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Bayesian Immature Survival Analysis of the Largest Colony of Common Murre (*Uria aalge*) in the Baltic Sea

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Abstract.—In long-lived species, such as seabirds, immature survival is the most important life history parameter after adult survival. The assessment of immature survival has often been difficult due to extended periods in which young birds remain unobservable at sea. This study presents results on survival of immature Common Murre (*Uria aalge*) obtained from an extensive mark-recapture study of a large colony at Stora Karlsö in the Baltic Sea, Sweden. This colony, in contrast with other colonies, has the unique feature that many 1-year-old birds return to the colony (12%). Between 2006 and 2016, 28,930 chicks were marked at fledging, of which 5,493 individuals were later resighted in the colony. Annual survival and recapture probabilities were estimated using Bayesian Cormack-Jolly-Seber models with four age classes for survival probability, and recapture probability being age and time dependent. Informative prior distributions were used to correct partial observability problems in older age classes (observed at breeding ledges). The estimated survival probability of 1-year-old birds was 0.53 (95% CI = 0.49-0.58), 2-year-old birds was 0.87 (0.79-0.96), 3-year-old birds was 0.96 (0.90-0.99), and 4-to-10-year old bird survival probability was 0.63 (0.61-0.64). Survival estimates for younger age classes were consistent with previous studies. Several biological factors may contribute to the observed decline in survival for older age classes. *Received 8 December 2018, accepted 1 July 2019.*

Key words.—Annual survival, Cormack-Jolly-Seber models, first-year survival, juvenile survival, partial detectability, recapture probability.

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Seabirds are of particular conservation concern due to their vulnerability to human activities, including climate change, bycatch, invasive species, and oil spills (Sandvick *et al.* 2005; Martínez-Abraín *et al.* 2006; Lewison *et al.* 2012), and many species of seabirds are listed under some category of threat, in part because they are long-lived with low reproductive rates (Croxall *et al.* 2012). In long-lived species such as seabirds, population dynamics are sensitive to changes in adult survival, reproductive success, and juvenile survival (Lewison *et al.* 2012). For seabirds, estimation of age- or stage-specific demographic parameters is particularly important, because declines in breeding populations can be influenced by non-breeders and immature birds (Votier *et al.* 2008). However, seabirds often have long periods of immaturity, remaining unobservable at sea for several years until they return to the colony (Croxall and Rothery 1991; Sandvik *et al.* 2008), making survival

estimation of immature stages difficult (Lee *et al.* 2008; Votier *et al.* 2008). Moreover, published estimates of juvenile survival (defined as survival from fledging to recruitment) exist for less than 2% of seabird species (Lewison *et al.* 2012).

One large colony of Common Murres (*Uria aalge*) from Stora Karlsö, in the Baltic Sea, Sweden, in contrast with other colonies, has the unique feature that many 1-year-old birds return to the colony (12%, this study). This Common Murre colony shows an important behavioral heterogeneity, involving several phases of club attendance, ledge attendance, pair bonding, and ledge establishment. Indeed, in this colony, 1-year-old individuals are almost exclusively resighted at clubs (flat boulders 2-5 m in diameter, located in the water beneath breeding cliffs, 10-20 m from shore, and holding aggregations of non-breeding birds), while subsequent ages gradually shift over to only being observed at breeding ledges (this

study). Other studies have reported this behavioral heterogeneity in several colonies (Halley *et al.* 1995; Nettleship and Birkhead 1985), but so far, few studies have considered it as a factor in survival models (Crespin *et al.* 2008; Lee *et al.* 2008; Votier *et al.* 2008).

Age is an important factor affecting survival and recapture probabilities in animal populations (Crespin *et al.* 2006; Harris *et al.* 2007; Morrison *et al.* 2009), and commonly in most species, first-year survival is lower than in later ages (Harris *et al.* 2007). In order to determine possible differences in survival among age classes, capture-mark-recapture data can be used in Cormack-Jolly-Seber models with age effects to jointly estimate survival and recapture probabilities of immature individuals, while taking into account that these models estimate “apparent” (instead of true) survival probabilities, as death and permanent emigration are confounding factors (King *et al.* 2010; Kéry and Schaub 2011). A strong assumption of capture-mark-recapture models is that animals remain faithful to the study area (Newman *et al.* 2014). Seabirds, in particular Common Murre, are philopatric to the breeding colony, but also to the sub-colony where they were hatched (Halley *et al.* 1995; Harris *et al.* 1996a; Harris *et al.* 1996b). As immature birds get older, they are increasingly present on breeding ledges and engaged in prospecting behavior in preparation for breeding (Oro and Pradel 2000; Kadin 2007). Hence, individuals hatched on monitored breeding ledges will have a higher recapture probability than birds hatched outside them.

