

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

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24 **Abstract:**

25 Capture-Recapture (CR) approaches are extensively used to estimate demographic parameters.  
26 Their robustness relies on the selection of suitable statistical models, but also on the sampling  
27 design and effort deployed in the field. In colonial or territorial species faithful to their breeding  
28 site, some recurrent local perturbations such as predation-induced breeding failure may lead  
29 individuals to disperse locally, potentially outside the study area. This might induce  
30 heterogeneity in CR histories and biases in demographic parameter estimates. Here, we assessed  
31 the effects of buffers areas and multi-site designs on dataset homogeneity and survival estimate  
32 accuracy. First, from a local multi-site long-term monitoring survey carried out in a colony of  
33 black-legged kittiwakes, we tested the homogeneity of individual CR histories and compared  
34 survival estimates from three datasets including one or several cliffs with or without buffer  
35 areas. Then, using simulated data with or without a multi-site design and buffer areas, we  
36 compared survival estimates for different scenarios involving contrasted local and regional  
37 dispersal. For field-based CR data, implementing a multi-site design and adding buffer areas  
38 did not improve dataset homogeneity, as all three datasets suffered from strong trap-dependence  
39 possibly due to individual breeding success conditioning site fidelity. Nevertheless, it  
40 significantly improved the accuracy of annual survival estimates. Results from simulations  
41 confirmed that a multi-site survey provided estimates that matched true survival probabilities  
42 with reduced confidence intervals while a single-site design consistently led to underestimated  
43 survival probabilities or greater confidence intervals. Similarly, a multi-site survey allowed  
44 detecting significant temporal trends while a single-site survey did not. Adapting the spatial  
45 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.

52

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53 **Introduction**

54 Monitoring and understanding how natural populations vary in space and time is a  
55 crucial issue in ecology and conservation. Demographic parameters such as annual adult  
56 survival rate, breeding probabilities or emigration rates, strongly influence population  
57 trajectories but are challenging to estimate directly in the field. Capture-recapture (CR)  
58 approaches have been developed to analyze incomplete data of individual life histories obtained  
59 from the monitoring of marked individuals (Lebreton et al. 1992, Williams et al. 2002). They  
60 are based on two crucial steps: the implementation of a study design in the field to mark and  
61 recapture/resight individuals and the application of statistical estimation models (Kendall et al.  
62 2009).

63 One difficulty with CR data is to properly deal with the imperfect detection of marked  
64 individuals in the field, which can bias demographic parameters and reduce their accuracy,  
65 especially if there is strong heterogeneity in individual detection probabilities (Archaux et al.  
66 2012, Fletcher et al. 2012, Tyre et al. 2003). Variation in detection probabilities can be induced  
67 by intrinsic factors associated with individual characteristics and behaviour (age, sex, breeding  
68 or social status, etc...), but also by extrinsic factors induced by the implementation of the  
69 sampling design itself (Crespin et al. 2008, Sanz-Aguilar et al. 2010). In particular, the spatial  
70 scale at which the sampling design is implemented may play a role in inducing heterogeneity  
71 in individual capture histories because dynamic environments or recurrent perturbation events  
72 acting at local scales may affect individual behaviour and movements. For example, predation-  
73 induced breeding failure in colonial or territorial species can lead individuals to disperse over a  
74 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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97 population is open to immigration and emigration, and secondary occasions, during which the  
98 population is closed (Williams et al. 2002). Therefore, even though complex CR models allow  
99 estimating survival probabilities closer to true survival with greater accuracy, their use is not  
100 always appropriate or straightforward (Lindberg 2012). Moreover, sophisticated models often  
101 require solid knowledge of the underlying mathematical processes, which may prevent non-  
102 specialist statisticians or conservation practitioners from easily using them.

103 Another way to mitigate individual heterogeneity is to implement a sampling design  
104 adapted to the biology and behaviour of the monitored species, as outlined by Kendall et al.  
105 (2009) for seabirds. The inclusion of buffer areas (BA), i.e. areas surrounding the monitored  
106 plots (Kendall et al. 2009), has been suggested as an efficient way to avoid edge effects of local  
107 dispersal movements (Cilimburg et al. 2002, Horton and Letcher 2008, Marshall et al. 2004).  
108 Accordingly, implementing a sampling design with BA that would allow accounting for the  
109 potential indirect effects of local environmental perturbation events such as predation should  
110 be beneficial for reducing heterogeneity and improving the accuracy of demographic parameter  
111 estimates. Using such an approach is nevertheless not necessarily obvious as monitoring  
112 surveys are often conducted on single plots that are assumed to hold a sufficient number of  
113 faithful individuals undergoing the same environmental conditions as the whole population.

