohorts are marked with a different plain colour-ring per colony, in a large-scale multi-site chick ringing study where the engraved colour-rings are all the same colour).

5.5.2 Annual ringing fieldwork

Timing of ringing activity

Adult Kittiwakes can be relatively easily caught from incubation to mid chick-rearing, prior to when chicks become more mobile. The exact timing will vary by colony, as breeding seasons start slightly later the further North the colony is located. It can also vary annually, so a good overall understanding of the timings at individual ringing sites is required. This can prove challenging for volunteers, especially those not living close to the colony, since they may be unable to alter the timing of visits in response to prevailing conditions.

This is also true for chick colour-ringing. For accessing chicks there is a balance to be struck between the chicks being large enough to be able to safely put a ring on them, and them being too large which would mean they will have an increased level of mobility that makes it hard to get them settled back into their nests and increases the chance of them fledging prematurely.

Ringing effort

At the beginning of an adult colour-ringing study, a high level of annual ringing effort is necessary to reach the target bird number as quickly as possible. The target bird number of a colour-ringing study is the confirmed number of colour-ringed birds (adults or chicks) at the colony in any given season. With the exception of the first year, when this sample will only consist of newly ringed birds, this will include resighted birds and birds that were newly ringed to top up the sample to the target number. For an adult colour-ringing study, the target number will depend on the number of accessible nests (for ringing and resighting) and ringing/resighting effort available at a given site (assessed in section 3).

While data collected before the target bird number is reached are often included in the final analysis, the study only attains its full power once the target number is reached. Afterwards annual ringing effort is likely to decrease as the number of colour-ringed birds only needs to be topped-up, depending on how many have been resighted (e.g. if the target number is 150 birds and only 88 of them have been resighted in a given year, 62 additional birds need to be colour-ringed during the same season).

For chick colour-ringing there is no difference in effort across years. Due to the likely post-natal dispersal, and because the need to estimate variability in juvenile/immature survival rates requires a new sample each year, an equally high number should be ringed each year. As this is sometimes not possible at one site, it is an option to spread the ringing effort across multiple sites in one colony (if the colony is large) or even across multiple adjacent colonies along a coastline.

Adults and/or chicks should be caught at the same site/s each year. While it is advisable to only target one adult per nest in a given year to reduce disturbance, it is completely acceptable and often necessary to target the second adult later on.

5.5.3 Annual resightings

Timing of resighting activity

While resightings can occur all year around, there are times that are more suitable than others, specifically the breeding season. First of all, birds are more likely to be seen during the breeding season or just before as this is the time when Kittiwakes spend more of their time on land, but even during the breeding season there are times that are better than others. Focussing any resighting activities at these times will result in higher resighting probability per unit effort (e.g. per hour of observation). The best time for resightings of colour-rings on any Kittiwake independent of their age class is the time around nest building before laying and incubation (Harris & Calladine 1993; Chambert *et al.* 2012). There is a lot of activity and movement in the colony during courtship and nest building, and pairs tend to spend a substantial amount of time at the nest together. Not only breeders return but also immatures (potentially including birds that have been colour-ringed as chicks in previous years) and birds that are about to take a sabbatical. In contrast, incubation which follows shortly after is the worst time for resightings with incubating birds sitting tight for hours without showing their legs and their partners being out at sea. Once the chick fledges, movement returns and towards the end of chick guarding adults shuffle around so much that ring reading becomes easier again. However, by then observers might have missed the opportunity to read rings of birds that failed early on (as well as birds of other age groups) and overall attendance of adult birds at the colony will continue to drop towards the fledging period.

Thus, pre-incubation is undoubtedly the optimal time for resighting adult colour-ringed Kittiwakes. As with the ringing activities, the exact timing can also vary, so regular colony checks early in the season can be helpful to not miss the window of opportunity.

Resighting effort

Compared to ringing activity, the annual resighting activity has a less tangible end to it, and it can be hard to decide whether certain birds were missed due to effort or them simply not being there. This will also depend on timing as outlined above. During visits, the site(s) should be scanned multiple times for colour-ringed birds until the observer is satisfied that they did not miss any colour-ringed birds that might be there. Also important to record is the date, time and duration of each visit. This will provide a reliable record of effort which can help to correct effort induced variability in survival rate estimates later on.

It can be relatively easy to coordinate resighting effort by dedicated observers, and in many situations it might be possible to motivate trained volunteer observers (e.g. members of bird observatories or ringing groups) to visit sites at certain times of the year, make multiple visits and take records of their effort. However, it can be much more difficult to achieve sufficient, and properly documented, resighting effort from untrained members of the wider public. Successfully coordinating an adequate resighting effort solely based on public records is unlikely to be effective in improving estimates of the parameters of interest in this review.

In the right circumstance and (easily accessible) location, however, public engagement in resighting activity can provide valuable insights and can be highly complementary to a more dedicated resighting effort. This is particularly true for resightings beyond the ringing colony and its neighbouring colonies to increase the spatial coverage when assessing dispersal. Increasing the spatial coverage of resighting effort is particularly important in chick colour-ringing studies as post-natal dispersal tends to be common, and individuals may move further than in incidences of adult dispersal.

Targeting specific public observer groups such as photographers or fishers can also help to increase resightings in less frequently visited locations, even offshore. However, to be really effective in engaging new observer groups and ensuring that the correct information is recorded, establishing an easily accessible (online) reporting system that can provide almost instantaneous feedback (as is in place in other countries such as Norway), and a targeted awareness campaign, would be extremely valuable.

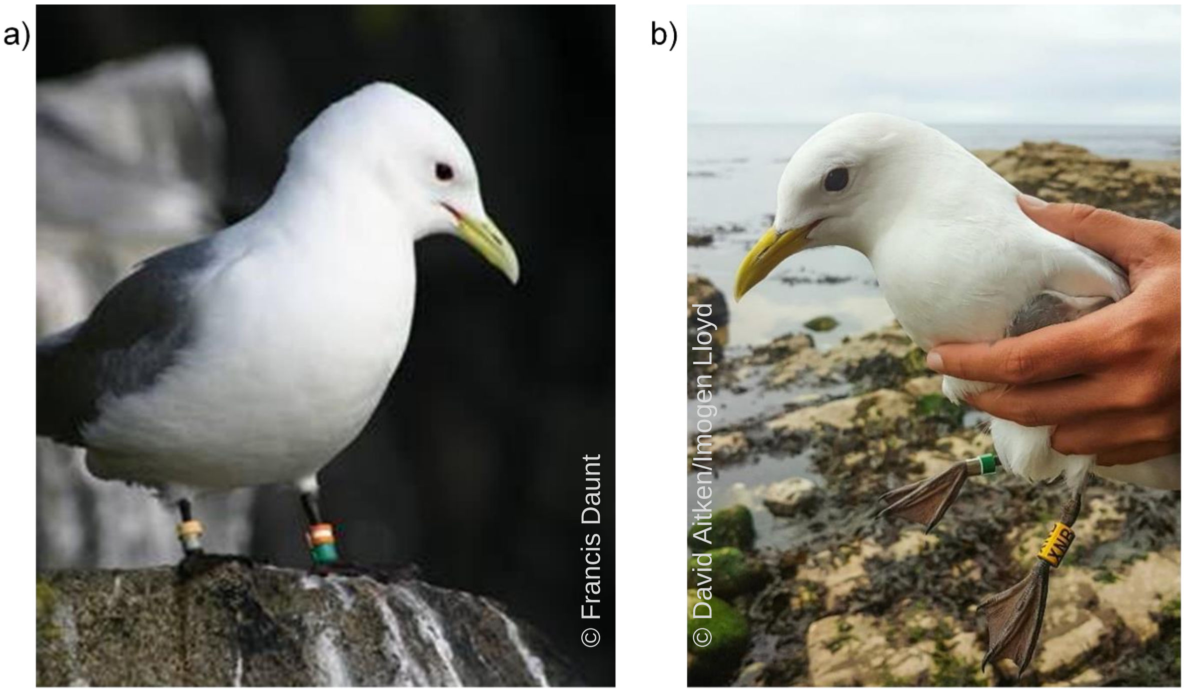


Figure 5.2. In general, there are two types of colour-rings that can be used to mark Kittiwakes: a) multiple single-colour-rings to code individual birds with colour combinations (usually two on one leg and one above the metal ring on the other) or b) an engraved colour-ring with a unique alpha-numeric code-colour combination, which may also be combined with a colony or year specific single-colour-ring above the metal ring.

5.6 How a large-scale Kittiwake colour-ringing project could be achieved

Colour-ringing is the most common approach used to obtain empirical data on Kittiwake demographic rates (section 2, Table 2.2), providing information on survival, age of first breeding, incidences of non-breeding and dispersal. It is also currently the only approach available given that other methods, involving technology or genetics, are currently not yet available to work in a Kittiwake context (section 5.7), although some may prove to be useful in the future, such as the Motus system.

To build on the review of current ringing effort (section 4) and the site suitability assessment and colour-ringing protocol (sections 5.1 – 5.5), below we demonstrate how a large-scale colour-ringing project of Kittiwake populations could actually be achieved in the UK to provide more accurate and up-to date empirical data on Kittiwake demographic rates that could be used to improve the parametrisation of current demographic models used during the consenting process of offshore wind developments.

5.6.1 Sampling design

The results of the power analysis (section 3) suggest that to obtain the indicative level of precision (within 2% of true values) of adult survival estimates at a single colony, a ringed population of around 100-150 individuals needs to be maintained. Considering levels of adult Kittiwakes ringed at colonies currently, this level of adult ringing may be achievable at some colonies; however, this will be influenced by colony size and the proportion of nests that are accessible (see sections 5.1 – 5.5). Generally, the power analyses suggested that, over the range of scenarios considered here, an increase in the number of birds sampled had a greater impact, in terms of increasing precision and power to estimate adult survival, than an increase in the resighting rate, matching results obtained in Common Guillemots *Uria aalge* (Lahoz-Monfort *et al.* 2014). As the scenarios were chosen to represent the range of plausible values for resighting rate and number of birds sampled, this suggests that, all else being equal, increasing the number of ringed birds to the upper end of what is realistically feasible is likely to have more benefit than increasing the resighting rate. A more thorough investigation of the relative importance of different factors in increasing precision/power would be possible in future work but would entail an additional analysis (e.g. sensitivity analysis / ANOVA, summarised through appropriate graphical outputs).

