

**Survival estimates strongly depend on capture-recapture designs in a
changing environment inducing dispersal**

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Abstract:

Capture-Recapture (CR) approaches are extensively used to estimate demographic parameters. Their robustness relies on the selection of suitable statistical models, but also on the sampling design and effort deployed in the field. In colonial or territorial species faithful to their breeding site, some recurrent local perturbations such as predation-induced breeding failure may lead individuals to disperse locally, potentially outside the study area. This might induce heterogeneity in CR histories and biases in demographic parameter estimates. Here, we assessed the effects of buffers areas and multi-site designs on dataset homogeneity and survival estimate accuracy. First, from a local multi-site long-term monitoring survey carried out in a colony of black-legged kittiwakes, we tested the homogeneity of individual CR histories and compared survival estimates from three datasets including one or several cliffs with or without buffer areas. Then, using simulated data with or without a multi-site design and buffer areas, we compared survival estimates for different scenarios involving contrasted local and regional dispersal. For field-based CR data, implementing a multi-site design and adding buffer areas did not improve dataset homogeneity, as all three datasets suffered from strong trap-dependence possibly due to individual breeding success conditioning site fidelity. Nevertheless, it significantly improved the accuracy of annual survival estimates. Results from simulations confirmed that a multi-site survey provided estimates that matched true survival probabilities with reduced confidence intervals while a single-site design consistently led to underestimated survival probabilities or greater confidence intervals. Similarly, a multi-site survey allowed detecting significant temporal trends while a single-site survey did not. Adapting the spatial scale of sampling design to the local environment and species behaviour is essential to robustly

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46 provide parameters of key relevance for the monitoring and management of populations.
47 Implementing buffer areas or multi-site design may be especially beneficial for long-lived
48 species facing regular local perturbation events.

49
50 **Keywords:** Demography, environmental change, individual behaviour, population dynamics,
51 prospecting movements, transience, trap-dependence.

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Introduction

Monitoring and understanding how natural populations vary in space and time is a crucial issue in ecology and conservation. Demographic parameters such as annual adult survival rate, breeding probabilities or emigration rates, strongly influence population trajectories but are challenging to estimate directly in the field. Capture-recapture (CR) approaches have been developed to analyze incomplete data of individual life histories obtained from the monitoring of marked individuals (Lebreton et al. 1992, Williams et al. 2002). They are based on two crucial steps: the implementation of a study design in the field to mark and recapture/resight individuals and the application of statistical estimation models (Kendall et al. 2009).

One difficulty with CR data is to properly deal with the imperfect detection of marked individuals in the field, which can bias demographic parameters and reduce their accuracy, especially if there is strong heterogeneity in individual detection probabilities (Archaux et al. 2012, Fletcher et al. 2012, Tyre et al. 2003). Variation in detection probabilities can be induced by intrinsic factors associated with individual characteristics and behaviour (age, sex, breeding or social status, etc...), but also by extrinsic factors induced by the implementation of the sampling design itself (Crespin et al. 2008, Sanz-Aguilar et al. 2010). In particular, the spatial scale at which the sampling design is implemented may play a role in inducing heterogeneity in individual capture histories because dynamic environments or recurrent perturbation events acting at local scales may affect individual behaviour and movements. For example, predation-induced breeding failure in colonial or territorial species can lead individuals to disperse over a few hundred meters (e.g., Catlin et al. 2005, Danchin et al. 1998, Danchin and Monnat 1992,

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75 Forero et al. 1999, Öst et al. 2011), potentially outside the monitored study area. These
76 movements may induce heterogeneity in CR histories through temporary or permanent
77 emigration and may ultimately lead to underestimated survival probabilities, as survival is
78 confounded with site fidelity and mortality, with dispersal (Cilimburg et al. 2002, Ergon and
79 Gardner 2014, Kendall et al. 2013, Marshall et al. 2004, Peñaloza et al. 2014, Sanz-Aguilar et
80 al. 2016, Taylor et al. 2015). The potential effect of environmental perturbations responsible
81 for local dispersal in long-term surveys is thus particularly important to consider, as it may
82 directly affect the quality of CR datasets and thus the statistical methodology used and
83 subsequent results and inferences.

84 As adult annual survival primarily drives population dynamics and trajectories in long-
85 lived species (Sæther and Bakke 2000, Stearns 1976), its estimation and accuracy are crucial,
86 especially when subsequently used in population dynamics models (Fletcher et al. 2012,
87 Ponchon et al. 2015b). Numerous complex statistical methods have been developed to account
88 for different types of individual heterogeneities and improve the reliability and accuracy of
89 demographic parameter estimates. (e.g. Choquet et al. 2013, Gimenez and Choquet 2010,
90 Pledger and Phillpot 2008, Pledger et al. 2003).. They usually validate or relax general model
91 assumptions such as homogeneity of detection probabilities but suffer from issues related to
92 parameter identifiability. They also often multiply the number of estimated parameters which
93 may sometimes be difficult to interpret in terms of biological significance (Lindberg 2012,
94 Schaub et al. 2004). Likewise, robust-design models account for temporary emigration and
95 provide relatively unbiased estimates (Kendall et al. 1997). However, they require a substantial
96 field effort to resight individuals, because they rely on primary occasions between which the

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population is open to immigration and emigration, and secondary occasions, during which the population is closed (Williams et al. 2002). Therefore, even though complex CR models allow estimating survival probabilities closer to true survival with greater accuracy, their use is not always appropriate or straightforward (Lindberg 2012). Moreover, sophisticated models often require solid knowledge of the underlying mathematical processes, which may prevent non-specialist statisticians or conservation practitioners from easily using them.