114 In this context, using field-based and simulated data, we explored the effects of the  
115 spatial scale of sampling design on the heterogeneity of individual capture histories and the  
116 estimation and accuracy of adult survival estimates in a commonly surveyed and widely  
117 distributed abundant seabird species, the black-legged kittiwake *Rissa tridactyla* (Coulson  
118 2011, Frederiksen et al. 2005a). This species is particularly suitable for monitoring surveys

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

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

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

147

## 148 **Materials and methods**

### 149 1) FIELD-BASED DATA

#### 150 STUDY SITE AND SAMPLING DESIGN

151 The study colony is situated on the island of Hornøya (70°23'N, 31°09'E), Eastern  
152 Finnmark, Norway, where more than 10 000 pairs of kittiwakes nest each year (Krasnov et al.  
153 2007). The long-term monitoring survey started in 1998, with the capture of breeding adults  
154 which were marked with individual colour ring combinations. Each year, 18 plots, divided into  
155 three sectors and situated in different parts of the island (Fig. 1), have been monitored once  
156 every three days from late April, before kittiwakes start building their nest, until late July, at  
157 fledging. For each ringed individual resighted, the (i) plot name and nest site number, (ii)  
158 presence of ringed or non-ringed mate and (iii) individual activity (i.e. standing on a  
159 constructed/non constructed nest, squatting, incubating, brooding chicks...) have been  
160 recorded. Additional resighting efforts have been made outside the main monitored plots, at the  
161 beginning and end of the season, when detection probabilities can be high (Chambert et al.

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162 2012). This notably allowed the resighting of birds in BA, i.e. around the plots, and in dense  
163 parts of the colony (Fig. 1).

164

#### 165 DATA SELECTION

166 Because experiments involving the manipulation of the breeding success in 1998 and  
167 1999 were conducted in most of the monitored plots (Boulinier et al. 2008), we focused the  
168 analyses on the period from 2003 to 2012. Individuals ringed before 2003 were included only  
169 if they were resighted at least once as breeders within the monitored plots between 2003 and  
170 2011. Moreover, as individuals can be resighted in different locations during the same season,  
171 the nest site assigned for a given season corresponded to the site where individuals reproduced  
172 or where they were most often seen during the season. Although each plot was visited ~30 times  
173 each season, we summarized observations as single yearly occasions to avoid additional intra-  
174 season temporal heterogeneity in individual detection probabilities potentially related to local  
175 breeding performances (Chambert et al. 2012). This means that resighted and non-resighted  
176 individuals were respectively coded 1 and 0 for a given year.

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

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

187

#### 188 GOODNESS-OF-FIT ANALYSIS

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

203

#### 204 MODEL SELECTION

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

210

## 211 2) SIMULATED DATA

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

219 In a first scenario, we fixed a constant true annual survival probability  $s$  of either 0.5,  
220 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.  
221 Dispersing individuals could come back to their initial site. We ran simulations over 8 yearly  
222 occasions and we compared the estimates of survival and detection probability obtained from a  
223 CJS model and a multistate model with an unobservable state (hereafter multistate model;  
224 Schaub et al. 2004) for the single-site design and a multisite model (Lebreton et al. 2003) for  
225 the multi-site design.

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226 In a second scenario, we fixed a constant survival  $s$  of 0.9 and we tested the effect of  
227 different values for local dispersal  $L$  towards buffer areas and regional dispersal  $r$  to a second  
228 site over 8 yearly occasions. We also tested whether a temporary increase of local dispersal  
229 (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  
230 estimates of survival and detection probability with the same statistical models used in scenario  
231 1.