One way to deal with the partial monitoring problem for birds older than 2-years-old is a subjective Bayesian approach incorporating former knowledge about the proportion of breeding birds on monitored ledges in the area of study (Olsson and Hentati-Sundberg 2017 in the case of our study). The use of informative prior distributions has been (and still is) a controversial issue in Bayesian inference (King *et al.* 2010; Golchi 2016). However, when relevant information is available, informative prior distributions are an appropriate way of introducing expert opin-

ion or information related to the study (McCarthy and Masters 2005; Christensen *et al.* 2011; Martínez-Abraín *et al.* 2014; Golchi 2016).

Our objective in this study was to use capture-mark-recapture data from a long term banding effort to estimate immature survival and incorporate possible differences in survival among age classes using Cormack-Jolly-Seber models with age effects to jointly estimate apparent survival and recapture probabilities of immature Common Murres. The study colony is one of the only colonies where immature individuals of the species are easily observed to allow such survival estimates.

METHODS

Study Site and Field Methods

We studied the survival of juvenile Common Murres at the island of Stora Karlsö (57° 17' 03" N, 17° 58' 23" E), west of the island of Gotland in the Baltic Sea, Sweden. The breeding population was 15,700 pairs in 2014, about two-thirds of the Baltic Sea population (Olsson and Hentati-Sundberg 2017). Between 2006 and 2015, chicks were marked in late June and early July on a beach under the cliffs with the largest sub-colony of the island (for colony details see Hedgren and Linnman 1979). The fledging age in Common Murre is around 20 days (Hedgren 1981; Birkhead and Nettleship 1986), therefore, since in our study all marked birds were chicks, we established that all the individuals were < 1-year-old at the time they were banded.

Throughout the study, we used the official triangular stainless-steel band with a unique ID code on one leg, provided by the Ringing Centre at the Swedish Museum of Natural History and manufactured by IÖ Mekaniska, Bankeryd, Sweden. Additionally, we used the following complementary bands with IDs and color-codes on the other leg: round plastic bands (Protouch Engraving and Signage, Saskatoon, Saskatchewan, Canada) 2006-2008 and 2013-2015; round aluminium bands (IÖ Mekaniska, Bankeryd, Sweden) 2009; and large triangular steel bands 2010-2012 (IÖ Mekaniska, Bankeryd, Sweden). All types of bands were possible to read with a spotting scope from above at all monitoring sites, resulting in minimal disturbance. Resightings were made during the breeding season (May to July) for 10 consecutive years (2007 to 2016) at five different locations in the colony, two different clubs and three breeding ledges (Fig. 1). We determined the birds' ID from both the official stainless-steel bands and the complementary bands. Mean seasonal resighting effort was 82.80 hr per year, with a maximum of 138 hr (year 2015) and a minimum of 57 hr (year 2008).