For chicks, the power analysis indicated that estimates of survival for immature age-classes could be estimated to within 10% of true values with 500 chicks ringed per colony per year for ten years. At present, this level of ringing is not carried out at any individual Kittiwake colony and is unlikely to be achievable at any individual colony, with the highest levels of ringing being on average between 70 and 100 chicks per year currently (section 3). This suggests that immature survival will need to be estimated at a regional level, pooling estimates from ringing at adjacent colonies.

In terms of resighting effort, evidence from the resighting analysis results indicate that to achieve a resighting probability of 0.9 between 5 and 10 visits (depending on the colony) should be made to each colony during the breeding season (Figure 3.19), ideally concentrated early in the breeding season, pre-incubation. Adult resighting probabilities of 0.75 – 0.8 are still achievable with 6-8 visits to each colony, even in the worst-case scenarios considered. Therefore, to maximise the number of colonies that can be monitored during each breeding season, we recommend at least 8 resighting visits to each colony.

Given the level of effort required, in terms of both ringing and resighting effort, concentrating effort on one section of the UK coast, large enough to capture the majority of dispersal instances, rather than selecting colonies geographically dispersed across the UK is likely to be a more feasible option. Selection of such regions should be based around those areas of highest interest to the offshore wind farm industry such as the North Sea.

The advantages of this approach include:

i) reducing the number of chicks needed to be ringed at a single colony, and instead ringing the sample sizes required across clusters of adjacent colonies;
ii) increasing the likelihood that colour-ringed individuals will be detected through concentrating resighting effort across specific areas, given that the majority of dispersal events are thought to occur within 100 km;
iii) increasing the likelihood of detecting colour-ringed individuals that disperse away from where they were ringed to improve estimates of local dispersal and connectivity between colonies, especially given that the frequency of natal dispersal of Kittiwakes is relatively high; and
iv) reducing the bias in estimates of apparent survival for colonies if local dispersal/emigration can be accounted for.

5.6.2 Site selection

In this section we focus site selection on the feasibility of ringing and resighting colour-ringed chicks and adults. Priority of locations from an offshore wind farm perspective is the focus of the recommendations (section 6).

East coast of England and Scotland

The east coast of the UK (for example, between Bempton, Yorkshire and Buchan Ness, Aberdeenshire, Figure 5.3b) was identified as a feasible region to focus Kittiwake colour-ringing efforts on for several reasons:

i) this section of coast supports the greatest number of breeding Kittiwakes;
ii) there are already several colonies along this stretch of coast where ringing of Kittiwakes takes place;
iii) the coastline is relatively straight (compared to the many headlands and offshore islands in other parts of the UK, such as the Northwest Scotland, which can make accessing and resighting at multiple colonies difficult); and
iv) this region has a relatively high population of people from which volunteers / citizen scientists could potentially be recruited from.

Given the length of the proposed stretch of east coast, and the number of Kittiwake colonies (Figure 5.3b), we recommend dividing the coastline into at least four regions to focus and co-ordinate ringing and resighting effort.

Along this stretch of coast adults and chicks are already ringed at 11 colonies (see section 4). Three colonies are registered RAS sites (Isle of May; Gateshead, Tyneside; and Flamborough, North Yorkshire), of which Isle of May and Gateshead also ring chicks. A further eight colonies ring both adults and chicks (Whinnyfold, Aberdeenshire; Inchkeith and Dunbar in the Firth of Forth; Farne Islands, Coquet Island and Cullernose in Northumberland; Hartlepool; and Scarborough, North Yorkshire). There is also an additional Kittiwake RAS further south along the east coast in Lowestoft, Suffolk, which colour-rings both adults and chicks. Although, this colony is not within the proposed east coast region, there is the potential that individuals colour-ringed in this region are resighted at Lowestoft, and vice versa.

An additional option would be the establishment of supplementary RAS sites at long-term Kittiwake research colonies (such as sites regularly used for GPS tagging). Kittiwakes might already be colour-ringed at some of these colonies as part of the research projects and increasing the sample size to the RAS minimum might be achievable with little extra effort, especially if trained ringers and observers are already present to conduct the ringing and resighting. However, combining both activities (research project vs. colour-ringing) is necessary and discussions with funders etc. of the research work is essential as additional resources may be required (e.g. colour-rings or staff time). In the near future, there are several seabird tracking projects planned that are funded by the offshore wind industry and that will be at colonies without a local RAS site (e.g. Buchan Ness, Fowlsheugh (both Grampian) and St. Abbs Head (Scottish Borders). These colonies might be good starting points as there should also be interest from industry to see more RAS sites established.

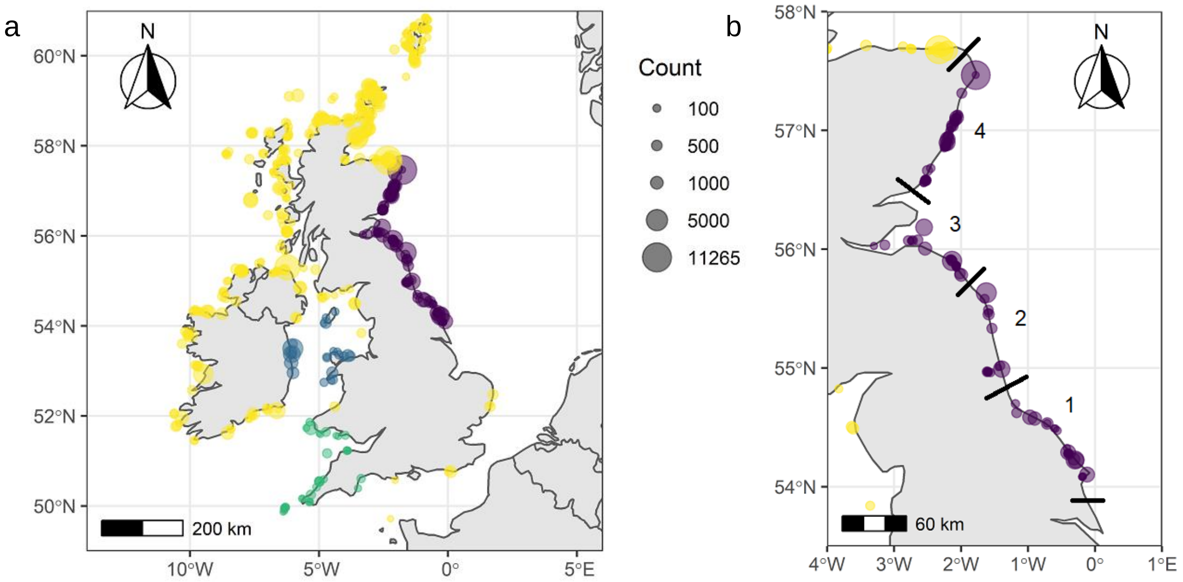


Figure 5.3. Location and size of Kittiwake colonies across a) the UK and Ireland, with the proposed east coast of Britain region in purple, zoomed in b); South Wales and southwest England in green; North Wales, Isle of Man and east Ireland in blue; and remaining areas in yellow. Figure b provides an example of how the east coast could be divided to focus ringing and resighting efforts. The point size relates to the size of the colony based on the most recent count available from JNCC for Britain, and from the Seabird Monitoring Programme dataset for Ireland (last updated 22 October 2010).

Additional regions

Focusing the majority of ringing and resighting effort on the east coast does have the disadvantage of restricting our understanding of regional variation in Kittiwake demographic rates outside of the selected focus region, especially of adult survival. Given the extent of potential offshore wind developments away from the North Sea, we recommend that additional ringing of adult Kittiwakes, ideally through registered RAS sites, should also be encouraged along the west coast to increase the regional coverage and obtain more accurate estimates of adult survival rates. Increased chick ringing should also be encouraged on the west coast given that Kittiwake productivity differs between the east and west of Britain (Cook & Robinson 2010) and immatures survival, especially of juveniles, may also differ between the two coasts.

Given the importance of understanding regional variability in demographic rates, there is the potential to include additional semi-independent clusters of colonies to the colour-ringing project, for example: south Wales and southwest England; and north Wales, Isle of Man and east Ireland (Figure 5.3a). Northwest Scotland is another option however, this will be more challenging due to the large number of Kittiwake colonies that would need to be searched for dispersed individuals across a more complex coastline, many of which will likely be difficult to access and observe.

Benefits to including additional regions on the west coast to colour-ringing efforts include: improving our understanding of regional differences in demographic rates; determining whether there may be any dispersal of individuals between the west and east coast of the UK (acknowledging that it will not be possible to search all colonies on the west coast); and understanding recruitment to specific colonies on the west coast. For example, for this last point, increasing ringing and resighting effort at colonies on the west coast where ringing currently occurs, such as Canna, could provide colony-specific data on age of recruitment and natal philopatry.

5.6.3 Implementation

A substantial amount of effort will be required to establish a colour-ringing project of Kittiwakes given the extent of ringing and resighting effort over the large spatial and temporal scales that are necessary to provide precise demographic rates estimates. Furthermore, the coordination of a large number of colour-ring combinations across multiple colonies and ringing groups, in addition to providing personal feedback to people who report resightings of colour-ringed Kittiwakes is a time consuming process that most individual ringing groups do not have the capacity to take on. A highly motivated coordinator with excellent interpersonal and organizational skills will be critical to the success of the project.