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

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

240

## 241 Results

### 242 1) Field-based data

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

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

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

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

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270

## 271 2) Simulated data

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

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

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

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

295 In the last scenario, which implemented a decrease of annual survival probability from  
296 0.9 to 0.75, two models were equivalent for the single-site, both with the CJS and multistate  
297 model, as the difference between their QAICc was lower than 2 (Table 4). The best-ranked CJS  
298 and multistate model gave a constant survival probability of 0.72 and 0.77 respectively. The  
299 second best models gave a time-dependent survival probability (Fig. 5), which temporal trends  
300 were not significant, as the confidence interval included 0 (95% confidence interval for the CJS  
301 model: -0.16 ; 0.032; 95% confidence interval for the multistate model: -0.20; 0.04). In the two-  
302 site design, the survival probability obtained from the best-ranked model was time-dependent  
303 and the associated negative trend was significant (95% confidence interval: -0.20 ; -0.033).  
304 Overall, the two-site design led to higher and more accurate survival estimates, closer to true  
305 survival compared to the single-site one, regardless of CR models, and allowed detecting  
306 temporal decrease in annual survival probabilities.

307

## 308 Discussion

309 In this study, we combined field-based and simulated data to test the effects of the spatial  
310 scale of sampling design on dataset homogeneity, estimation and accuracy of survival annual  
311 and subsequent inferences when individuals disperse locally in buffer areas or at larger scales.  
312 We found consistent differences between the results provided by the single-site dataset and the  
313 two other multi-site ones in the field based-study and these were confirmed by the simulation  
314 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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336 heterogeneity may originate from temporary emigration but also from individual site fidelity  
337 conditioned by individual and conspecific breeding performance,

338

#### 339 ACCURACY AND PRECISION OF SURVIVAL ESTIMATES

340 In the field-based study, the constant survival probability obtained from the single-site  
341 dataset was underestimated or less precise compared to the ones estimated from the multi-site  
342 datasets (Table 3). The cliff selected to constitute the single-site dataset has been irregularly  
343 impacted by predation on eggs and/or chicks (rarely adults) by ravens *Corvus corax*. This has  
344 resulted in regular massive local breeding failures and a progressive desertion of the area, likely  
345 involving adult dispersal towards other breeding cliffs (Boulinier et al. 2008, Danchin et al.  
346 1998, Ponchon et al. 2017b). In the case of the single-site survey design, the dispersing failed  
347 birds may not be detected anymore and may be considered as dead while they are still alive but  
348 somewhere else, which may directly decrease apparent survival (Cilimburg et al. 2002, Ergon  
349 and Gardner 2014, Horton and Letcher 2008, Marshall et al. 2004, Sanz-Aguilar et al. 2016,  
350 Zimmerman et al. 2007). On the contrary, in the multi-site survey, although some monitored  
351 cliffs have also been affected by predation, these local effects may have been buffered by the  
352 spatial scale considered. Individuals may have potentially dispersed to other monitored cliffs  
353 where they could still be detected, which resulted in estimations of higher annual survival  
354 probabilities, probably closer to the true survival probability. This interpretation is strengthened  
355 by the simulation results, which clearly show that not accounting for local dispersal by  
356 monitoring a single site may lead to a strong underestimation of annual survival probability,  
357 especially for long-lived species (Fig. 4). Likewise, scenario 3 from the simulation study

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

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

370

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

372 The survival estimate for the multi-site dataset including BA is only slightly higher  
373 (0.876) than the one without BA (0.872), and the confidence interval, slightly lower  
374 (respectively 0.854-0.896 and 0.846-0.894). Nevertheless, the dataset with BA is more  
375 homogenous, as only one trap-dependence effect is detected (Table 1). Thus, in our field-based  
376 CR study, although 9% of observations occurred in BA, the inclusion of these data did not  
377 markedly help improve survival estimates and confidence intervals, but efficiently improve  
378 dataset homogeneity and detection probabilities for birds not resighted on the previous  
379 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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402 Implementing the appropriate sampling design at the beginning of a long-term study  
403 primarily depends on the purpose of long-term monitoring surveys, but it also depends on the  
404 time to be spent in the field to collect data, sample size, potential individual heterogeneity and  
405 the precision needed to make demographic inferences (Field et al. 2005, Lahoz-Monfort et al.  
406 2014, Lindberg 2012, Nichols and Williams 2006). Enlarging the monitored area often requires  
407 more time spent in the field and may be constrained by logistical or financial issues. However,  
408 the number of marked individuals and the proportion of population monitored should not be  
409 neglected, because small sample sizes or too small monitored areas lead to underestimated  
410 annual survival probabilities and larger confidence intervals (Devineau et al. 2006, Sanz-  
411 Aguilar et al. 2016, Zimmerman et al. 2007), which would in the end, weaken ecological  
412 inferences. The advantage of a multi-site design is that it may account for a larger proportion  
413 of the area encompassing the population and it may not necessarily imply more individuals to  
414 resight/capture, as the initial number of ringed individuals in one area can be scattered in several  
415 ones (Fig. 2). Additionally, identifying the periods when individuals are the most detectable  
416 may help optimize a multi-site design, reduce field effort and mitigate individual heterogeneity  
417 (Chambert et al. 2012, Field et al. 2005, Lahoz-Monfort et al. 2014). Finally, the duration of  
418 the long-term surveys should also be carefully considered, as it may strongly bias survival  
419 estimates towards the end of the time series (Langtimm 2009, Peñaloza et al. 2014).