Another way to mitigate individual heterogeneity is to implement a sampling design adapted to the biology and behaviour of the monitored species, as outlined by Kendall et al. (2009) for seabirds. The inclusion of buffer areas (BA), i.e. areas surrounding the monitored plots (Kendall et al. 2009), has been suggested as an efficient way to avoid edge effects of local dispersal movements (Cilimburg et al. 2002, Horton and Letcher 2008, Marshall et al. 2004). Accordingly, implementing a sampling design with BA that would allow accounting for the potential indirect effects of local environmental perturbation events such as predation should be beneficial for reducing heterogeneity and improving the accuracy of demographic parameter estimates. Using such an approach is nevertheless not necessarily obvious as monitoring surveys are often conducted on single plots that are assumed to hold a sufficient number of faithful individuals undergoing the same environmental conditions as the whole population.

In this context, using field-based and simulated data, we explored the effects of the spatial scale of sampling design on the heterogeneity of individual capture histories and the estimation and accuracy of adult survival estimates in a commonly surveyed and widely distributed abundant seabird species, the black-legged kittiwake *Rissa tridactyla* (Coulson 2011, Frederiksen et al. 2005a). This species is particularly suitable for monitoring surveys

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because breeding individuals can be readily detected once marked and many populations are monitored across the species' range, notably to detect potential effects of changes in environmental conditions on the temporal dynamics of adult survival probabilities (Frederiksen et al. 2005b, Oro and Furness 2002, Reiertsen et al. 2014, Sandvik et al. 2005).

In the first part of our study, we used CR data from a long-term monitoring program carried out on the island of Hornøya (Norway), where the kittiwake colony numbers thousands of breeding pairs (Krasnov et al. 2007). We constituted three datasets corresponding to three different spatial scales covered in the survey to compare survival estimates, associated confidence intervals and detection probabilities obtained from simple CR models dealing with individual heterogeneity. The first dataset, based on a single-site design, included a single cliff of the kittiwake colony (Fig. 1), where heavy predation on eggs and/or chicks by ravens *Corvus corax*, has been regularly recorded over the years (rarely on adults). The second and third datasets, based on a local multi-site design respectively without and with BA, included the cliff of the first dataset and a series of other nesting cliffs (Fig. 1). In a second part, using simulated data from a single-site design with or without buffer areas and a three-site design (Fig. 2), we tested the capacity of statistical models to match true survival for different survival and dispersal values. We also tested the effects of simultaneous local and regional dispersal on the estimates of survival and detection probabilities. Finally, we tested whether negative temporal trends in survival probabilities could be detected within a single-site or a two-site design. We hypothesized that by increasing the spatial scale of sampling, i.e. by adding BA and by extending the number of monitored plots, we would better account for local individual movements and thus be more likely to consider a locally-closed population system. As a result,

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we expected survival estimates closer to true survival and lower confidence intervals for the multi-site datasets in the field-based and simulated data analyses (Cilimburg et al. 2002, Horton and Letcher 2008, Marshall et al. 2004). Moreover, we expected the bias in survival estimates to be more important for high dispersal rates. Finally, we expected a better detection of temporal trends for a multi-site design compared to a single-site one in the simulated data analysis (Zimmerman et al. 2007).

Materials and methods

1) FIELD-BASED DATA

STUDY SITE AND SAMPLING DESIGN

The study colony is situated on the island of Hornøya (70°23'N, 31°09'E), Eastern Finnmark, Norway, where more than 10 000 pairs of kittiwakes nest each year (Krasnov et al. 2007). The long-term monitoring survey started in 1998, with the capture of breeding adults which were marked with individual colour ring combinations. Each year, 18 plots, divided into three sectors and situated in different parts of the island (Fig. 1), have been monitored once every three days from late April, before kittiwakes start building their nest, until late July, at fledging. For each ringed individual resighted, the (i) plot name and nest site number, (ii) presence of ringed or non-ringed mate and (iii) individual activity (i.e. standing on a constructed/non constructed nest, squatting, incubating, brooding chicks...) have been recorded. Additional resighting efforts have been made outside the main monitored plots, at the beginning and end of the season, when detection probabilities can be high (Chambert et al.

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2012). This notably allowed the resighting of birds in BA, i.e. around the plots, and in dense parts of the colony (Fig. 1).

DATA SELECTION

Because experiments involving the manipulation of the breeding success in 1998 and 1999 were conducted in most of the monitored plots (Boulinier et al. 2008), we focused the analyses on the period from 2003 to 2012. Individuals ringed before 2003 were included only if they were resighted at least once as breeders within the monitored plots between 2003 and 2011. Moreover, as individuals can be resighted in different locations during the same season, the nest site assigned for a given season corresponded to the site where individuals reproduced or where they were most often seen during the season. Although each plot was visited ~30 times each season, we summarized observations as single yearly occasions to avoid additional intra-season temporal heterogeneity in individual detection probabilities potentially related to local breeding performances (Chambert et al. 2012). This means that resighted and non-resighted individuals were respectively coded 1 and 0 for a given year.

To constitute the single-site dataset, we chose a cliff where predation on eggs and/or chicks by ravens *Corvus corax* had been recorded over years. Predation pressure was nevertheless irregular over years, with years of high predation events (i.e. Ponchon et al. 2017b) and other with very few. We only selected birds that had been ringed in this cliff and thereafter we considered only resightings in this cliff. All other observations made outside the cliff were thus coded 0, as if the birds had not been seen for that year. Overall, the single- and the multi-site datasets included respectively 92 and 779 marked individuals, representing a total of 319

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and 3306 observations over 10 yearly occasions. To constitute the multi-site dataset without BA, all ringed birds assigned to BA, i.e. observed outside the monitored plots after the first occasion, were coded 0. Observations in BA represented 9.1% of the total multi-site dataset.