We therefore recommend employing a dynamic and pro-active project coordinator (1.0 FTE in the first instance) to:

- i) engage and build relationships with ringing groups;
- ii) encourage the set-up of Kittiwake RAS across the UK;
- iii) coordinate the distribution of alpha-numeric engraved colour-rings;
- iv) organise resighting field workers;
- v) collate colour-ring resightings / database management;
- vi) engage with local volunteers and citizen scientists, including providing feedback on resighting submissions; and
- vii) provide a mix of in-person and online training to potential volunteer resighters.

Ringing effort

To encourage ringing groups to get involved in a national-scale Kittiwake colour-ring project, we recommend covering the cost of metal and alpha-numeric engraved colour-rings (approx. £2 per bird), as well as providing an annual payment (or honorarium, estimated at up to £600 based on the average cost of current ringing activities – section 4.1) to contribute to the ringers' expenses incurred during ringing visits to colonies.

We recommend that chick ringing effort is focused at up to five colonies within each region, with a target of ringing 100 chicks per year at each colony, to achieve a sample size of 500 chicks ringed per year per region. We also recommend that adult ringing effort is focused at the same colonies as chick ringing occurs, with the target of maintaining a colour-ringed population of 100-150 adults per colony. This is likely to mean increased effort at colonies where ringing occurs currently. For some large regions, such as the east coast of Britain, it may be useful to split the region into sub-regions to focus ringing and resighting effort further (Figure 5.3b).

Due to the large number of unique colour-rings that would be required for this, and to reduce errors associated with misreads, and in fitting combinations of multiple rings, the use of alpha-numeric engraved colour-rings are recommended for such a large-scale Kittiwake ringing project (Figure 5.2). Four-character rings, which are already used on Kittiwakes as well as Black-headed Gulls *Chroicephalus ridibundus* (which take similar-sized rings) would provide more than enough unique combinations (~390,000) for the proposed number of adults and chicks to be ringed, even with a reduced character set to minimise reading error. Having an additional (non-engraved) colour-ring to identify different colonies/regions might facilitate higher resighting rates and help identify broad movement patterns, even if the full engraved combination is not legible.

These colonies within each region would form focal colonies where adult and chick ringing efforts are concentrated. To ensure high resighting probabilities, resighting effort should be undertaken at all Kittiwake colonies within the sub-regions. There is also the potential for nest monitoring and breeding success data to be collected during resighting work by fieldworkers, providing important contextual information.

Resighting effort

The number of visits required to obtain high (greater than 90%) resighting probabilities means that we cannot rely on volunteers to provide all the resighting data. Furthermore, one assumption of the power analysis, in terms of the effort required to ring and resight colour-ringed individuals, is that field effort is relatively constant over time. This will be difficult to achieve within and between breeding seasons if volunteers are relied on. However, with compensated effort to control field schedules, it is possible to reduce variability in field effort. Therefore, dedicated fieldworkers will be required to obtain resighting data.

Along the proposed stretch of the east coast of England and Scotland we recommend employing at least four fieldworkers, with the target of carrying out 8 resighting visits to every colony during the breeding season to resight colour-ringed Kittiwakes. Based on monitoring two colonies per day over 12 weeks of the breeding season, with more visits allocated to pre-incubation, we estimate that four fieldworkers should be able to cover 40-50% of all colonies along this stretch of coast, although it should be noted that the actual number of colonies that can be monitored will vary depending on the size of the colony, distance between colonies and access (section 5), meaning effective coverage will be higher. It is also unlikely that it will be possible to resight all colonies, or all nests within each colony. To ensure coverage of as many colonies as possible, efforts to recruit volunteers to cover resighting at some colonies will also be necessary.

Digital infrastructure and analysis

If implemented successfully, this project will quickly generate a lot of data, which needs to be collated effectively, validated and subsequently analysed to produce meaningful results. Critical to this will be some underlying digital infrastructure to collect and store the data. This will need to comprise four parts:

1. collecting and storing ringing data – the identity of each bird and associated biometric data;
2. collecting and storing colour-ringing resighting data;
3. collecting and storing nest and colony metadata to provide important contextual information to interpret the quantified demographic rates; and
4. a field recording app – to enable data to be recorded efficiently and more accurately because validation (e.g. of possible misread errors) can happen in (near) real-time.

In practice, items 1 through 3 can (and should) build on existing systems of recording data for the British and Irish ringing schemes (1,2) and the Seabird Monitoring Programme (3). Detailed specifications, depending on the scope of the project envisaged, would be needed before the additional resourcing requirements can be determined, both for the creation and maintenance of such systems.

Collecting data is of no use unless it is subsequently analysed robustly to quantify the demographic rates concerned. Given the nature of the data, this is unlikely to be a trivial task, and will require a statistician with some expertise in the analysis of mark-recapture data. Maintaining a rolling program of analysis and review (~0.2 FTE) of the data will be essential to refine protocols, with a larger more formal analysis/review in year 5 (~0.5FTE). If the project is maintained for longer additional analysis/reporting time may well be beneficial since a dataset of this size and quality is likely to yield many avenues for providing insight into Kittiwake demography and its interactions with offshore infrastructure.

Costs

Information on staff and equipment costs for implementing a large-scale colour-ringing project on Kittiwakes is provided in Table 5.1, for the high priority area, in terms of feasibility, along the east coast of England and Scotland, as well as for if the two additional colony clusters were to be included (South Wales and southwest England, and North Wales, Isle of Man and east Ireland).

Note that all time allocations are indicative. Any quote for work will be based on further discussion of the detailed project specifications and the rates prevailing at the time at which any tender may be issued.

Table 5.1. Schedule of work to concentrate Kittiwake colour-ringing effort in Britain and Ireland.

Staff and equipment required	**E Britain[1] (118 colonies)**	**S Wales, SW England[2] (36 colonies)**	**Irish Sea[3] (22 colonies)**
Feasibility	High	Medium	Medium
Project management[5]	0.1 FTE	0.1 FTE	0.1 FTE
Project coordinator[5]	0.8 FTE Y 1 0.6 FTE Y 2-5	0.7 FTE in Y 1 0.4 FTE in Y 2-5	0.7 FTE Y 1 0.4 FTE Y 2-5
IS Technical Support[5]	0.3 FTE Y 1 0.1 FTE Y 2-5	0.3 FTE Y1 0.1 FTE Y2-5	0.3 FTE Y 1 0.1 FTE Y 2-5
Analysis/Reporting[5]	0.3 FTE Y 2-5	0.25 FTE Y 2-5	0.25 FTE Y 2-5
Resighting: Field Time[5]	0.25 FTE per Y x 4	0.25 FTE per Y x 2	0.25 FTE per Y x 3
Resighting: T&S	48 nights, 2000 miles per field worker	48 nights, 1000 miles per field worker	48 nights, 1000 miles per field worker
Ringing: Support/ Equip[4]	10 sites	4 sites	6 sites

[1] Covering the coastline, for example, between Bempton, Yorkshire and Buchan Ness, Aberdeenshire, Figure 5.3b. Three colonies are currently registered as RAS sites in this region (Isle of May; Gateshead, Tyneside; and Flamborough, North Yorkshire).
[2] Covering south Wales and southwest England (Cornwall and the Isles of Scilly; Figure 5.3). Two RAS sites are currently registered in this region (Skomer, Pembrokeshire and Trewavas Head, Cornwall).
[3] Covering north Wales, the Isle of Man and west coast of Ireland (Figure 5.3). One RAS site is currently registered in this region (Puffin Island, Anglesey).
[4] Support for qualified ringers (non-staff), rings, contribution to project costs.
[5] All figures to nearest 0.1 FTE.

5.7 Review of alternative methodologies

Colour-ringing studies are the commonly adopted approach to quantify adult and juvenile survival rates and dispersal but often require a high effort that is maintained over long periods of time. Here, we provide a brief overview of some alternative and/or complementary approaches that might require less effort and/or can provide results more readily. Most of these approaches are not yet completely adapted/tested to work in a Kittiwake context (e.g. most of the technological alternatives described in section 5.7.1 below) and feasibility studies are needed to assess their suitability. Others have been shown to be ineffective for Kittiwakes, despite being very successful in other species (e.g. genetic approaches), and we will only briefly summarise their mechanisms.

5.7.1 Technological alternatives

The use of technology such as bird-borne devices to assess survival and dispersal seems like a natural choice given how successful it has been in answering these questions in other species, some of which are substantially smaller and appear more restrictive to work on than Kittiwakes (e.g. Strandberg *et al.* 2010; Mckinnon *et al.* 2019).

However, it is not the weight that limits their application to Kittiwakes but the availability of a safe, long-term attachment method. For example, commonly-used methods to attach GPS devices on Kittiwakes during the breeding season (e.g. Tesa taping and glue mounting to the back) will only last for up to a month (Wischnewski *et al.* 2017), but to get insights into survival and dispersal rates, attachments have to last for a year at least. The only currently available method that would allow such deployment lengths in a proven safe manner is ring mounting, which has been used to deploy geolocators and time-depth recorders on Kittiwakes over the winter (Mcknight *et al.* 2011; Christensen-Dalsgaard *et al.* 2018). For devices to fit on a ring they need to be: a) even smaller and lighter than the conventional GPS devices deployed on the back; b) compact, without external antennas; and c) sturdy and watertight to withstand the occasional pecking and submergence in water.

Another long-term attachment method commonly used in other species such as passerines, waders and larger gulls are wing or leg-loop harnesses. There are different types of harnesses, but none have been thoroughly tested on Kittiwakes. There is a general concern that they will affect Kittiwakes negatively due to their pelagic lifestyle. Previously, harness deployments have been attempted on other pelagic seabird species such as Great Skuas *Catharacta skua* with detrimental effects (Thaxter *et al.* 2016). However, other, larger gull species that spend less time offshore, such as Lesser Black-backed Gulls *Larus fuscus,* seem to suffer fewer problems with harness attachments (Thaxter *et al.* 2016). Some initial trials on Kittiwakes outside of the UK suggest severe negative effects of back-pack and leg-loop harnesses (Aurore Ponchon, personal communication), but details are not clear and further trials are needed to assess their suitability for Kittiwakes; such trials are planned in the UK, on a small sample of individuals, in 2021 by the BTO.