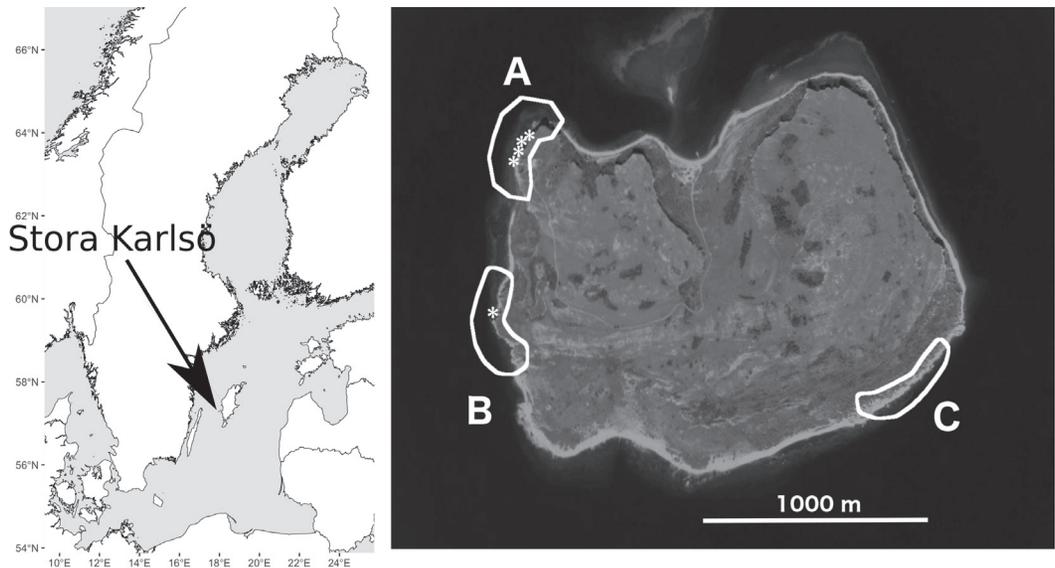


Figure 1. Location of a large Common Murre (*Uria aalge*) breeding colony on the island of Stora Karlsö in the Baltic Sea (left), where immature birds were captured, banded, and resighted from 2006-2016. Map of the island (right) shows the location of the main breeding ledges used by murre (areas A, B and C) and locations that were monitored to resight marked birds (indicated with asterisks). Chicks were captured and banded in area A.

Survival Modelling

We estimated annual survival and annual resighting probabilities using an m-array formulation (Lebreton *et al.* 1992; Kéry and Schaub 2011; King *et al.* 2010). Our main objective was to establish robust, stage-specific demographic parameter estimates for the colony. Although survival can be year-dependent (due to variation in food availability or extreme weather events; Votier *et al.* 2008; Harris *et al.* 2000), in this study we modelled survival probability as age dependent because previous studies performed in the colony suggested that the population trajectory is both stable and positive (Hentati-Sundberg and Olsson 2016; Olsson and Hentati-Sundberg 2017). Since the type (plastic/aluminium/steel) of complimentary bands used changed over the years of the study and varied in their durability, which could affect annual resighting probabilities, we modelled recapture probability as age and time dependent.

The number of age classes established were different in survival and recapture probabilities. Let R be the set of age classes established for survival, $R = \{1,2,3,4\}$, in this case 1-year-old, 2-years-old, 3-years-old and 4-10-years-old. Similarly, R' denoted the set of age classes for recapture probability, $R' = \{1,2,3\}$, corresponding to 1-year-old, 2-years-old, and 3-10-years-old. Moreover, ϕ_t denoted the annual survival probability from time t to $t+1$ of an individual belonging to age class r ($r \in R$ and $t = 1, \dots, T-1$), while $p_{r,t}$ denoted the recapture probability at time t of an individual which belonged to age class r' ($r' \in R'$ and $t = 2, \dots, T$). We selected these age categories because the main focus of the paper was to analyze immature survival, while at the same time taking into

account that mature individuals (from 3-years-old onward) became less resighted due to their movement to unobserved parts of the colony.

Posterior Inference

Bayesian statistics allows models to incorporate not only the data into the inferential process, but also all the available prior knowledge about the unknown parameters. This information needs to be expressed in probabilistic language in the so-called prior distributions. Bayes' theorem combines both types of information and provides the posterior distribution, which contains all the relevant knowledge about the parameters of interest (McCarthy and Masters 2005; King *et al.* 2010; Christensen *et al.* 2011; Kruschke 2011).

Most of the time, Bayesian inferential processes are based on vague or non-informative prior distributions, because no information is available. Nevertheless, Martínez-Abraín *et al.* (2014) stated that ecologists should make a greater effort to make use of available prior information because this is their most legitimate contribution to the inferential process. In other words, when information about the parameters is available, we should try to incorporate it.