GOODNESS-OF-FIT ANALYSIS

Analyses started with the Cormack-Jolly-Seber (CJS) model assuming time-dependent survival and detection probabilities (Lebreton et al. 1992). This model allows estimating two parameters: the annual apparent survival probability s , i.e. the probability that an individual is alive and available for detection in the monitoring area and detection probability p , i.e. the probability of resighting an individual at the monitored site given that it is alive in the monitoring area.. The inter-individual homogeneity assumption of the CJS model was assessed for each dataset independently using the U-CARE software (Choquet et al. 2009a). With this tool, the causes of some lack of fit can be identified. In particular, test 3.SR tests for the presence of transient individuals by comparing survival probabilities between newly marked individuals and individuals resighted at previous occasions. Test 2.CT examines trap-dependence effects by comparing detection probabilities between individuals already seen and those not seen at the previous occasion. Any significant test (p -value < 0.05) means that the homogeneity assumption of the CJS model (i.e. equal survival and detection probabilities among individuals) is violated.

MODEL SELECTION

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The program E-Surge (Choquet et al. 2009b) was used to build and fit the models. Model selection was performed based on the Quasi-likelihood Akaiques' Information Criterion, corrected for small sample size and overdispersion (QAICc, Burnham and Anderson 2002). The model with the lowest QAICc was considered to be the best model (see Appendix 1 for all models tested).

2) SIMULATED DATA

To highlight further potential biases induced by the spatial scale of the sample design on demographic parameters and subsequent inferences, we conducted a second analysis based on simulated data. We compared survival probabilities estimated from one virtual single-site design where 100 individuals were ringed at first occasion and one two-site design where 50 individuals were ringed in each site at first occasion as well (Fig. 2). We did not implement transience and trap-dependence effects in individual capture histories to avoid confounding effects.

In a first scenario, we fixed a constant true annual survival probability s of either 0.5, 0.7 or 0.9, a local dispersal rate d of 0.1 or 0.3, and a constant detection probability p of 0.7. Dispersing individuals could come back to their initial site. We ran simulations over 8 yearly occasions and we compared the estimates of survival and detection probability obtained from a CJS model and a multistate model with an unobservable state (hereafter multistate model; Schaub et al. 2004) for the single-site design and a multisite model (Lebreton et al. 2003) for the multi-site design.

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In a second scenario, we fixed a constant survival s of 0.9 and we tested the effect of different values for local dispersal L towards buffer areas and regional dispersal r to a second site over 8 yearly occasions. We also tested whether a temporary increase of local dispersal (0.05 from occasion 1 to 3, 0.2 for occasion 4 and 5 and 0.05 for occasion 6 to 8) could bias the estimates of survival and detection probability with the same statistical models used in scenario 1.

In a third scenario, we implemented a fixed dispersal rate d of 0.3 but a time-dependent survival probability, decreasing from 0.9 to 0.75 over 10 yearly occasions. In this case, we tested whether CJS and multistate models were able to detect this negative trend by estimating a time-dependent survival probability depending on study design.

To avoid multiple Monte-Carlo simulations, we built a single three-sitedataset for each combination of dispersal and survival values using a numerical approach based on expected values (see Devineau et al. 2006 for procedure details) using M-SURGE software (Choquet et al. 2004).

Results

1) Field-based data

Goodness-of-fit tests did not reveal any transience effect, but a very strong trap-dependence effect in the three datasets (Table 1). The multi-site dataset without BA was the one with the strongest over-dispersion, as the two tests of trap-dependence (Test 2.CT and 2.CL) were significant. The multi-site dataset including BA and the single-site dataset were more homogeneous, with only one significant trap-dependent test (Test 2.CT; Table 1).

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Consequently, we applied a trap-dependent model (Pradel 1993) for the three datasets and we additionally applied a multistate model (Schaub et al. 2004) on the single-site dataset. This model accounts for temporary emigration and allows individuals to enter an unobservable state when they temporarily or permanently move outside the study area. Additional lack of fit was taken into account by adding corresponding overdispersion coefficients \hat{c} calculated as the sum of chi-squares χ^2 divided by the sum of degrees of freedom df (Table 1).

The model selections gave a constant survival for the three datasets (Table 2), but the ones calculated from the single-site was 0.01 to 0.05 lower compared to the ones from the multi-site datasets that were higher, very similar and relatively accurate (0.876 ± 0.011 for the multisite design with BA and 0.872 ± 0.012 for the multisite design without BA; Table 3). The survival estimate obtained with the multistate model was 0.04 higher than the one obtained with the trap dependent model for the single-site dataset but the confidence intervals was as large (Table 3).

Detection probabilities were constant for the single-site dataset, both with the trap-dependent and multistate model. On the contrary, they were time-dependent for the two other datasets but values were relatively similar (Fig. 3). Detection probabilities for individuals seen the previous occasion were very high, between 0.80 and 0.93 for the two multi-site datasets and fixed at 0.909 ± 0.031 and for the single-site dataset. Those for individuals not seen the previous occasion were consistently lower, fluctuating between 0.18 to 0.58 for the two multi-site datasets and constant at 0.330 ± 0.159 for the single-site dataset with the trap-dependent model. The addition of buffer areas seemed to improve the detection probabilities for individuals not seen the previous occasion (Fig. 3).

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2) Simulated data

The results from the simulated data showed that as expected, the type of design and model choice strongly influenced both the estimates of annual survival and detection probabilities (Fig. 4).