Motus

Parameters	***Measurable with Motus?***
Adult survival	Potentially, with sufficient sample size
Juvenile / immature survival	Potentially, with sufficient sample size
Dispersal between colonies (adults)	Yes if tag can be miniaturised
Dispersal between colonies (juvenile/immatures)	Yes if tag can be miniaturised
Origin of birds in wind farms (year-round)	Yes if tag can be miniaturised

The Motus wildlife tracking system (motus.org) is an automated radio telemetry system that uses a receiver station network to automatically detect (bird-mounted) radio transmitters once they come within range. Each radio transmitter has a unique frequency signature making it possible to identify individuals. It has been used successfully for years in the Western Hemisphere to monitor migratory movements of passerines, waders and other bird and bat species (Taylor *et al.* 2017; Mckinnon *et al.* 2019); even some seabirds (mostly terns and gulls) have been tagged (Loring *et al.* 2019).

Overall, data from the system will resemble a spatially explicit capture-mark-recapture study and could therefore be seen as a colour-ringing study where resighting effort is automated and constant once a suitable network of receiver stations is in place. Thus, the numbers of birds needing to be marked is similar to that discussed in section 3, albeit with a “resighting” probability of close to 1. They can be positioned on land across SPAs and other seabird colonies but also offshore such as within wind farms, on oil rigs, or even on moving vessels. The distance at which tags can be detected by receivers depends on a number of factors, such as local geography, but is often in the order of kilometres.

Dependent on the sampling frequency tags are set to (i.e. how often they emit a radio signal) they can last for multiple years. While they are most frequently deployed using harnesses or glue mounting, tags are potentially small enough to be deployed on leg rings once the external antenna can be changed to an internal one. The development of tags with internal antennas is already in progress for larger species (geese) but it is likely that it is possible to miniaturise them further in the medium-term (Lotek Wireless Inc and Cellular Tracking Technologies, *pers. comms*.).

If large-scale, long-term leg deployments on Kittiwakes are possible and a suitable receiver network is in place across UK seabird colonies, this system could potentially collect reliable adult and juvenile survival rates (though there may be issues with sample sizes, of both ringed birds and receivers, required for robust estimates), and information on dispersal between colonies, in a shorter timespan than required for a colour-ringing study (though the delayed maturation of Kittiwakes imposes the same absolute minimum time of 5 years as colour-ringing to estimate immature survival and dispersal). If receiver stations are also positioned within wind farms, it would be possible to assess the year-round connectivity between tagged birds and certain offshore wind developments. It is potentially even possible to reconstruct flight paths if the receiver station network is dense enough.

Due to the substantial potential in applying the Motus system to an offshore wind context, the Offshore Wind Strategic Monitoring Research Forum (OWSMRF) identified a Motus feasibility study as a key research opportunity, for which funding is currently being sought via the Offshore Wind Evidence and Change Programme (OWEC). If this funding bid is successful, the project will include work to miniaturise tags to fit on kittiwake leg rings and test these in the field from 2022/2023.

Icarus

Parameters	***Measurable with Icarus?***
Adult survival	Not with current tags/attachments
Juvenile / immature survival	Not with current tags/attachments
Dispersal between colonies (adults)	Not with current tags/attachments
Dispersal between colonies (juvenile/immatures)	Not with current tags/attachments
Origin of birds in wind farms (year-round)	Not with current tags/attachments

Icarus (“International Cooperation for Animal Research Using Space”; icarus.mpg.de) is a relatively new satellite-based animal tracking system. Mini-transmitters are deployed on animals and the data they collect is transmitted to a receiver station in space which then sends the data back to the ground station.

The benefits of Icarus are very similar to Motus; in fact it has the potential to be more beneficial since data is returned via satellite without the need for the bird to be close to a receiver, so spatial coverage could be greater, although currently coverage extends to only 55°N/S, which will exclude many UK Kittiwake colonies. Transmitters can last for years (they have solar panels for recharging) and are incredibly small, but the data collected are at a much higher spatial resolution and not reliant on a receiver station network. However, transmitters currently have extremely long antennas and there is no plan to make them suitable for ring deployments, yet. They are so far only suitable for deployment on birds using harnesses or temporary plumage attachments.

GPS

Parameters	***Measurable with GPS?***
Adult survival	Not with current tags/attachments
Juvenile / immature survival	Not with current tags/attachments
Dispersal between colonies (adults)	Not with current tags/attachments
Dispersal between colonies (juvenile/immatures)	Not with current tags/attachments
Origin of birds in wind farms (year-round)	Not with current tags/attachments

The limitation of using GPS tags to determine survival and dispersal in Kittiwakes is almost exclusively due to the attachment method. Remote download satellite or GSM (Global System for Mobile Communications) tags with solar panels that could last for years are available but require harness attachments as they are too big to be mounted on a leg ring and often have external antennas (which preclude leg-ring attachment). In recent years, discussions about miniature GPS tags that can be deployed on leg rings have increased but direct communication with several tag manufacturers[1] revealed that further development time is needed. The current main hindrance is battery size. Additionally, any miniature GPS tags developed in future for use on leg rings are very unlikely to be satellite or GSM tags (as these types of tags require more components and more power so are more difficult to miniaturise) but most likely archival tags that either need to be retrieved or, in the best case, send data to a local base station (Madsen 2015) . This limits the benefit of their usage to assess survival and dispersal in Kittiwakes compared to a conventional colour-ringing study.

Camera monitoring

Parameters	***Measurable with Camera Monitoring?***
Adult survival	Probably not
Juvenile / immature survival	Probably not
Dispersal between colonies (adults)	Yes, in combination with colour-ringing
Dispersal between colonies (juvenile/immatures)	Yes, in combination with colour-ringing
Origin of birds in wind farms (year-round)	Yes, in combination with colour-ringing

Not a bird-borne device, but remote camera monitoring at colonies, or elsewhere, might be able to provide resightings for colour-ringing studies. Cameras are unlikely to be able to identify individuals as in most cases they won't be close enough to record individual alpha-numeric codes or detailed colour combinations in a legible manner (though this may be possible in some sites, using high quality cameras), but they might be able to capture age or colony (if rings are colour coded by colony). It must be emphasised that, while cameras can provide a valuable addition to resighting, analysis time would increase, as the footage needs to be analysed and this can be very time-consuming. Remote cameras with zoom-lenses in visitor centres can provide an effective engagement tool for visitors and lead to additional records but are unlikely to generate the required level of sightings. In some circumstances, it may be possible to use cameras to enhance resighting rates at sites where access is difficult, particularly if the angle and zoom of the camera can be remotely controlled by a trained observer recording resightings. A wireless HD Nature Cam system at the DuPont Nature Center in Delaware has been used to resight colour-ringed waders (https://vimeo.com/171021867). Birds need to be relatively close to the camera for rings to be readable (within a few tens of metres), so this type of system would likely work only where a camera could be positioned relatively close to a cliff face where colour-ringed birds nest.

5.7.2 Molecular alternatives

Parameters	***Measurable with these Molecular Techniques?***
Adult survival	No
Juvenile / immature survival	No
Dispersal between colonies (adults)	Not with current available methods
Dispersal between colonies (juvenile/immatures)	Not with current available methods
Origin of birds in wind farms (year-round)	No

Analyses of blood or feathers samples from birds can sometimes provide valuable information on their origin, which can be useful for estimating dispersal in some circumstances. However, whilst these methods are safe and have minimal effects on birds when conducted properly, it is always important to consider animal welfare when taking

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[1] Icarus, Ornitela, Technosmart, Pathtrack, Ecotone, Lotek and Microwave Telemetry

samples, so appropriate training and licensing is required for taking blood or feather samples.

While genetic studies cannot be used to assess adult and juvenile survival rates, they can be a powerful tool to determine population structures and therefore connectivity between colonies, which in turn provides insight into dispersal and metapopulation dynamics (Bicknell *et al*. 2012; Yannic *et al*. 2016; Young 2010). Conventional genetic analyses, for example using microsatellite markers, can be done almost instantly from blood samples, but they require some level of genetic diversity between birds from different colonies to provide useful results.

An initial study in the North Atlantic using microsatellite markers showed that Kittiwake populations are only genetically structured at large spatial scales, with weak patterns of isolation by distance, suggesting that substantial dispersal occurs across large distances (McCoy *et al*. 2005). Interestingly, the same study found that looking at the birds' parasites (in this case ticks) can sometimes be more informative due to their stronger regional population structure. Another potential alternative could be looking into infectious agents and antibodies in the birds' blood. Similarly, if there is a regional structure in diseases that the birds have been exposed this can lead to differences in antibodies in the birds' blood. Whilst the study of parasites and pathogens has the potential to help with understanding population structure in the future, considerable further development of these methods would be required in order to understand whether information about Kittiwake dispersal can be measured with such techniques.

Even if more conventional genetic approaches using microsatellites were not successful, genomics (analyses of the whole genome rather than specific segments of DNA) might be able to provide further insights into the population structure by picking up on more subtle differences, but this will be costly and time consuming and is currently some way from practical implementation.

Analyses of stable isotope ratios in birds' feathers can provide useful information on the diet and location of the bird at the time the feathers were grown and therefore can measure avian dispersal in some circumstances (Inger & Bearhop 2008). However, it is unlikely to be a useful approach for elucidating the inter-colony dispersal of kittiwakes because of the life-history and moult cycles of this species, which means the feathers birds are carrying when they arrive at a new colony are not likely to have been grown at the colony they dispersed from. For juvenile dispersal, there are several years between birds leaving the nest (where their first feathers are grown) and recruiting to a breeding colony. During the intervening period they will have undergone several complete moults, most likely far away from the colony where they hatched. Adult moult usually happens after the end of the breeding season when birds are likely to have left their breeding site. We have therefore ruled out stable isotopes as a useful approach for measuring inter-colony dispersal in this species.