In our case, we incorporated expert prior information about the partial monitoring of this colony in the Cormack-Jolly-Seber model. Based on a recent census of the colony, Olsson and Hentati-Sundberg (2017) found that the size of the monitored breeding ledges represented 19% of breeding pairs in area A (Fig. 1). Furthermore, individuals of age class three were mainly observed at breeding ledges, not at the clubs, due to the gradual settlement of the prospecting individuals

on breeding ledges (Kadin 2007; this study). Therefore, we used informative prior distributions, but only for the recapture probabilities for individuals 3-10-years-old. We used non-informative prior distributions for the remaining parameters of the model, in particular, Uniform (0,1). The probability of seeing an individual that is alive $P(p_i=1|z_i=1)$ can be expressed as,

$$\begin{aligned} P(p_i=1|z_i=1) &= P(p_i=1, M|z_i=1) + P(p_i, \bar{M}|z_i=1) = \\ P(p_i=1|M, z_i=1) * P(M|z_i=1) &+ P(p_i=1|\bar{M}, z_i=1) * \\ P(\bar{M}|z_i=1) &= P(p_i=1|M, z_i=1) * 0.19, \end{aligned}$$

where the event M indicates that the individual is in a monitored breeding ledge, and \bar{M} indicates the opposite. Additionally, even though a bird is present at a ledge, it is not certain that its band could be read, mainly because individuals are standing close to each other and not always showing their bands. In order to be the less informative, we considered that we could see all the individuals (which is far from reality), and so, the recapture probabilities should not be greater than $1*0.19=0.19$. In other words, we used informative prior distributions that constrained the parametric space for the recapture probabilities in the 3-10-years-old age class in order not to exceed that 0.19 value.

As usual in this context, the resulting posterior distributions containing all the information about the system have no closed expression, so we need numerical approaches to approximate them. A feasible possibility is to use Markov Chain Monte Carlo (MCMC)

methods (Robert and Casella 2011). In this study, we used MCMC through the *jags* software (Plummer 2003) implemented in the R software (R Core Team 2019). We obtained the final approximate random sample using three chains, 200,000 iterations, discarding the first 20,000 and saving 1 of every 300 of the remaining (to avoid autocorrelation).

RESULTS

A total of 28,930 chicks were banded between years 2006 and 2016. Mean banding effort was 2,893 individuals per year, with a maximum of 4,956 individuals (year 2015) and a minimum of 1,965 individuals (year 2007). A total of 7,625 resightings was achieved (mean = 762.5 resightings per year), with a maximum of 1,284 individuals resighted (year 2016) and a minimum of 174 individuals resighted (year 2007). The total number of resightings were of 5,493 unique individuals (19% of banded birds), and each individual was observed an average of 1.38 times. The most common age of resighted birds was 2-years-old, followed by 3-years-old, 4-10-years-old, and 1-year-old (Fig. 2).