In a first scenario testing different combinations of annual survival and dispersal rates (Fig. 4, left panel), the design including buffer areas led to survival values that matched the true parameter with reduced confidence intervals. The one obtained from the trap-dependent model for the single-site design led to constantly lower and less accurate survival values and the bias was exacerbated for high survival and dispersal rates. The multistate model gave survival estimates close to true survival but with large confidence intervals and performed worse when survival and dispersal rates were high. The same pattern was observed for detection probabilities (Fig. 4).

In the second scenario (Fig. 4, right panel), the annual survival probabilities were only correctly estimated within a three-sites design or a site including buffer areas when local dispersal L was high (0.3). When local dispersal L was low (0.05), regardless of regional dispersal r , survival probability was 0.03 to 0.15 lower than the true parameter and confidence intervals were larger. Time-dependent local dispersal rates led to slightly lower survival estimates compared to constant ones. It has to be noted that for both high local and regional dispersal rates ($L0.3/r0.2$), the model overestimated survival for the single-site design and strongly underestimated detection probabilities. In case of high local and/or regional dispersal, the single-site design led to strongly biased detection probabilities. The multistate model applied on the single-site dataset gave similar survival estimates as the multisite model applied

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on the two-site design, except when local dispersal was high ($L=0.3$). However, estimates had larger confidence intervals.

In the last scenario, which implemented a decrease of annual survival probability from 0.9 to 0.75, two models were equivalent for the single-site, both with the CJS and multistate model, as the difference between their QAICc was lower than 2 (Table 4). The best-ranked CJS and multistate model gave a constant survival probability of 0.72 and 0.77 respectively. The second best models gave a time-dependent survival probability (Fig. 5), which temporal trends were not significant, as the confidence interval included 0 (95% confidence interval for the CJS model: -0.16 ; 0.032; 95% confidence interval for the multistate model: -0.20; 0.04). In the two-site design, the survival probability obtained from the best-ranked model was time-dependent and the associated negative trend was significant (95% confidence interval: -0.20 ; -0.033). Overall, the two-site design led to higher and more accurate survival estimates, closer to true survival compared to the single-site one, regardless of CR models, and allowed detecting temporal decrease in annual survival probabilities.

Discussion

In this study, we combined field-based and simulated data to test the effects of the spatial scale of sampling design on dataset homogeneity, estimation and accuracy of survival annual and subsequent inferences when individuals disperse locally in buffer areas or at larger scales. We found consistent differences between the results provided by the single-site dataset and the two other multi-site ones in the field based-study and these were confirmed by the simulation study.

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315

316 INDIVIDUAL HETEROGENEITY

317 In the field-based data analysis, all datasets suffered from a strong trap-dependence
318 effect (Table 1). This heterogeneity in detection probabilities may result from the species
319 behaviour and movements related to breeding site selection. Indeed, during the breeding season,
320 kittiwake behaviour may be influenced by individual and conspecific breeding performance
321 (Ponchon et al. 2015a, Ponchon et al. 2017b), which may itself conditions site fidelity the
322 following year (Boulinier et al. 2008, Danchin et al. 1998, Naves et al. 2006, Ponchon et al.
323 2015a, Ponchon et al. 2017b). If individuals successfully breed within a monitored plot, they
324 will be more likely to remain faithful to their breeding site and thus their probability to be
325 resighted the following year may be higher. On the contrary, failed breeding individuals are
326 more likely to disperse to a new breeding site, especially when their neighbours are also in
327 failure, which might decrease their detection probabilities (Boulinier et al. 2008, Danchin et al.
328 1998). Moreover, black-legged kittiwakes frequently display prospecting movements to other
329 breeding areas when they are failed or non-breeders (Boulinier et al. 1996, Cadiou et al. 1994,
330 Danchin et al. 1998, Ponchon et al. 2017a, Ponchon et al. 2013). This means that even if
331 individuals have dispersed out of the monitored area, they may occasionally come back to the
332 monitored area for prospecting, notably if they have failed breeding. This might induce
333 temporal heterogeneity in detection probabilities, intra-seasonally (Chambert et al. 2012) but
334 also possibly inter-annually, as kittiwake breeding success can be highly variable in time and
335 space (Paredes et al. 2014, Ponchon et al. 2014). Therefore, in the current case study,

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heterogeneity may originate from temporary emigration but also from individual site fidelity conditioned by individual and conspecific breeding performance,

ACCURACY AND PRECISION OF SURVIVAL ESTIMATES

In the field-based study, the constant survival probability obtained from the single-site dataset was underestimated or less precise compared to the ones estimated from the multi-site datasets (Table 3). The cliff selected to constitute the single-site dataset has been irregularly impacted by predation on eggs and/or chicks (rarely adults) by ravens *Corvus corax*. This has resulted in regular massive local breeding failures and a progressive desertion of the area, likely involving adult dispersal towards other breeding cliffs (Boulinier et al. 2008, Danchin et al. 1998, Ponchon et al. 2017b). In the case of the single-site survey design, the dispersing failed birds may not be detected anymore and may be considered as dead while they are still alive but somewhere else, which may directly decrease apparent survival (Cilimburg et al. 2002, Ergon and Gardner 2014, Horton and Letcher 2008, Marshall et al. 2004, Sanz-Aguilar et al. 2016, Zimmerman et al. 2007). On the contrary, in the multi-site survey, although some monitored cliffs have also been affected by predation, these local effects may have been buffered by the spatial scale considered. Individuals may have potentially dispersed to other monitored cliffs where they could still be detected, which resulted in estimations of higher annual survival probabilities, probably closer to the true survival probability. This interpretation is strengthened by the simulation results, which clearly show that not accounting for local dispersal by monitoring a single site may lead to a strong underestimation of annual survival probability, especially for long-lived species (Fig. 4). Likewise, scenario 3 from the simulation study

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revealed that a multi-site design was essential to detect a slow but significant decrease of annual survival probability over time (Fig. 5).