6 Conclusions and Recommendations

Determining the impact of offshore wind farms on seabird populations using demographic models is a vital part of the consenting process (section 1). However, the lack of empirical data on Kittiwake demographic rates to parametrise these models can result in considerable uncertainty when assessing the impact of renewable developments on seabird populations (Cook *et al*. 2018). The literature review (section 2) highlighted the paucity of data on all Kittiwake demographic rates, particularly those prior to breeding. Adult survival was better quantified, but regional representivity could be improved.

To increase the predictive accuracy of demographic models, and our confidence in how Kittiwake populations will respond to potential impacts of offshore installations, we require up to date, accurate and, ideally, precise empirical data on most demographic rates (Table 6.1). These conclusions are based on information drawn from the previous sections, particularly the literature review (section 2), the power analysis (section 3) and consultation with a range of experts and stakeholders (section 4.2).

Survival rates, of all age-classes, have the greatest influence on estimating population viability, although PVAs are most sensitive to misspecification of juvenile/immature rates because a relatively wide range of values can be considered plausible. Recruitment of breeding individuals to colonies was highlighted as an important quantity by workshop participants. This additionally requires knowledge on natal dispersal, since rates of adult dispersal are low.

Currently, a large-scale colour-ringing project is the only feasible means of quantifying levels of survival, of any age-class; details of how this might be organised are provided in section 5.6. Technological solutions are currently not ready to be deployed on Kittiwakes (section 5.7) and current molecular approaches do not appear to be applicable to Kittiwakes (which lack a strong population structure, presumably due to widespread natal dispersal).

Table 6.1. Qualitative assessment of the importance of each demographic rate in determining population dynamics and reducing uncertainty in PVAs, and whether colour-ringing is a feasible option to improve estimates of these rates.

Demographic Rate	**Importance in determining population size / growth**[1]	**Sensitivity in the PVA**[2]	**Feasibility to obtain data through colour-ringing**[3]	**Is it possible to estimate this rate through colour-ringing, and hence begin to reduce uncertainty in PVAs, within:**[3]		**Could a precision of 2% (adult survival) or 10% (juvenile and immature survival) be achieved within:**[4]	
				5-years	**10-years**	**5-years**	**10-years**
Adult survival	High	Moderate	High	Yes	Yes	No	Yes
Juvenile and immature survival	High	High	Moderate	No	Yes	No	Yes
Age of first breeding	Moderate	Low	Moderate	No	Yes	N/A	N/A
Incidences of non-breeding	Low	Low	Low (Ideally requires automated recording)	Yes	Yes	N/A	N/A
Natal dispersal	High	High	Low-Moderate	No	Yes	N/A	N/A
Adult dispersal	Low	Low	Moderate	No	Yes	N/A	N/A

[1] Informed by the literature review (section 2) and drivers of Kittiwake population change (section 2.4).
[2] Informed by the PVA outcome in section 2.5.
[3] Informed by the review of the literature (section 2) and current ringing effort in the UK (section 4).
[4] Informed by the power analysis (section 3).

6.1 Importance of specific demographic rates

6.1.1 Adult survival

Adult survival is a key demographic rate, which generally has the greatest proportional effect on seabird population growth rates (Gressetvold 2013). One of the key points that came out of the expert workshop (section 4.2.1) was not to lose sight of the importance of estimating adult survival, especially given that in the UK, our current adult survival estimates are restricted geographically (so may not be applicable to particular areas of future development interest), and some are based on out-dated data.

Mark-recapture methods are the only currently available approach used to quantify adult survival rates. For adult survival, we observed that reasonably precise estimates (within 2% of the true value) could be achieved for most of the levels of ringing and resighting effort we considered for studies of 10 or more years in length (section 3). However, 5-year studies were insufficient to consistently achieve estimation of adult survival rates within 2% of the true value on a consistent basis. Successfully estimating a step-change in survival required higher levels of ringing effort and could only be done in the context of long-term studies.

Adult survival is relatively less variable than other rates, so may be less likely to be badly mis-specified (i.e. using data which may not be accurate or precise) than for example juvenile or immature survival (section 2.5). However, PVAs, and the decision metrics derived from them, are particularly sensitive to misspecification of this rate (Cook & Robinson 2016). From an offshore wind farm development perspective, understanding regional variation is an important part of the consenting process as population-specific adult survival rates are required to assess the potential impact of mortality from offshore wind farms on nearby populations, especially where Kittiwakes are identifying features of SPAs. Increasing the number and geographical spread of colonies where adults are colour-ringed will reduce this misspecification risk.

6.1.2 Juvenile and immature survival

Recruitment of individuals into the breeding population (the product of fecundity, survival to age at first breeding and dispersal rates) can have a large impact on seabird population dynamics (Sandvik *et al.* 2012). However, while rates of fecundity are relatively well characterised, juvenile and immature survival rates are very poorly quantified and highly uncertain due to the lack of empirical data available on these age classes, especially in a UK context. Therefore, it is vital that we improve our knowledge of these rates.

From an offshore wind farm development perspective, rate of recruitment is particularly important where adult mortality is elevated (e.g. through additional mortality caused by collisions with wind turbines), as the impact this mortality will have on the population may, or may not, be mitigated by how many immatures are able to recruit to the breeding population.

The power analysis results indicated that up to five hundred chicks per colony per year should be ringed to obtain precise estimates of survival for immature age-classes within 10% of true values. Although this will generally not be possible at a single colony, there are clusters of colonies in certain areas of the UK where ringing this level of chicks is likely to be achievable (section 4.3). Due to the delayed maturation of Kittiwakes, with age of first breeding being around 4 years on average, colour-ringing studies of longer than 5 years are essential to obtain estimates of juvenile and immature survival; the power analyses (section 3) suggested a minimum of 10 years was likely to be necessary. Obtaining empirical data to inform juvenile and immature survival estimates will also require substantial resighting effort both at the natal colony but also at surrounding colonies (potentially within 100 km), given a relatively high frequency of natal dispersal.

Colour-ringing is currently the only feasible method that will provide empirical data on juvenile and immature survival rates. There is potential that automated technology systems, especially Motus, will become a feasible option in the future, for chicks and adults, if tags can be miniaturised sufficiently, especially as a complementary approach to colour-ringing. Motus will likely have the greatest benefit for detecting juveniles and immatures given their low probability of detection at the colony but could also be useful for adults. However, the technology is not yet adapted or tested to work in a Kittiwake context (section 5.7).

Based on the results of the Leslie matrix model, juvenile and immature survival rates showed the greatest sensitivity in the PVA, with derived annual population growth rates varying by up to 14 percentage points (section 2.5) therefore, there is substantial uncertainty induced by the misspecification of survival of these age classes in the model. While the power analysis (section 3) indicates that achieving reliable estimates of juvenile/immature survival is not possible in five years, narrowing the range of plausible values to the chosen level of precision (±10%) for juvenile (Table 6.2, row 4) and immature (row 7) would approximately halve the uncertainty in population growth rate (λ) compared to current levels (rows 1, 5) of uncertainty (which essentially amount to no knowledge). Thus, the range of projected growth rates at the lower and upper bounds of the plausible juvenile survival decreases from 0.90-1.04 to 0.94-1.00, and similarly for immature survival from 0.87-1.00 to 0.93-1.00; note the precise values are of less interest here than the differences between them. This means any empirical data collected has the potential to substantially improve our confidence in the PVA outputs (section 6.2.1).

Table 6.2. Impact of reducing the plausible range of ϕjuv on population growth rate (λ). BS: Breeding Success (number of chicks per pair, based on JNCC 2020); pB: proportion of adults breeding (all adults are assumed to breed for simplicity); Age: at first breeding; ϕjuv: apparent survival of first-year birds; ϕimm: apparent annual survival of immature (between age 2 and first-breeding age) birds; ϕad: apparent annual survival of adult birds. Importance in the PVA models is indicated by the difference (Δλ) in values of λ.

BS	pB[1]	Age	ϕ_{juv}[1]	ϕimm[1]	ϕad	λ min	λ max	Δλ
0.65	1.0	4	0.1 - 0.6	0.8	0.85	0.899	1.041	0.142
0.65	1.0	4	0.2 - 0.6	0.8	0.85	0.937	1.041	0.104
0.65	1.0	4	0.2 - 0.5	0.8	0.85	0.937	1.019	0.082
0.65	1.0	4	0.2 - 0.4	0.8	0.85	0.937	0.995	0.058
0.65	1.0	4	0.35	0.4 – 0.85	0.85	0.874	1.000	0.126
0.65	1.0	4	0.35	0.5 – 0.85	0.85	0.893	1.000	0.107
0.65	1.0	4	0.35	0.65 – 0.85	0.85	0.933	1.000	0.067

[1] Note these values are indicative, similar values would be obtained for equivalent ranges of ϕ_{juv} centered on different values (e.g. for the last row 0.3-0.4 or 0.4-0.5).

6.1.3 Age of first breeding

Under stable population conditions, average age at first breeding is likely to vary little (although there may be more variation between individuals). Where populations show sustained directional population change there is a greater likelihood of variation as the relative availability of unoccupied nest sites changes. Age of first breeding has relatively little impact on the outcome of PVAs, so does not need to be a focus of empirical data gathering (section 2.5). However, if a colour-ringing programme to estimate immature survival is in operation, this will also provide estimates of age at first-breeding, which can inform the PVA process.

6.1.4 Incidences of non-breeding

Incidences of non-breeding (or skipped breeding) in adult Kittiwakes are poorly quantified with data from very few studies. However, variation in incidences of non-breeding had relatively little impact on the example PVA outcome (section 2.5), so obtaining more precise estimates is unlikely to reduce uncertainty in PVAs significantly. Incidences of non-breeding can be determined through long-term colour-ringing studies that monitor individual-level breeding success and are derivable from colour-ring studies that are aimed at estimating adult survival and which achieve a sufficiently high re-encounter rate.

6.1.5 Natal dispersal

Although natal dispersal is frequent, empirical data are scarce. However, it is important to quantify natal dispersal as immigration and emigration between colonies will influence population size and growth and the potential impact of developments on populations that are features of SPAs.