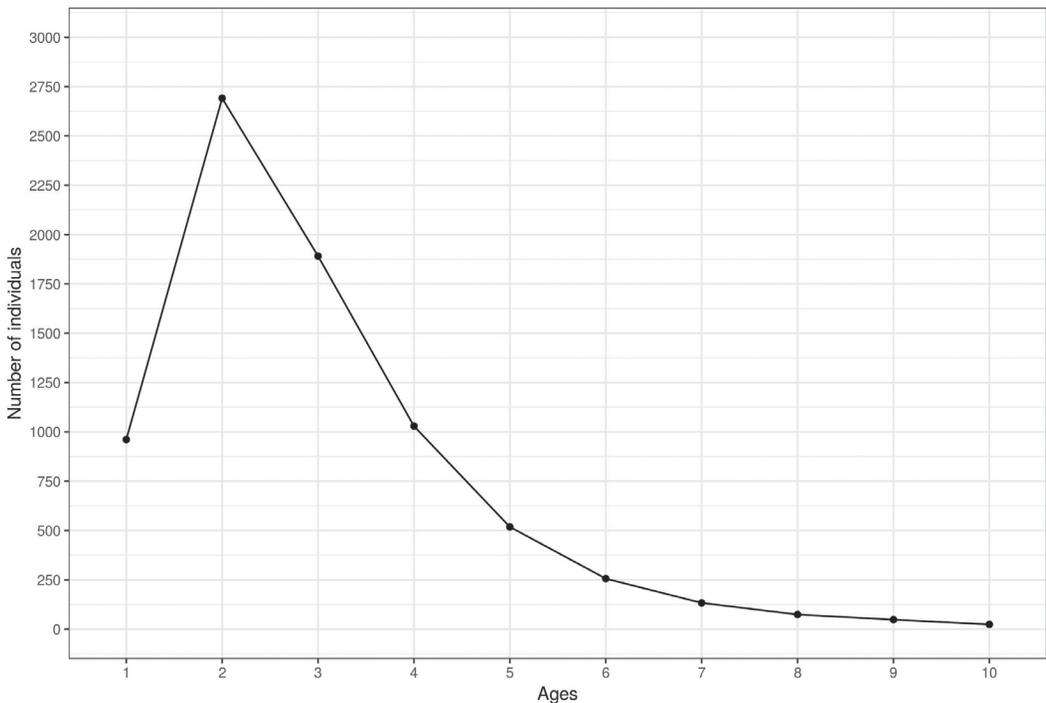


Figure 2. Number of banded Common Murre (*Uria aalge*) individuals resighted for each age class in a large Common Murre (*Uria aalge*) breeding colony on the island of Stora Karlsö in the Baltic Sea from 2006-2016.

The 1-year-old birds were almost exclusively resighted at the clubs, and only a few (5%) on the ledges (Table 1). In subsequent age classes, there was a clear trend that the proportions of birds seen only at the breeding ledges were increasing drastically with age, observing 89% of 3-10-years-old birds only at breeding ledges (Table 1).

Survival probabilities differed among age classes and were highest for 2-years-old and 3-years-old birds (Fig. 3). As expected, survival to 1-year-old was the lowest among the age classes. Resighting probability for 1-year-old birds was extremely low (Fig. 4), peaking at 2-years-old, and was close to the upper bound of the informative prior for the older age class, as expected based on visibility of the ledges. Recapture probability showed interannual variation among years, but it is important to remark that all the age classes showed the same pattern of variability between years.

DISCUSSION

Through the use of Bayesian Cormack-Jolly-Seber models, we provide new estimations of annual survival and resighting probabilities of young birds at the largest Common Murre colony in the Baltic Sea. The large number of banded and resighted birds offered a robust database to obtain relevant inferences. Unique among Common Murre colonies, a number of birds re-

Table 1. Age and number (with percentage) of banded Common Murres (*Uria aalge*) resighted at clubs, breeding ledges, and both areas in a large breeding colony on the island of Stora Karlsö in the Baltic Sea, Sweden from 2006-2016.

Age	Clubs	Breeding ledges	Both
1	704 (95%)	32 (4.31%)	5 (0.68%)
2	1183 (52.77%)	930 (41.48%)	129 (5.75%)
3	285 (17.71%)	1306 (81.17%)	18 (1.12%)
4	57 (6.38%)	830 (92.95%)	6 (0.67%)
5	8 (1.65%)	477 (98.35%)	0 (0.00%)
6	4 (1.62%)	243 (98.38%)	0 (0.00%)
7	1 (0.78%)	127 (99.22%)	0 (0.00%)
8	1 (1.39%)	71 (98.61%)	0 (0.00%)
9	1 (2.17%)	45 (97.83%)	0 (0.00%)
10	1 (4.76%)	20 (95.24%)	0 (0.00%)

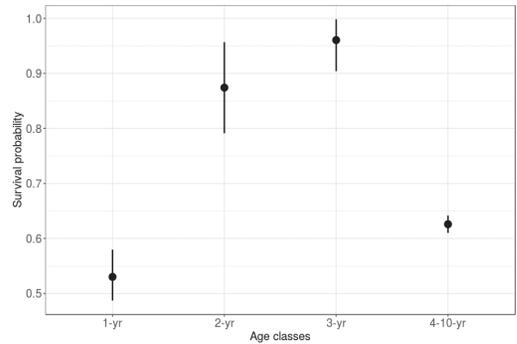


Figure 3. Mean and 95% CI of the marginal posterior distribution of annual survival probabilities among age classes of Common Murres (*Uria aalge*) from an extensive banding study in a breeding colony on the island of Stora Karlsö in the Baltic Sea from 2006-2016.