Overall, the use of a multistate model accounting for temporary emigration within a single-site design provided values close to true survival, as the ones obtained within a multisite design but had larger confidence intervals (Fig.4). Moreover, some models suffered from identifiability issues (Appendix 1), leading to less robust results than the ones obtained within a multisite design. A robust design (Kendall et al. 1997) may not have helped obtain better estimated because populations are not closed within secondary occasions due prospecting movements which unevenly occur during the breeding season (Boulinier et al. 1996, Chambert et al. 2012, Ponchon et al. 2015a). Therefore, our results emphasize the necessity to match species biology by implementing the right design before developing complicated and potentially ineffective CR models..

BENEFITS AND IMPLICATIONS OF BUFFER AREAS OR MULTI-SITE STUDY DESIGNS

The survival estimate for the multi-site dataset including BA is only slightly higher (0.876) than the one without BA (0.872), and the confidence interval, slightly lower (respectively 0.854-0.896 and 0.846-0.894). Nevertheless, the dataset with BA is more homogenous, as only one trap-dependence effect is detected (Table 1). Thus, in our field-based CR study, although 9% of observations occurred in BA, the inclusion of these data did not markedly help improve survival estimates and confidence intervals, but efficiently improve dataset homogeneity and detection probabilities for birds not resighted on the previous occasions (Fig. 3). This highlights that in our field study, a multi-site design is more efficient

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380 than just locally extending one monitored area to estimate annual survival probabilities.
381 Nevertheless, simulations provide contrasted results. Scenario 2, notably testing the effects
382 local and regional dispersal, shows that in case of high local dispersal ($L=0.3$), a buffer area is
383 sufficient to obtain relatively unbiased survival estimates, even when regional dispersal is high
384 (Fig. 4).

385 In addition to estimating survival probabilities closer to true survival and allowing more
386 robust ecological inferences thanks to reduced confidence intervals, a multi-site sampling
387 design may provide wider perspectives in terms of species management and conservation, but
388 also population ecology. It may allow a better understanding of local movements and thus local
389 population dynamics, by the possibility of estimating dispersal rates using more sophisticated
390 statistical models, such as multi-site (Lebreton et al. 2003), multi-event (Pradel 2005) or
391 spatially explicit CR models accounting for locations associated with individual detection
392 (Borchers and Fewster 2016). If such design could further be implemented in several
393 populations, this would lead to a hierarchical design enhancing efficient conservation and
394 management efforts both at a local and regional scale. This could provide information on the
395 variation of survival estimates (Frederiksen et al. 2005a), revealing specific local demographic
396 and dispersal rates but also regional connectivity (Barlow et al. 2013, Fernández-Chacón et al.
397 2013). More importantly, a multi-site design may anticipate changes in the local environment,
398 which may avoid ending with a completely empty monitored area after years of bad local
399 environmental conditions. This kind of design would therefore be beneficial for species more
400 likely to disperse to other surrounding breeding areas because of recurrent local perturbations
401 such as predation or man-induced disturbance.

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Implementing the appropriate sampling design at the beginning of a long-term study primarily depends on the purpose of long-term monitoring surveys, but it also depends on the time to be spent in the field to collect data, sample size, potential individual heterogeneity and the precision needed to make demographic inferences (Field et al. 2005, Lahoz-Monfort et al. 2014, Lindberg 2012, Nichols and Williams 2006). Enlarging the monitored area often requires more time spent in the field and may be constrained by logistical or financial issues. However, the number of marked individuals and the proportion of population monitored should not be neglected, because small sample sizes or too small monitored areas lead to underestimated annual survival probabilities and larger confidence intervals (Devineau et al. 2006, Sanz-Aguilar et al. 2016, Zimmerman et al. 2007), which would in the end, weaken ecological inferences. The advantage of a multi-site design is that it may account for a larger proportion of the area encompassing the population and it may not necessarily imply more individuals to resight/capture, as the initial number of ringed individuals in one area can be scattered in several ones (Fig. 2). Additionally, identifying the periods when individuals are the most detectable may help optimize a multi-site design, reduce field effort and mitigate individual heterogeneity (Chambert et al. 2012, Field et al. 2005, Lahoz-Monfort et al. 2014). Finally, the duration of the long-term surveys should also be carefully considered, as it may strongly bias survival estimates towards the end of the time series (Langtimm 2009, Peñaloza et al. 2014).

CONCLUSION

In a context of current climate change, CR surveys are frequently used to study the effects of environmental factors on the survival of potentially sensitive species, but their

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robustness is sometimes questioned (Grosbois et al. 2009). The accuracy and reliability of survival estimates based on an appropriate study design and statistical models are crucial to draw reliable demographic inferences, especially when estimated parameters are used to correlate demography and climate variability at large spatial scales (Grosbois et al. 2008, Tavecchia et al. 2016), predict population response to environmental change (Ponchon et al. 2015b) or make decisive conservation and management plans (Kendall et al. 2009, Williams et al. 2002, Zimmerman et al. 2007). The lower survival probability obtained from our field-based single-site dataset and the results from the simulation analysis highlight the need to implement adapted study designs to closely match species biology and behaviour and avoid biases due to local environmental factors or perturbation events that might alter individual behaviour and detection at local and regional scales.

In addition to spatial scale, the timing of surveys could also affect heterogeneity through strong temporal variation in detection probabilities of individuals (Chambert et al. 2012). An increasing number of studies have shown that species may change their phenology to match new environmental conditions driven by climate change (Walther et al. 2002), breeding earlier (Moyes et al. 2011) or delaying their hibernation emergence (Lane et al. 2012). Consequently, monitoring surveys should thus not only be implemented to match the species' spatial ecology, as highlighted here, but should also possibly be fine-tuned to the local conditions, which may vary at various temporal scales (Chambert et al. 2012, Hurley et al. 2013).