420

#### 421 CONCLUSION

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

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424 robustness is sometimes questioned (Grosbois et al. 2009). The accuracy and reliability of  
425 survival estimates based on an appropriate study design and statistical models are crucial to  
426 draw reliable demographic inferences, especially when estimated parameters are used to  
427 correlate demography and climate variability at large spatial scales (Grosbois et al. 2008,  
428 Tavecchia et al. 2016), predict population response to environmental change (Ponchon et al.  
429 2015b) or make decisive conservation and management plans (Kendall et al. 2009, Williams et  
430 al. 2002, Zimmerman et al. 2007). The lower survival probability obtained from our field-based  
431 single-site dataset and the results from the simulation analysis highlight the need to implement  
432 adapted study designs to closely match species biology and behaviour and avoid biases due to  
433 local environmental factors or perturbation events that might alter individual behaviour and  
434 detection at local and regional scales.

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

443

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457

458 **Author contribution statement:**

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

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DOI [10.1111/ecoq.03334](https://doi.org/10.1111/ecoq.03334)



465 **References**

- 466 Archaux, F. et al. 2012. When can we ignore the problem of imperfect detection in comparative  
467 studies? — *Methods in Ecology and Evolution* 3: 188-194.
- 468 Barlow, E. J. et al. 2013. Estimating dispersal distributions at multiple scales: within-colony  
469 and among-colony dispersal rates, distances and directions in European Shags  
470 *Phalacrocorax aristotelis*. — *Ibis* 155: 762-778.
- 471 Borchers, D. and Fewster, R. 2016. Spatial Capture-Recapture Models. — *Statist. Sci.* 31: 219-  
472 232.
- 473 Boulinier, T. et al. 1996. Timing of prospecting and the value of information in a colonial  
474 breeding bird. — *J. Avian Biol.* 27: 252-256.
- 475 Boulinier, T. et al. 2008. Public information affects breeding dispersal in a colonial bird:  
476 kittiwakes cue on neighbours. — *Biol. Lett.* 4: 538-540.
- 477 Burnham, K. P. and Anderson, D. R. (eds.) 2002. Model selection and multimodel inference: a  
478 practical information-theoretic approach. — Springer.
- 479 Cadiou, B. et al. 1994. Prospecting in the kittiwake, *Rissa tridactyla*: different behavioural  
480 patterns and the role of squatting in recruitment. — *Anim. Behav.* 47: 847-856.
- 481 Catlin, D. H. et al. 2005. The effects of nesting success and mate fidelity on breeding dispersal  
482 in burrowing owls. — *Canadian Journal of Zoology* 83: 1574-1580.
- 483 Chambert, T. et al. 2012. Heterogeneity in detection probability along the breeding season in  
484 Black-legged Kittiwakes: implications for sampling design. — *Journal of Ornithology*  
485 152: 371-380.
- 486 Choquet, R. et al. 2009a. U-CARE: Utilities for performing goodness of fit tests and  
487 manipulating CApture-REcapture data. — *Ecography* 32: 1071-1074.

**Ponchon, Aurore; Choquet, Rémi; Tornos, Jérémy; McCoy, Karen D.; Tveraa, Torkild; Boulinier, Thierry.**

Survival estimates strongly depend on capture-recapture designs in a disturbed environment inducing dispersal. *Ecography* 2018 ;Volum 41.