Substantial ringing of chicks and resighting effort of colour-ringed individuals, at the natal colony and at surrounding colonies, and studies of longer than 5 years will be necessary to provide data on natal dispersal given the delayed maturation of Kittiwakes. In the absence of empirical data on frequency and length of dispersal events it is impossible to quantify the impact of reducing uncertainty in this metric. However, natal dispersal away from the focal colony can be considered to be broadly numerically equivalent to a change in immature survival in PVA, so we would expect similar improvements in outputs. Estimates of natal dispersal will naturally be achieved through a co-ordinated colour-ringing programme at multiple colonies within a region (since what evidence there is suggests most dispersal is within 100 km).

Other methods such as Motus may provide a useful complementary approach to colour-ringing in the future, especially at colonies where it is difficult to visually resight individuals. However, this technology is currently not available to work in a Kittiwake context as the tags cannot yet be attached to a leg ring (section 5.7.1). Modelling approaches, specifically meta-population modelling, also have the potential to improve our understanding of connectivity among populations and therefore the importance of dispersal in maintaining Kittiwake populations (section 3.6; section 4.2.1). Bayesian meta-population modelling based on population trends, productivity and distance could potentially be used to estimate natal dispersal, and to move away from the assumption of closed populations in impact assessments (e.g. recent University of Glasgow model for Shetland colonies (Ruffino *et al*. 2020). However, these approaches have additional data requirements and so will only be feasible in regions with good data coverage, and long-term data on breeding numbers, productivity and adult survival. Data on productivity is available for 68 populations across the UK (Horswill *et al*. 2021), however there are few colonies with frequent whole-colony counts of breeding numbers.

6.1.6 Adult dispersal

Dispersal by breeding adults is poorly characterised, both in terms of frequency and the spatial scale over which individuals disperse, however, the evidence that does exist suggests that incidences of adult dispersal are infrequent.

Long-term colour-ringing at colonies has provided empirical data on adult dispersal, however, it is necessary to search for colour-ringed individuals within other areas of the breeding colony (to pick up within-colony movements) and surrounding colonies (between-colony movements).

Given the likely limited nature of adult dispersal, we suggest that efforts to quantify it more extensively are unlikely to have a major impact on PVA outcomes, so we recommend this is not a primary focus of future data-gathering.

6.2 Colour-ring programme operation

6.2.1 Length of project

What can be achieved in 5 years

Building on existing effort, obtaining better empirical data on adult survival to reduce uncertainty in PVAs is achievable 5-years after implementing a Kittiwake colour-ringing project. It is also likely that some information on incidences of non-breeding could be obtained over this time frame.

The power analysis showed that 5-year studies were unable to obtain even moderate levels of precision (within 10% of true values) of survival estimates across all juvenile and immature age classes, even under the highest levels of ringing effort. Therefore, to obtain more accurate immature survival estimates studies of at least 10 years duration are necessary.

A 5-year study would also not provide sufficient empirical data to accurately quantify for age of first breeding, or natal and adult dispersal. However, **some information on juvenile survival may be obtained after 5 years** depending on the number of colour-ringed individuals that return and are resighted 3 - 4 years after ringing, although the level of precision will likely be low.

At present the values used in PVAs for juvenile and immature survival are based on extremely limited empirical data and so there is a high amount of uncertainty around how accurate these values are. An immature survival value of 0.79 is frequently used in PVA analysis (i.e. Searle *et al.* 2020). However, this value is estimated from a very small sample size (84 ring recaptures) using ad hoc methods at a time when Kittiwake population trends were increasing in contrast to recent declines (Coulson & White 1959). Furthermore, Coulson (2011) subsequently suggested that juvenile survival was more likely to be around 0.63, after re-calculating estimated first year mortality to take into account that mortality risk is likely to be higher during an individual's first year compared to later years. Therefore, any additional empirical data of juvenile and immature survival rates will be valuable to help determine whether the current survival rate estimate of 0.79 used in PVAs is close to the current 'true' value.

Given the length of project required to obtain useful empirical data on Kittiwake demographic rates, a coordinated effort to colour-ring adults and chicks needs to start as soon as possible.

What can be achieved in 10 years

Colour-ringing studies of 10 years can provide high levels of precision (within 2% of true values) of adult survival estimates and moderate levels (±10%) for juvenile/immature survival rates with the required levels of ringing effort dependent on the age classes of interest.

Studies of this length will also allow the collection of empirical data to quantify natal and adult dispersal if a sufficient density of colony coverage can be achieved; this will be easier in some regions than others (section 5.6).

We recommend that a coordinated colour-ringing programme of Kittiwakes should be planned in two phases. Initially, it should be operated for five years, at which point the number of re-encounters achieved should be assessed, including some analysis, to ensure they are in line with expectations before commencement of a second 5-year phase. Realistically, **the full 10 years of operation is likely to be needed to generate estimates that are useful for populating PVA models**, however, the data achieved after five years is likely to be helpful in narrowing the frame of uncertainty around some of these rates in the models, particularly juvenile survival. The cost (ex-VAT) of setting up a coordinated colour-ringing programme for Kittiwakes is estimated to be between £900k and £1,400k over five years and £1,800k and £2,800k over 10 years, depending on which priority regions are selected (Table 6.3, section 5.6).

6.2.2 Site selection based on high priority areas for industry

Given the importance of obtaining empirical data on adult survival rates from a geographically representative spread of colonies to understand regional variation in this rate, we recommend expanding the current number of Kittiwake RAS sites across Britain and Ireland, with an improved focus on generating re-encounter data at these sites. This is particularly pertinent given the expected increase in offshore wind development around the UK, particularly in the North Sea, Irish Sea and off the west coast of Scotland (Table 6.3). **Increasing adult ringing and resighting effort across the UK will enable regionally relevant adult survival rates to be used during the consenting process of specific wind farms.**

Given the large number of chicks required to be ringed to obtain estimates of survival for immature age-classes, selecting specific regions of the UK to focus chick ringing effort was deemed more appropriate than aiming for a large, but more scattered, geographical spread of individual colonies. Considering the regions which have a high interest for offshore wind farm developers, as well as where it is feasible to ring large numbers of chicks (section 5.6), the highest priority region to focus chick ringing and resighting effort is the east coast of Britain between North Yorkshire and Aberdeenshire; with the Irish Sea being the second highest priority region (Table 6.3). Ringing of adults should also be encouraged in these areas as concentrated resighting effort to search for immature birds will also increase the changes that colour-ringed adults are also detected. Concentrating ringing and resighting effort in a specific region is expected to improve the detection rate of immatures and adults that disperse locally (within 100 – 200 km) to provide empirical data on immigration and emigration rates, which will improve our understanding of connectivity between Kittiwake colonies and help reduce uncertainty in demographic models around the assumption that population are closed.

Table 6.3. Priority regions to implement Kittiwake colour-ringing around Britain and Ireland based on relevance to the offshore wind industry and feasibility ring, and resight, Kittiwakes.

Region[1]	**Feasibility to ring/resight adults**[2]	**Feasibility to ring/resight chicks**[2]	**Importance to offshore wind development**
East coast of Britain North Sea	High	High	High
North Wales, Isle of Man and east Ireland Irish Sea	High	Medium	High
West coast of Scotland	High	Low	High
South Wales and southwest England Celtic Sea	High	Medium	Medium

[1] Regions are defined in Figure 5.3.

[2] Informed by the feasibility of ringing adults and chicks in different regions as discussed in section 5.6.2.

We recommend **increasing the number of colonies where adult Kittiwakes are colour-ringed across the UK to provide empirical data to estimate regionally relevant adult survival rates.**

We recommend that **colour-ringing of chicks is focused on specific regions of the UK, concentrating on the east coast of Britain in the first instance** due to the importance of the North Sea to the offshore wind farm industry, and the greater feasibility of ringing high levels of chicks in addition to adults along this coastline.

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Appendix 1

A. Model Likelihood

The set of parameters used to generate the capture history for a population of ringed individuals is denoted by $\boldsymbol{\theta} = (\phi_c, \phi_a, p_1, p_2, p_3, p_{4+})$. For a given vector $\boldsymbol{\theta}$ we can simulate an N by T matrix of capture histories, $\boldsymbol{h}$, where N is the total number of individuals ringed and T is the length of the study in years, by applying a series of binomial probabilities to the chick and adult ringing schedules, $\boldsymbol{r_c}$ and $\boldsymbol{r_a}$, as described in Figure 3.2. We can then write down the likelihood of a set of parameter values given the observed data, $L(\boldsymbol{\theta}; \boldsymbol{h})$ as follows. Let the capture history matrix, $\boldsymbol{h}$, be constructed such that the first N_a rows correspond to individuals ringed as adults and rows $N_a + 1$ to $N_a + N_c$ correspond to individuals ringed as chicks. Also let R_i denote the year on which individual i was ringed for $i = 1, 2, \ldots, N$. The likelihood of a given set of parameter values, $\boldsymbol{\theta}$, given some observed capture history matrix, $\boldsymbol{h}$, is given by

$$L(\boldsymbol{\theta}; \boldsymbol{h}) = \prod_{i=1}^{N_a} \prod_{j=R_i+1}^{T} \left({\phi_a}^{j-R_i} p_{4+}\right)^{h_{ij}} \left(1 - {\phi_a}^{j-R_i} p_{4+}\right)^{1-h_{ij}}$$

$$\prod_{i=N_a+1}^{N_a+N_c} \prod_{j=R_i+1}^{T} \left(\phi_c {\phi_a}^{j-R_i-1} p_{j-R_i} I(j-R_i)\right)^{h_{ij}} \left(1 - {\phi_a}^{j-R_i-1} p_{j-R_i} I(j-R_i)\right)^{1-h_{ij}}$$