turned to this colony in their first summer, i.e. when 1-year-old (Kadin 2007). Our results showed that 1-year-old individuals were almost exclusively observed at clubs, but the subsequent age classes gradually shift over to almost only being observed at breeding ledges. The clubs help the youngest birds learn social and sexual behaviors without the risk of being attacked by breeding birds, as well as to gain experience in locating fishing grounds near the colony (Halley *et al.* 1995). We considered that resightings in clubs were not biased because birds used the boulders randomly, that is, all the individuals that belonged to the sub-colony where we banded them had the same probability of being resighted there. However, this assumption did not hold true for monitored breeding ledges and older birds (> 1-year-old).

Our results for detection of older birds were in accordance with our assumption that only 19% of the birds on the ledges would be observable. Birds that are > 1-year-old begin to prospect the breeding ledges in order to learn the competences for breeding (Halley *et al.* 1995; Harris *et al.* 1996b). Seabirds, and in particular the Common Murre, are philopatric to natal colony, but also to the sub-colony where they hatched (Halley *et al.* 1995; Harris *et al.* 1996a; Harris *et al.* 1996b). Hence, individuals that settle in monitored breeding ledges will have a higher resighting probability compared to individuals settling in other ledges in the same sub-colony

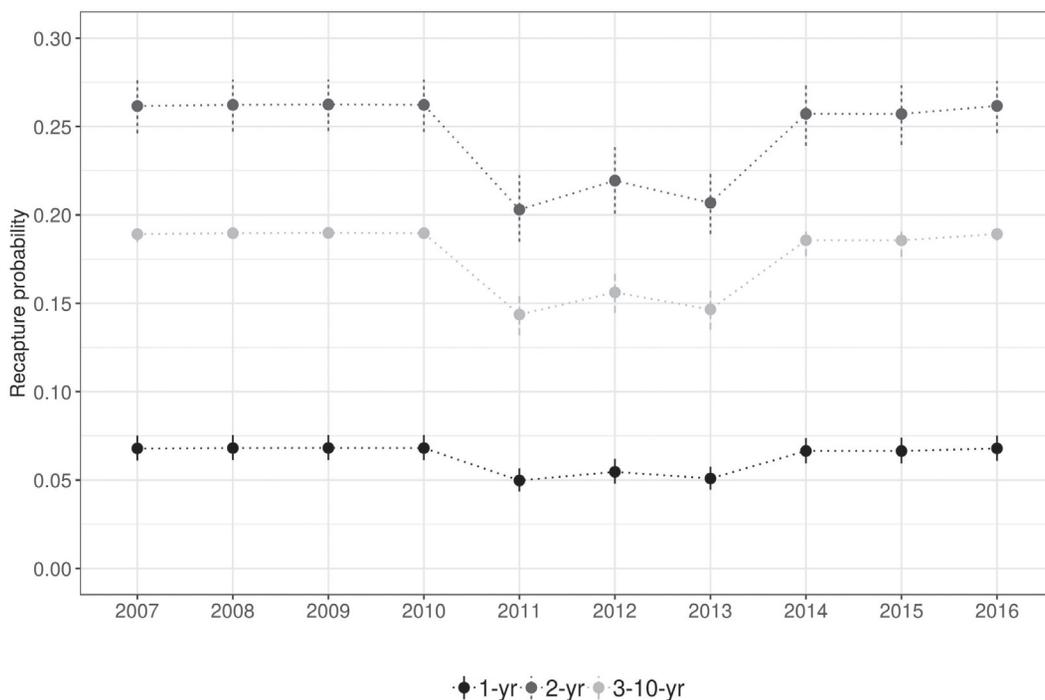


Figure 4. Mean and 95% CI of the marginal posterior distribution of recapture probabilities among age classes of Common Murres (*Uria aalge*) from an extensive banding study in a breeding colony on the island of Stora Karlsö in the Baltic Sea from 2006-2016.

– risking underestimation of survival estimates (Lebreton *et al.* 1992; Sanz-Aguilar *et al.* 2016).