DOI [10.1111/ecoq.03334](https://doi.org/10.1111/ecoq.03334)



- 488 Choquet, R. et al. 2004. M-SURGE: new software specifically designed for multistate capture-  
489 recapture models. — *Anim. Biodivers. Conserv.* 27: 207-215.
- 490 Choquet, R. et al. 2009b. Program E-Surge: software application for fitting multievent models.  
491 — In: Thomson, D. et al. (eds), *Modeling demographic processes in marked*  
492 *populations*. Springer US, pp. 845-865.
- 493 Choquet, R. et al. 2013. Estimating demographic parameters from capture–recapture data with  
494 dependence among individuals within clusters. — *Methods in Ecology and Evolution*  
495 4: 474-482.
- 496 Cilimburg, A. B. et al. 2002. Effects of dispersal on survival probability of adult yellow  
497 warblers (*Dendroica petechia*). — *The Auk* 119: 778-789.
- 498 Coulson, J. C. 2011. *The kittiwake*. — T & AD Poyser.
- 499 Crespin, L. et al. 2008. Is heterogeneity of catchability in capture–recapture studies a mere  
500 sampling artifact or a biologically relevant feature of the population? — *Popul. Ecol.*  
501 50: 247-256.
- 502 Danchin, E. et al. 1998. Conspecific reproductive success and breeding habitat selection:  
503 implications for the study of coloniality. — *Ecology* 79: 2415-2428.
- 504 Danchin, E. and Monnat, J. Y. 1992. Population dynamics modelling of two neighbouring  
505 Kittiwake *Rissa tridactyla* colonies. — *Ardea* 80: 171-180.
- 506 Devineau, O. et al. 2006. Planning Capture–Recapture studies: straightforward precision, bias,  
507 and power calculations. — *Wildl. Soc. Bull.* 34: 1028-1035.

**Ponchon, Aurore; Choquet, Rémi; Tornos, Jérémy; McCoy, Karen D.; Tveraa, Torkild; Boulinier, Thierry.**

Survival estimates strongly depend on capture–recapture designs in a disturbed environment inducing dispersal. *Ecography* 2018 ;Volum 41.

DOI [10.1111/ecoq.03334](https://doi.org/10.1111/ecoq.03334)



- 508 Ergon, T. and Gardner, B. 2014. Separating mortality and emigration: modelling space use,  
509 dispersal and survival with robust-design spatial capture–recapture data. — *Methods in*  
510 *Ecology and Evolution* 5: 1327-1336.
- 511 Fernández-Chacón, A. et al. 2013. When to stay, when to disperse and where to go: survival  
512 and dispersal patterns in a spatially structured seabird population. — *Ecography* 36:  
513 1117-1126.
- 514 Field, S. A. et al. 2005. Optimizing allocation of monitoring effort under economic and  
515 observational constraints. — *J. Wildl. Manage.* 69: 473-482.
- 516 Fletcher, D. et al. 2012. Bias in estimation of adult survival and asymptotic population growth  
517 rate caused by undetected capture heterogeneity. — *Methods in Ecology and Evolution*  
518 3: 206-216.
- 519 Forero, M. G. et al. 1999. Causes and consequences of territory change and breeding dispersal  
520 distance in the Black Kite. — *Ecology* 80: 1298-1310.
- 521 Frederiksen, M. et al. 2005a. Inter-population variation in demographic parameters: a neglected  
522 subject? — *Oikos* 111: 209-214.
- 523 Frederiksen, M. et al. 2005b. Regional patterns of kittiwake *Rissa tridactyla* breeding success  
524 are related to variability in sandeel recruitment. — *Mar. Ecol. Prog. Ser.* 300: 201-211.
- 525 Gimenez, O. and Choquet, R. 2010. Individual heterogeneity in studies on marked animals  
526 using numerical integration: capture-recapture mixed models. — *Ecology* 91: 951-957.
- 527 Grosbois, V. et al. 2008. Assessing the impact of climate variation on survival in vertebrate  
528 populations. — *Biological Reviews* 83: 357-399.