where $I(j - R_i)$ is an indicator function for the dispersal such that

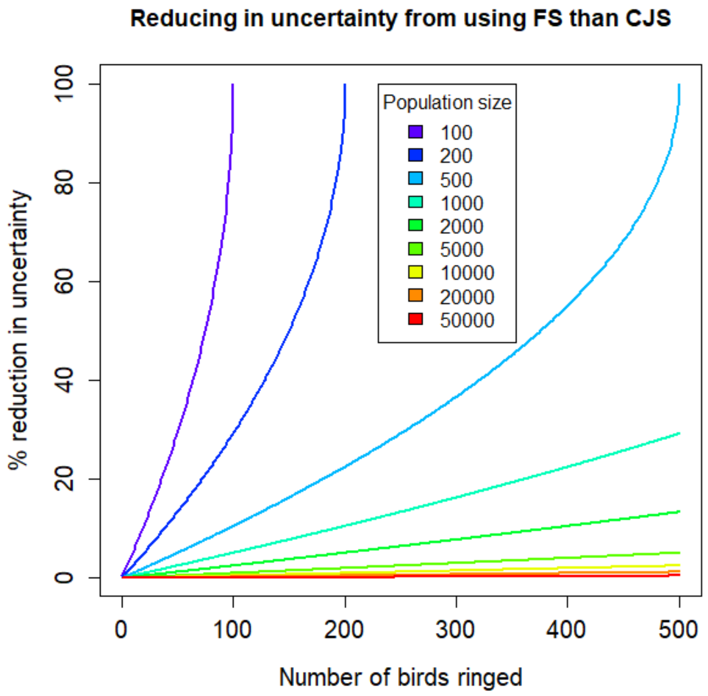
$$I(j - R_i) = \begin{cases} 1 - d, & j - R_i = 4, \\ 1, & \text{otherwise.} \end{cases}$$

B. Potential reduction in uncertainty with a finite sampling approach

The percentage reduction in uncertainty (i.e. size of standard error) associated with the finite sampling approach can easily be calculated, and is equal to

100 * (1 – SQRT((1 – (number of ringed birds / population size))))

For large colonies this implies (figure below that the two approaches are likely to yield similar results, but for smaller colonies the finite sampling approach may, particularly with high levels of ringing, yield substantially higher precision than the CJS modelling approach (Figure 3.1). (We note that when sample size (n) is less than 5% of total population size (N), the finite population correction factor, the multiplier is between 0.95 and 1.)



Further, we note that due to imperfect resighting (possible emigration from the colony) finite population inference for the fraction surviving is more complicated than in a “standard” finite population sampling framework. In the simplest, and unrealistic, case where the resighting probability was known with certainty, the underlying sampling design can be viewed as a two-stage sample: sample one is randomly selecting M birds to be ringed, and sample two is randomly selecting a sample from the subset of M birds that have survived, noting that the size of the second sample is random. The theory for this setting is somewhat non-standard and theoretical development time is an unknown—but would make a good MSc project in statistics.

C. Sample size and precision/power in the absence of resighting

The multinomial models that underly the general CJS framework are complex enough that closed form, analytic sample size determination for estimating parameters, e.g. survival and capture probabilities, with a specified precision or to achieve a specified power is not possible. Variances for maximum likelihood estimates of these parameters are typically based on the inverted matrix of second derivatives of the log likelihood. In rare cases analytical formulae for the variances are available and one can then analytically link sample sizes to these variances (and covariances). More often, however, such matrices are calculated numerically, and the effects of changing sample sizes are most easily examined by simulation studies, as was the approach taken here.

Some insight into what lower bounds for achievable precision might look like can be gained by examining a highly oversimplified setting, in particular a purely Bernoulli distribution setting where randomly selected individuals have the same probability of surviving, denoted ϕ. Note that we are in the infinite population setting, a “process model” perspective, where one can repeat the Bernoulli process over and over.

In the table below, assuming ϕ=0.80, we calculated the margin of error, namely 2*standard error, for estimates of ϕ that will be achieved for an array of sample sizes, denoted M, in this highly oversimplified setting. The sample sizes, M, were chosen to achieve common margins of error (0.01 to 0.05). The 3rd column shows what the average margin of error, based on a simulation study with 10,000 simulations, would be for a simple mark/resight study where there were two resightings and the probability of resighting was 0.60. The achieved margins of error in the mark/resighting case are about 75% larger than for the simplified setting, which is a largely a consequence of needing to estimate another parameter, namely the resighting probability. Another way to view these differences is to compare the sample size (number marked) to achieve a specific margin of error in the mark/resighting case to the sample size in the simple case; e.g., to achieve a margin of error of about 0.05, a sample of over 700 is needed, while 256 is needed in the simple case.

M	Bernoulli: 2*SE, ϕ=0.80	Mark/2 Resightings: ϕ=0.80, p=0.60
256	0.05	0.088
400	0.04	0.070
711	0.03	0.052
1600	0.02	0.035
6400	0.01	0.017

D. Sketch of a hierarchical modelling framework

As an example consider the following spatial-temporal hierarchical model for survival $\phi_{s,t}$ where space (s) is represented by C=10 colonies and time (t) spans T=15 years.

$$\alpha_s \sim \text{Normal}(\mu_s, \sigma_s^2), \qquad s = 1, \ldots, C$$
$$\beta_t \sim \text{Normal}(\mu_t, \sigma_t^2), \quad t = 1, \ldots, T$$
$$\phi_{s,t} = \exp(\alpha_s + \beta_t)/(1 + \exp(\alpha_s + \beta_t))$$
$$y_{s,t} \sim \text{Binomial}(M_{s,t}, \phi_{s,t})$$

The term α_s represents a spatial random effect, β_t represents a temporal effect, $M_{s,t}$ is the number marked (or total number) at colony s for year t, and $y_{s,t}$ is the number that survive. The parameters of primary interest could be the averages and variances of the spatial and temporal effects. Note that there could be three sets of sample size problems: number of colonies C, number of years of sampling T, and the numbers of birds to mark at the different colonies in different years.

An alternative model could include some spatial dependency, where the α_s values for colonies that relatively close to each other are similar, there are patterns or dependencies in the temporal component, β_t, and/or various environmental covariates may used to model the spatial and temporal effects.

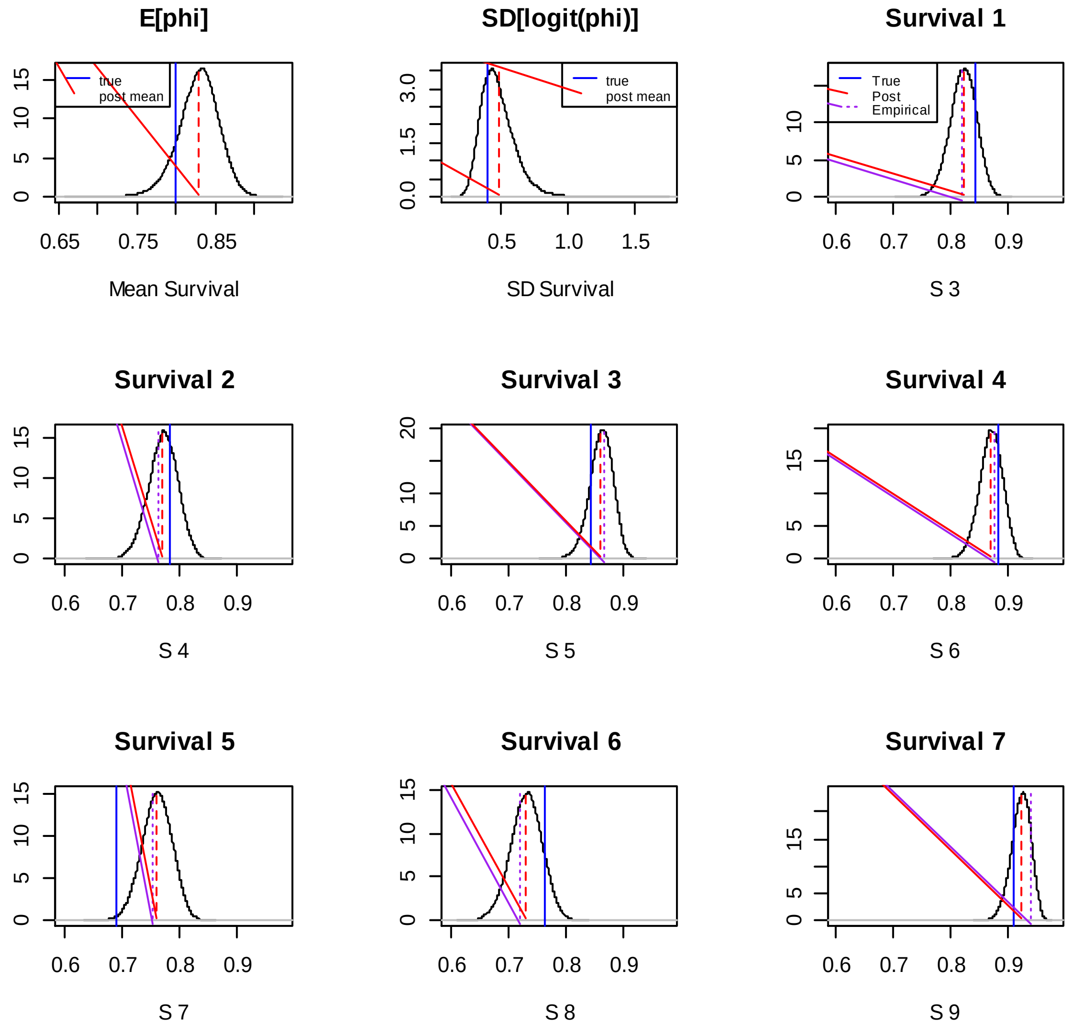
Referring to the above example, JAGS could produce posterior distributions for the fixed parameters, namely μ_s, σ_s^2 , μ_t, σ_t^2 that generate the space and time random effects α_s and β_t.