We were able to compare our annual survival estimates with those obtained in other studies at the Isle of May, Scotland (Crespin *et al.* 2006; Harris *et al.* 2007; Reynolds *et al.* 2009), Skomer Island, Wales (Birkhead and Hudson 1977; Votier *et al.* 2008; Meade *et al.* 2013), and Farallon Island, California (Lee *et al.* 2008), keeping in mind differences with regard to data sources and statistical methodology (Table 2). Our estimate of survival to 1-year-old is the lowest value reported for Common Murre, whereas for 2-years-old it is the highest value reported. This is likely because no 1-year-old individuals were seen alive in the other studies, so inference in first year survival probability was done without that information. In our study, however, 12% of 1-year-old birds and 35% of 2-years-old birds were resighted. Our results showed that birds in our study had higher mortality during their first winter than during the second, confirming earlier studies that high-

light the first winter as a critical period for Common Murres, as indicated by over-representation in bycatch recoveries (Olsson *et al.* 2000a). Other comparable outputs are those for survival up to 2-years-old, which we can easily calculate combining survival of the 1-year-old and 2-years-old age classes. This calculated survival probability up to 2-years-old is 0.34 (0.58²) in Crespin *et al.* (2006), while it is 0.49 (0.70²) in Votier *et al.* (2008), and it is 0.41 (0.54*0.76) in Reynolds *et al.* (2009). In our study, the posterior mean and 95% CI of survival up to 2-years-old was 0.46 (0.44-0.49), which is similar to the calculated estimations for the other studies.

Our estimate of survival to 3-years-old was also similar to other studies. In particular, the posterior mean was close to the estimations obtained by Votier *et al.* (2008) and Reynolds *et al.* (2009). Also, and previously mentioned, in order to compare our results with those by Birkhead and Hudson (1977) and Meade *et al.* (2013) (in which the estimations were for individuals up to 3-years-old), we have to consider the calculated posterior

Table 2. Previously reported survival probability estimates for Common Murre (*Uria aalge*) from various colonies (expressed in terms of the mean, the mean and 95% CI, or the mean \pm SD; estimates are for annual survival probability except Skomer Island studies, which report cumulative survival probabilities).

Colonies, Studies and Time period	Survival estimates	Age class	Banded chicks
Farallon island, Lee <i>et al.</i> (2008). 1986-2004	0.59	1-yr	375
	0.67	2-yrs	
	0.75	3-yrs	
	0.80	4-yrs	
Isle of May, Crespin <i>et al.</i> (2006). 1983-2001	0.58 [0.44,0.71]	1-2-yrs	—
	0.86 [0.81,0.91]	3-4-yrs	
	0.70 [0.65,0.73]	5-18-yrs	
Isle of May, Harris <i>et al.</i> (2007). 1983-2002	0.56 [0.54, 0.59]	1-yr	96-237 year ¹
	0.79 [0.72,0.85]	2-yrs	
	0.92 [0.87,0.95]	3-yrs	
	0.94 [0.87,0.98]	4-yrs	
	0.97 [0.94,0.98]	5+ yrs	
Isle of May, Reynolds <i>et al.</i> (2009). 1983-2003	0.54	1-yr	5,594
	0.76 [0.72, 0.81]	2-yrs	
	0.93 [0.89, 0.96]	3-yrs	
	0.91 [0.87, 0.94]	4-yrs	
Skomer island, Birkhead and Hudson (1977). 1972-1977	0.26 **	1-3-yrs	279
	0.21 **	1-5-yrs	
Skomer island, Votier <i>et al.</i> (2008). 1985-2005	0.70 \pm 0.04	1-2-yrs	1,522
	0.95 \pm 0.08	3-yrs	
	0.87 \pm 0.06	4-yrs	
	0.78 \pm 0.05	5-20 yrs	
Skomer island, Meade <i>et al.</i> (2013). 1985-2004	0.43 **	1-3-yrs	5,943
Stora Karlsö, This study. 2006-2016	0.53 [0.49-0.58]	1-yr	28,930
	0.87 [0.79-0.96]	2-yrs	
	0.96 [0.90-0.99]	3-yrs	
	0.63 [0.61-0.64]	4-10-yrs	

probability of the cumulative survival up to three years. In our study the posterior mean and 95% CI for survival to 3-years-old in Stora Karlsö colony was 0.44 (0.43-0.46), which was a similar result Meade *et al.* (2013).