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Author contribution statement:

TB, KDM and TT implemented the long-term monitoring survey and associated design. TB, JT, KDM, TT and AP participated to fieldwork to collect the data. AP and JT processed the data. AP and RC ran capture-recapture models from field-based and simulated data. AP led the writing of the manuscript. All authors contributed critically to the drafts of the manuscript and gave final approval for publication.

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Table 1: Goodness-of-fit tests of the Cormack-Jolly-Seber model for each field-based dataset. Significant chi-square statistics ($p < 0.05$) reflecting model assumption violations are in bold.

	Single-site dataset			Multi-site dataset without BA			Multi-site dataset with BA		
Goodness of fit components	χ^2	df	p	χ^2	df	p	χ^2	df	p
Test 3.SR	2.6	8	0.95	5.2	8	0.73	10.3	8	0.25
Test 3.SM	1.6	6	0.91	8.1	8	0.43	6.8	8	0.61
Test 2.CT	21.0	6	0.0019	421.9	7	<0.001	278.0	7	<0.001
Test 2.CL	0	4	1	17.5	7	0.014	10.7	6	0.10
\hat{c} with the CJS model		1.05			15.1			10.5	
\hat{c} for trap-dependent model		1			1.34			1.26	

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Table 2: Most parsimonious models selected based on QAICc for each of the three datasets.

s is the apparent survival probability, T is a transition probability, p is the detection probability,

i is a constant, t is time-dependence and a is a trap-dependant effect.

Model structure	Dataset	Model	Nb of parameters	Deviance	QAIC	QAICc
Multistate model with and unobservable state	Single-site dataset	$s(i)T(i)p(i)$	4	407.62	415.62	415.75
	Single-site dataset	$s(i) p(a)$	4	406.60	414.60	414.67
Trap-dependent model	Multi-site dataset without BA	$s(i) p(a+t)$	12	3925.18	2953.24	2953.30
	Multi-site dataset with BA	$s(i) p(a+t)$	12	3980.90	3183.45	3183.50

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Table 3: Estimates of annual apparent survival probability for the three field-based datasets with a trap-dependant (TD) or a multistate model with an unobservable state (UN).

Field design	Estimate ± SE	95% confidence interval
Single-site (TD)	0.823 ± 0.028	0.762 – 0.871
Single site (UN)	0.861 ± 0.024	0.806 – 0.902
Multi-site (TD)	0.872 ± 0.012	0.846 – 0.894
Multi-site + BA (TD)	0.876 ± 0.011	0.854 – 0.895

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Table 4: Model selection for the third scenario of simulations, parameterized with a true survival probability starting at 0.9 and decreasing of *ca.* 0.015 every year and detection probability of 0.7. In the models, survival *s*, transition *T* and detection probabilities *p* are either constant (i), time-dependent (t), or decreasing (slope). The best selected models are in bold. * indicates models with unidentifiable parameters.

Design	Model	Number of parameters	Deviance	QAIC	QAICc
Single-site (Multistate with an unobservable state)	s(i)T(i)p(i)	4	812.28	820.28	820.38
	s(slope)T(i)p(i)	5	810.69	820.69	820.84
	s(t)T(i)p(i)	12	810.68	834.68	835.47
	s(slope)T(i)p(t)	13	810.68	836.68	837.60
	s(t)T(i)p(t)	19	810.68	848.68	850.63
Single-site (CJS)	s(i), p(i)	2	828.06	832.06	832.09
	s(slope), p(i)	3	826.38	832.38	832.44
	s(slope), p(t)	11	825.44	847.44	848.11
	s(t), p(t)	17	825.27	859.27	860.84
Two-sites (CJS)	s(slope), p(i)	3	1488.34	1494.33	1494.36
	s(i), p(i)	2	1495.63	1499.63	1499.65
	s(t), p(i)	10	1488.28	1508.28	1508.56
	s(slope), p(t)	12	1488.31	1512.31	1512.71
	*s(t)p(t)	18	1488.28	1524.28	1525.16

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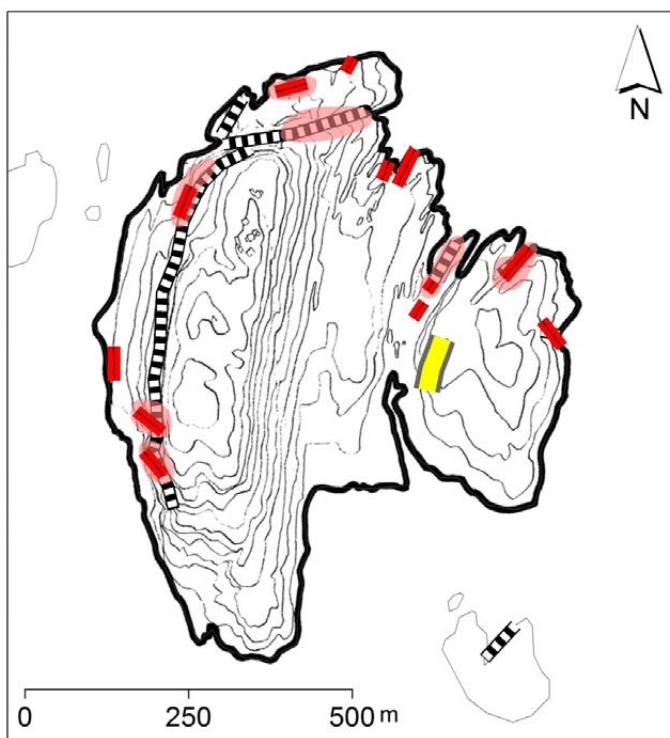
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Figures

Figure 1: Map of the different areas included in the single-site (thick yellow line) and multi-site (red lines) designs. All kittiwake nesting cliffs are represented by striped black and white lines and buffer areas, by light red areas.