R Code Example of simulating and fitting a hierarchical model. The R code below simulates a hierarchical model for survival (varying over 7 colonies or years, say), and the resulting posterior distributions are shown in the figure at the end of the code.

```
#---- Demonstration using JAGS and rjags to fit a Hierarchical Model
library(rjags)

#----simulate a hierarchical model for survival alone ----
mu.phi <- 0.8
mu.logit.phi <- log(mu.phi/(1-mu.phi))
sd.logit.phi <- 0.4
num.groups   <- 7
n.per.group  <- 250

set.seed(939)
logit.phi.set <-
rnorm(n=num.groups,mean=mu.logit.phi,sd=sd.logit.phi)
survival.set <- expit(logit.phi.set)
print(survival.set)
# [1] 0.8409425 0.7842963 0.8432466 0.8832093 0.6906955 0.7643955
0.9077750

y <- rbinom(n=num.groups,size=n.per.group,prob=survival.set)
print(y)
# [1] 205 191 217 219 188 180 235

# Set up for running JAGS
hier.data <- list(m=num.groups,n=rep(n.per.group,num.groups),y=y)
num.chains <- 3
hier.init <- list()
for(i in 1:num.chains) {
  hier.init[[i]]  <- list(mu.logit.phi=
rnorm(n=1,mean=mu.logit.phi,sd=sd.logit.phi),
                         sd.logit.phi=
rlnorm(n=1,meanlog=log(sd.logit.phi),sdlog=0.2))
}

hier.model <-
"model  {
mu.logit.phi ~ dnorm(1.5,1/0.3)
sd.logit.phi ~ dlnorm(-1.6,1/0.3)
tau.logit.phi <- 1/pow(sd.logit.phi,2)

for(i in 1:m) {
 logit.phi[i] ~ dnorm(mu.logit.phi,tau.logit.phi)
 survival[i]  <- exp(logit.phi[i])/(1+exp(logit.phi[i]))
 y[i]         ~ dbinom(survival[i], n[i])
 }

}"

# create JAGS object
hier.compile <- jags.model(file=textConnection(object=hier.model),

data=hier.data,inits=hier.init,n.chains=num.chains)

# burn-in
burnin <- 1000
update(object=hier.compile,n.iter=burnin)
```

```
#  Generate sample: use coda.samples to generate a mcmc.list object
num.iters <- 10000
hier.samples <- coda.samples(model=hier.compile,

variable.names=c("mu.logit.phi","sd.logit.phi","survival"),
                             n.iter=num.iters)
class(hier.samples) # [1] "mcmc.list"
summary(hier.samples)

hier.matrix.samples <- as.matrix(hier.samples)

par(mfrow=c(3,3))
 x <- hier.matrix.samples[,"mu.logit.phi"]
 est.mu.phi <- exp(x)/(1+exp(x))
 plot(density(est.mu.phi),type="l",xlab="Mean
Survival",ylab="",main="E[phi]")
 abline(v=mu.phi,col="blue")
 abline(v=mean(est.mu.phi),col="red",lty=2)
 legend("topleft",legend=c("true","post mean"),lty=1:2,
        col=c("blue","red"),cex=0.6)

 est.sd.phi <- hier.matrix.samples[,"sd.logit.phi"]
 plot(density(est.sd.phi),type="l",xlab="SD
Survival",ylab="",main="SD[logit(phi)]")
 abline(v=sd.logit.phi,col="blue")
 abline(v=mean(est.sd.phi),col="red",lty=2)
 legend("topright",legend=c("true","post mean"),lty=1:2,
        col=c("blue","red"),cex=0.6)


 my.xlim <- c(0.6,0.98)
 for(i in 3:(num.groups+2)) {
  x <- hier.matrix.samples[,i]
  plot(density(x),type="l",xlab=paste("S",i),ylab="",
       main=paste("Survival",i-2),xlim=my.xlim)
  abline(v=survival.set[i-2],col="blue",lty=1)
  abline(v=y[i-2]/n.per.group,col="purple",lty=3)
  abline(v=mean(x),col="red",lty=2)
  if((i-3)==0) legend("topleft",legend=c("True","Post","Empirical"),
                      col=c("blue","red","purple"),
                      lty=1:3,cex=0.6)
 }
par(mfrow=c(1,1))
```

The figure below shows the posterior distributions for different parameters with the true value indicated by a vertical blue line and the estimated posterior mean by a red dashed line.



Appendix 2

Kittiwake workshop on estimating demographic rates from colour-ringing

Date: 22nd February 2021

Time: 18:00-20:00 GMT

Workshop objectives. The UK is expanding the number of offshore renewable developments, and they have the potential to negatively affect seabirds through collisions and displacement. The kittiwake is a species of particular concern because of recent sharp declines (~65% since 1986) and their potential vulnerability to both collision and displacement. However, our ability to assess potential impacts on populations of Kittiwakes is hampered by a paucity of data on demographic rates. While there are good data on productivity from many UK colonies, adult survival is only estimated at a small number of colonies and data on immature survival and immigration/emigration is very limited. BTO, UKCEH, BioSS and RSPB are currently undertaking a project commissioned by Vattenfall and project managed by JNCC that is looking at the feasibility of colour-ringing across a network of colonies to deliver estimates of these key demographic rates, including the extent to which they vary regionally.

The purpose of this workshop is to bring together key experts in kittiwake demography to exchange views on this potential approach to get better empirical information on all key demographic rates that will enable more biological realism to be introduced into impact assessments of offshore renewable developments.

AGENDA
18:00 Welcome, Introductions and Workshop Objectives (Francis Daunt, UKCEH)
18:10 Rationale for the project (Jesper Larsen, Vattenfall)
18:15 Project objectives (Rob Robinson, BTO).
18:20 Demography of Kittiwakes: current studies (Nina O’Hanlon, BTO)
18:30 Informing project design using power analysis (Dave Ewing, BioSS)

18:40 Break-outs Session

1. The lost years: estimating immature survival, dispersal, recruitment and age at first breeding using colour-ringing
2. Demography of adults: estimating survival, breeding dispersal and non-breeding using colour-ringing
3. Alternative approaches to estimating demographic rates: MODUS, GPS and other technologies

19:05 Break-outs (same themes repeated, participants rotate)
19:30 Break-out reports
19:45 Final discussion
20:00 Finish

ATTENDEES:

Invited participants
Paul Acker (NTNU)
Tycho Anker-Nilsson (NINA)
Thierry Boulinier (CNRS)
Emmanuelle Cam (University of Western Brittany)
Kyle Elliott (McGill University)
Morten Frederiksen (Aarhus University)
Mike Harris (UKCEH)
Scott Hatch (ISRC)
Cat Horswill (ZSL/UCL)
David Irons (FWS)
Sasha Kitaysky (University of Alaska)
Kate Layton-Matthews (NINA)
Alyson McKnight (Unity College)
Daniel Oro (CSIC)
Aurore Ponchon (University of Aberdeen)
Sarah Wanless (UKCEH)
Shannon Whelan (McGill University)
Matt Wood (University of Gloucestershire)
Nigel Yoccoz (UiT)

Project Team
Adam Butler (BioSS)
Francis Daunt (UKCEH)
David Ewing (BioSS)
Esther Jones (BioSS)
Ken Newman (BioSS)
Nina O’Hanlon (BTO)
Liz Humphreys (BTO)
Rob Robinson (BTO)
Kate Searle (UKCEH)
Saskia Wischnewski (RSPB)

Project Steering Group
Orea Anderson (JNCC)
Danni Thompson (JNCC)
Michael Bailey (NRW)
Bob Furness (MacArthur Green)
Mel Kershaw (NE)
Jesper Kyed Larsen (Vattenfall)
Julie Miller (Marine Scotland)
Sue O’Brien (JNCC)

Appendix 3

Agenda

Kittiwake Colour-ringing Project – Logistics workshop

Date: 24th February 2021

Time: 19:00 – 21:00

In common with many seabirds, demographic parameters (such as survival and dispersal) that are important in determining population status and trends are poorly known in Kittiwakes, meaning it is hard to assess the population impact of future changes. BTO have been commissioned by JNCC to scope the extent to which colour-ringing can help us better quantify these. The purpose of this workshop is to seek views on what might be practicable, and ways in which this might best be achieved. These views will help refine our recommendations for a possible large-scale colour-ringing effort, including the quality of information that might be gained and what resources would be needed to deliver it.

19:00 Welcome
Housekeeping
Introductions

19:10 Background to the project and objectives of the workshop
Rob Robinson, BTO

19:20 Ringing and resighting protocols
Saskia Wischnewski, RSPB
Followed by a group discussion to identify additional considerations to be included in these protocols

19:45 Summary of our current knowledge of Kittiwake demography and where adults and chicks are currently ringed
Nina O'Hanlon, BTO
Followed by a group discussion on which existing and potential sites could be included in a large-scale UK wide colour-ringing project

20:10 Breakout room discussions
Participants will be assigned to one of the following breakout discussions:

1) How can we achieve high resighting rates of colour-ringed Kittiwakes?

2) Is it feasible to carry out large-scale chick ringing to obtain information on recruitment and immature survival?

20:35 Feedback from groups
20:45 Final discussion / Roundup Next steps and closing comments
21:00 Finish

ATTENDEES:

Participants
Andrew Rickeard (Gateshead)
Bob Swann (Canna)
Chris Redfern (Farnes)
Craig Thomas (Flamborough BO)
David Jardine (Highland)
Hayley Douglas (Tiree)
Jim Lennon (Shiants)
Lisa Morgan (SWW Wlidlife Trust)
Mark Grantham (Cornwall)
Mike Harris (UKCEH)
Raymond Duncan (Grampian)
Robin Ward (Treshnish Isles)
Sarah Wanless (UKCEH)

Project Team
Adam Butler (BioSS)
Francis Daunt (UKCEH)
David Ewing (BioSS)
Esther Jones (BioSS)
Nina O’Hanlon (BTO)
Rob Robinson (BTO)
Liz Humphreys (BTO)
Saskia Wischnewski (RSPB)
Lucy Wright (RSPB)

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Orea Anderson (JNCC)
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Rebecca Jones (NE)