Adult survival in seabirds is the life history characteristic of greatest importance for population growth, and it is crucial for colony maintenance (Sandvik *et al.* 2012). Österblom *et al.* 2004 suggested high adult survival estimates in this colony (0.937 excluding one year with a cholera outbreak). Additionally, the colony of Common Murre of Stora Karlsö has almost tripled from 1980 until present (Hentati-Sundberg and Olsson 2016; Olsson and Hentati-Sundberg 2017).

Our final age class (4-10-years-old) is considered to consist of young adult birds. Given our relatively low annual survival estimation

for birds in this age class, and current estimates of breeding success (0.6-0.7, Berglund 2016), there should not be a strong population increase without high immigration into the colony. However, as Stora Karlsö is by far the largest colony in the Baltic Sea (Olsson and Hentati-Sundberg 2017), and because no banded birds from other colonies have been observed at Stora Karlsö, we can rule out the possibility of high immigration. There is evidence of emigration, as birds banded at Stora Karlsö are breeding at several other locations, mainly in the Baltic Sea, but also in the Atlantic Ocean (Bird Ringing Centre, Swedish Museum of Natural History, unpubl. data).

We hypothesize that our annual survival of the 4-10-years-old age class was underestimated, despite our correction for limited resighting using prior information about the

colony. A potential reason for this could be that our database provided very little information about adult survival (indeed, it was designed to estimate immature survival). Interestingly, Votier *et al.* (2008) and Crespin *et al.* (2006) reported a similar survival decline with age, both in annual survival from the 4-year to 5-year age class, and from the 3-4-year to 5-18-year age class. Both studies suggested an over representation of non-breeders with low individual quality as a possible explanation to this survival decline. However, we speculate that the main explanation may be the clearly observable age variation in prospecting behavior. Individuals at a later stage of prospecting become increasingly difficult to observe when they recruit at non-observable ledges, and thus they become less likely to show up at monitored ledges. Another complementary explanation could be that emigration takes place after initial prospecting in the natal colony (Harris *et al.* 2007). Future studies involving resighting data from other colonies could help to clarify these hypotheses.

Although the official triangular stainless-steel band has remained the same throughout the study, wear of the complementary bands has been a difficult practical issue in this study and none of the band types used has been without drawbacks. The colored-plastic bands used for most years (2006-2008, 2013-2015) were initially clearly readable, even at large distances, but tended to wear heavily after a few seasons in the colony, and eventually became unreadable. Thus, those bands are best suited for observing young birds at clubs and less optimal for longer-term studies. The ID-codes of the aluminium bands (2009) were worn away very quickly, and those bands can therefore not be recommended. The large triangular steel bands (2010-2012) had good durability but were less easy to read at longer distances. However, we were able to identify a large proportion of resighted birds by reading the official stainless-steel bands, which alleviated the problem with complementary band types. Our estimate of the recapture probabilities revealed that the 2011-2013 time-period had the lowest

recapture probabilities. These years correspond to one year after the use of the large steel bands (2010-2012), suggesting a link between recapture probabilities and band readability.

In conclusion, in this work we present the results from an extensive study carried out in the largest Murre colony from the Baltic Sea on Stora Karlsö. The wide-spread colony attendance of 1- and 2-year-old birds reported in this paper is an aspect which appears unique among Common Murre colonies. Continued research is needed to investigate the drivers behind the strong positive population trends in Stora Karlsö. In addition, in this work we provide a potential solution to deal with the partial monitoring problem for this colony by incorporating expert knowledge to the inferential process through the use of prior distributions. One of the factors that can surely affect recapture probabilities is behavioral heterogeneity. An exciting way forward to obtain more accurate pre-breeding survival estimates would be to implement models that better account for the complex prospecting behavior in Common Murres. We foresee the possibility of using this Bayesian modelling framework with more detailed individual-specific recapture histories to shed light on these important issues. Future studies and existing ones with data that may be analysed with these things in mind will provide greater insight into this approach and the biology of colonial seabirds.

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