**Ponchon, Aurore; Choquet, Rémi; Tornos, Jérémy; McCoy, Karen D.; Tveraa, Torkild; Boulinier, Thierry.**

Survival estimates strongly depend on capture–recapture designs in a disturbed environment inducing dispersal. *Ecography* 2018 ;Volum 41.

DOI [10.1111/ecoq.03334](https://doi.org/10.1111/ecoq.03334)



- 529 Grosbois, V. et al. 2009. Modeling survival at multipopulation scales using capture-mark-  
530 recapture data. — Ecology 90: 2922-2932.
- 531 Horton, G. E. and Letcher, B. H. 2008. Movement patterns and study area boundaries:  
532 influences on survival estimation in capture-mark-recapture studies. — Oikos 117:  
533 1131-1142.
- 534 Hurley, V. G. et al. 2013. Techniques for optimising long-term, large-scale capture-mark-  
535 resighting raptor studies: climb hard, band fast. — Wildl. Res. 40: 269-280.
- 536 Kendall, W. L. et al. 2013. Combining dead recovery, auxiliary observations and robust design  
537 data to estimate demographic parameters from marked individuals. — Methods in  
538 Ecology and Evolution 4: 828-835.
- 539 Kendall, W. L. et al. 2009. Sampling design considerations for demographic studies: a case of  
540 colonial seabirds. — Ecol. Appl. 19: 55-68.
- 541 Kendall, W. L. et al. 1997. Estimating temporary emigration using capture-recapture data with  
542 Pollock's robust design. — Ecology 78: 563-578.
- 543 Krasnov, Y. V. et al. 2007. Status of black-legged kittiwakes (*Rissa tridactyla*), common  
544 guillemots (*Uria aalge*) and Brünnich's guillemots (*U. lomvia*) in Murman, north-west  
545 Russia, and Varanger, north-east Norway. — Polar Res. 26: 113-117.
- 546 Lahoz-Monfort, J. J. et al. 2014. Exploring the consequences of reducing survey effort for  
547 detecting individual and temporal variability in survival. — J. Appl. Ecol. 51: 534-543.
- 548 Lane, J. E. et al. 2012. Delayed phenology and reduced fitness associated with climate change  
549 in a wild hibernator. — Nature 489: 554-557.

**Ponchon, Aurore; Choquet, Rémi; Tornos, Jérémy; McCoy, Karen D.; Tveraa, Torkild; Boulinier, Thierry.**

Survival estimates strongly depend on capture-recapture designs in a disturbed environment inducing dispersal. *Ecography* 2018 ;Volum 41.

DOI [10.1111/ecoq.03334](https://doi.org/10.1111/ecoq.03334)



- 550 Langtimm, C. A. 2009. Non-random temporary emigration and the robust design: conditions  
551 for bias at the end of a time series. — In: Thomson, D. L. et al. (eds), Modeling  
552 Demographic Processes In Marked Populations. Springer US, pp. 745-761.
- 553 Lebreton, J. D. et al. 1992. Modeling survival and testing biological hypothesis using marked  
554 animals: a unified approach with case study. — *Ecol. Monogr.* 62: 67-118.
- 555 Lebreton, J. D. et al. 2003. Estimation by capture-recapture of recruitment and dispersal over  
556 several sites. — *Oikos* 101: 253-264.
- 557 Lindberg, M. S. 2012. A review of designs for capture-mark-recapture studies in discrete time.  
558 — *Journal of Ornithology* 152: 355-370.
- 559 Marshall, M. R. et al. 2004. Annual survival estimation of migratory songbirds confounded by  
560 incomplete breeding site-fidelity: study designs that may help. — *Anim. Biodivers.*  
561 *Conserv.* 27: 59-72.
- 562 Moyes, K. et al. 2011. Advancing breeding phenology in response to environmental change in  
563 a wild red deer population. — *Global Change Biol.* 17: 2455-2469.
- 564 Naves, L. C. et al. 2006. Breeding performance, mate fidelity, and nest site fidelity in a long-  
565 lived seabird: behaving against the current? — *Oikos* 115: 263-276.
- 566 Nichols, J. D. and Williams, B. K. 2006. Monitoring for conservation. — *Trends Ecol. Evol.*  
567 21: 668-673.
- 568 Oro, D. and Furness, R. W. 2002. Influences of food availability and predation on survival of  
569 kittiwakes. — *Ecology* 83: 2516-2528.
- 570 Öst, M. et al. 2011. Causes and consequences of fine-scale breeding dispersal in a female-  
571 philopatric species. — *Oecologia* 166: 327-336.