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655 **Figure 2:** Field designs tested with simulated datasets. In scenario 1, individuals disperse
 656 locally at rate L to buffer areas. They can be monitored (black lines) in buffer areas or not (grey
 657 lines) depending on study design. In scenario 2, individuals disperse locally to buffer areas at a
 658 constant (L) or time-dependent rate Lt and disperse regionally to another site with a constant
 659 rate r . Scenario 3 is similar to scenario 1 but true survival decreases over time.
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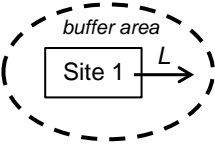
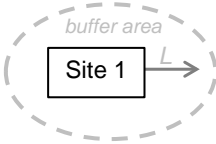
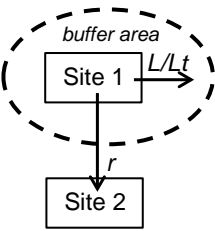
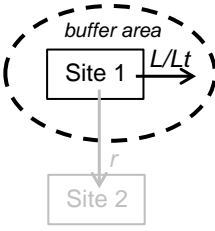
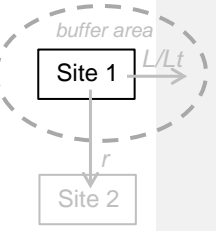
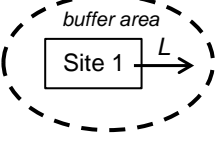
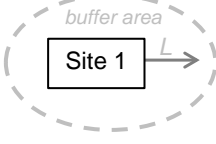
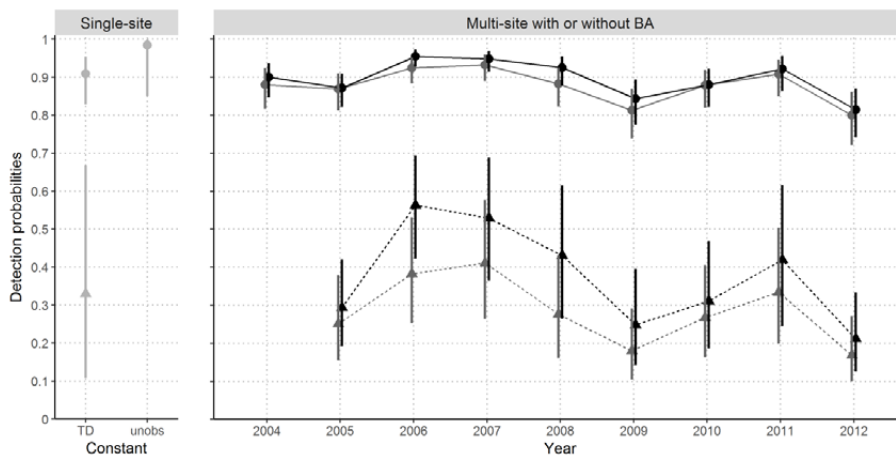
	Full dataset	Reduced dataset	
Scenario 1: Constant survival and dispersal rates tested	Single-site + BA design 	Single-site design 	
Scenario 2: Constant survival; different local and regional dispersal rates tested	Three sites design 	Single-site + BA design 	Single-site design 
Scenario 3: Decreasing survival and constant local dispersal rate tested	Single-site + BA design 	Single-site design 	

Figure 3: Detection probabilities and associated 95% confidence intervals estimated from the best selected models for the single-site field-based dataset analyzed with a trap-dependent model (TD) and a multistate model with an unobservable state (unobs) and the two multi-site field-based datasets analyzed with a trap-dependent model. Dark grey represents the multi-site dataset without BA and black, the multi-site dataset with BA. Points and triangles represent respectively the group of individuals seen the previous occasion and that of individuals not seen the previous occasion. Note that the multistate model with an unobservable state only has one group of detection probabilities.

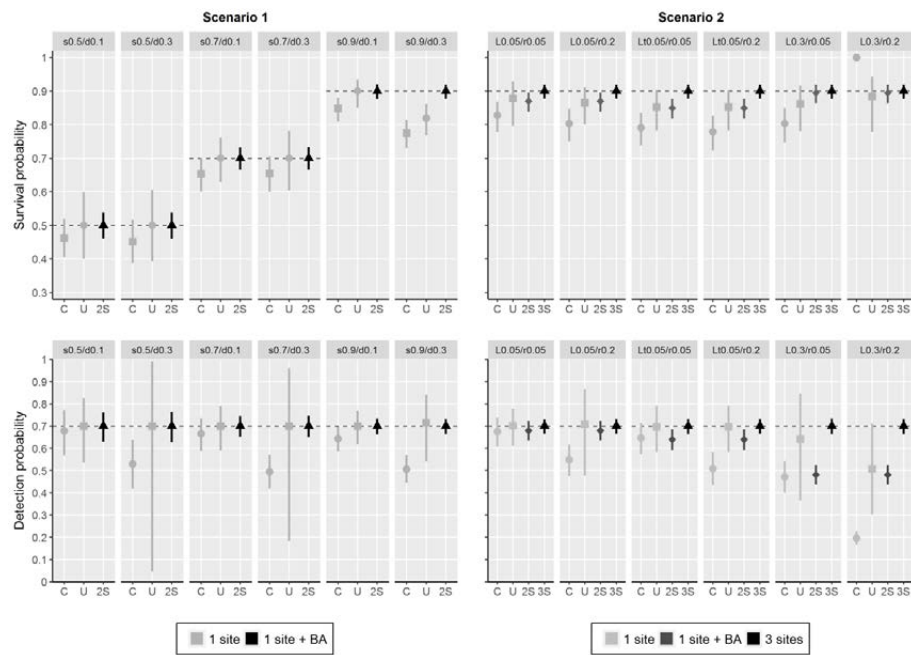


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Figure 4 : Estimates of survival (upper panel) and detection probabilities (lower panel) for a combination of survival and dispersal values. In scenario 1 (left panel), we tested how different survival (s) and dispersal (d) probabilities affected estimates depending on design and CR model. In scenario 2, with a constant survival fixed at 0.9, we tested how different combinations of constant (L) or time-dependant (L_t) local dispersal and regional dispersal (r) affected the estimates of survival and detection probabilities depending on design and CR models. Black triangles represents the full dataset whereas dark and light grey represent reduced datasets. Vertical bars represent the 95% confidence intervals and dashed horizontal lines, true implemented parameters. C: CJS model; U: multistate model with an unobservable state; 2S: two-site model; 3S: three-site model.



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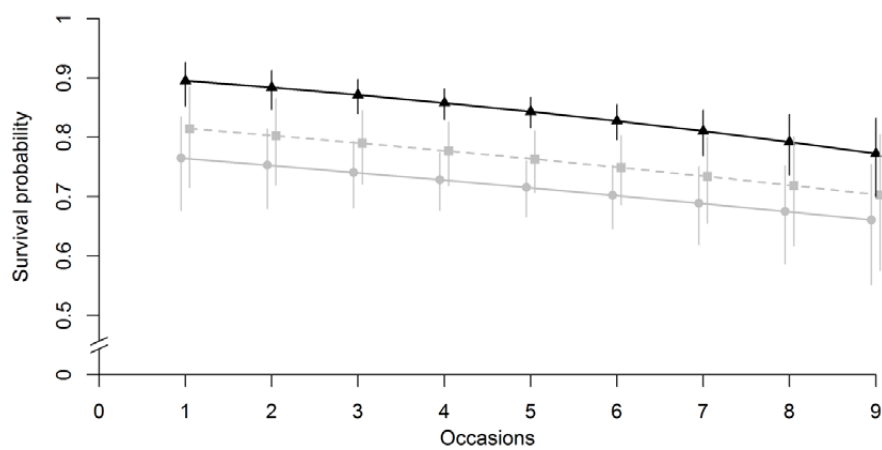
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686 **Figure 5:** Annual survival probabilities estimated from the best ranked-model for Scenario 3,
 687 implemented with a fixed dispersal rate of 0.3 and a time-dependent survival probability,
 688 decreasing from 0.9 to 0.75. Light grey points and squares respectively represent estimates
 689 obtained with a CJS and multistate model with a unobservable state applied on a single-site
 690 dataset. Black triangles represent estimates from a CJS model applied on a two-site design
 691 dataset. Vertical bars indicate 95% confidence intervals.



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695 **Supporting information:**

696 Model selection for the analysis of the field-based CR data. s is the annual apparent survival

697 probability, T is a transition probability, p is the detection probability, i is a constant, t is time-

698 dependence and a is a trap-dependent effect. Selected models for each dataset are in bold. *

699 indicates models with unidentifiable parameters.

700

Dataset and model applied	Model	Number of parameters	Deviance	QAIC	QAICc
Multi-site+BA	s(i)p(a+t)	12	3980.90	3183.44	3183.50
	s(i)p(a.t)	19	3964.10	3184.11	3184.24
	s(t)p(a+t)	19	3968.76	3187.81	3187.94
	s(t)p(a.t)	25	3956.04	3189.72	3189.94
Trap-dependent model	s(t)p(a)	12	3999.98	3198.58	3198.64
	s(i)p(a)	4	4033.04	3208.82	3208.84
	s(t)p(i)	11	4177.67	3337.61	3337.66
	s(i)p(i)	3	4208.40	3346.00	3346.00
Multi-site without BA	s(i)p(a+t)	12	3925.18	2953.24	2953.30
	s(i)p(a.t)	19	3908.96	2955.14	2955.28
	s(t)p(a)	12	3938.13	2962.90	2962.96
	s(t)p(a+t)	19	3920.83	2964.00	2964.13
Trap-dependent model	s(t)p(a.t)	25	3905.04	2964.21	2964.45
	s(i)p(a)	4	3962.56	2965.14	2965.14
	s(i)p(i)	3	4236.99	3167.93	3167.93
	s(t)p(i)	11	4219.17	3170.63	3170.68
Single-site	s(i)p(a)	4	406.60	414.60	414.67
	s(i)p(a+t)	12	397.61	421.61	422.18
	s(t)p(a)	12	400.73	424.73	425.30
Trap-dependent model	s(i)p(a.t)	19	391.85	429.85	431.25
	s(t)p(a+t)	19	394.27	432.27	433.67
	s(i)p(i)	3	432.26	438.26	438.30
	s(t)p(a.t)	25	388.57	438.56	440.99
Single-site	s(i)T(i)p(i)	4	407.62	415.62	415.75
	s(i)T(i)p(t)	12	400.60	424.60	425.62
	s(t)T(i)p(i)	12	401.55	425.55	426.57
	s(t)T(t)p(i)	20	391.34	431.34	434.16

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Multistate model with an unobservable state	*s(t)T(i)p(t)	19	394.66	432.66	435.20
	s(i)T(t)p(t)	20	392.78	432.78	435.60
	*s(t)T(t)p(t)	26	387.66	439.66	444.47
	s(i)T(t)p(i)	12	457.13	481.13	482.14

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