**Ponchon, Aurore; Choquet, Rémi; Tornos, Jérémy; McCoy, Karen D.; Tveraa, Torkild; Boulmier, Thierry.**

Survival estimates strongly depend on capture-recapture designs in a disturbed environment inducing dispersal. *Ecography* 2018 ;Volum 41.

DOI [10.1111/ecoq.03334](https://doi.org/10.1111/ecoq.03334)



- 572 Paredes, R. et al. 2014. Foraging responses of black-legged kittiwakes to prolonged food-  
573 shortages around colonies on the Bering Sea shelf. — PLoS ONE 9: e92520.
- 574 Peñaloza, C. L. et al. 2014. Reducing bias in survival under nonrandom temporary emigration.  
575 — Ecol. Appl. 24: 1155-1166.
- 576 Pledger, S. and Phillpot, P. 2008. Using mixtures to model heterogeneity in ecological capture-  
577 recapture studies. — Biometrical Journal 50: 1022-1034.
- 578 Pledger, S. et al. 2003. Open capture-recapture models with heterogeneity: I. Cormack-Jolly-  
579 Seber Model. — Biometrics 59: 786-794.
- 580 Ponchon, A. et al. 2017a. Spatial overlaps of foraging and resting areas of black-legged  
581 kittiwakes breeding in the English Channel with existing marine protected areas. —  
582 Mar. Biol. 164: 119.
- 583 Ponchon, A. et al. 2015a. Breeding failure induces large scale prospecting movements in the  
584 back-legged kittiwake. — J. Exp. Mar. Biol. Ecol. 473: 138-145.
- 585 Ponchon, A. et al. 2015b. Predicting population responses to environmental change: the  
586 importance of considering informed dispersal strategies in spatially structured  
587 population models. — Divers. Distrib. 21: 88-100.
- 588 Ponchon, A. et al. 2014. When things go wrong: intra-season dynamics of breeding failure in a  
589 seabird. — Ecosphere 5: Art. 4.
- 590 Ponchon, A. et al. 2013. Tracking prospecting movements involved in breeding habitat  
591 selection: insights, pitfalls and perspectives. — Methods in Ecology and Evolution 4:  
592 143-150.

**Ponchon, Aurore; Choquet, Rémi; Tornos, Jérémy; McCoy, Karen D.; Tveraa, Torkild; Boulinier, Thierry.**

Survival estimates strongly depend on capture–recapture designs in a disturbed environment inducing dispersal. *Ecography* 2018 ;Volum 41.

DOI [10.1111/ecoq.03334](https://doi.org/10.1111/ecoq.03334)



- 593 Ponchon, A. et al. 2017b. Intense prospecting movements of failed breeders nesting in an  
594 unsuccessful breeding subcolony. — *Anim. Behav.* 124: 183-191.
- 595 Pradel, R. 1993. Flexibility in survival analysis from recapture data: handling trap-dependence.  
596 — In: Lebreton, J. D. and North, P. M. (eds), *Marked individuals in the study of bird*  
597 *population*. pp. 29-37.
- 598 Pradel, R. 2005. Multi-event: an extension of multistate Capture-Recapture models to uncertain  
599 stats. — *Biometrics* 61: 442-447.
- 600 Reiertsen, T. K. et al. 2014. Prey density in non-breeding areas affects adult survival of Black-  
601 legged Kittiwakes *Rissa tridactyla*. — *Mar. Ecol. Prog. Ser.* 509: 289-302.
- 602 Sæther, B.-E. and Bakke, Ø. 2000. Avian life history variation and contribution of demographic  
603 traits to the population growth rate. — *Ecology* 81: 642-653.
- 604 Sandvik, H. et al. 2005. The effect of climate on adult survival in five species of North Atlantic  
605 seabirds. — *J. Anim. Ecol.* 74: 817-831.
- 606 Sanz-Aguilar, A. et al. 2016. Estimating recruitment and survival in partially-monitored  
607 populations. — *J. Appl. Ecol.* 53: 73-82.
- 608 Sanz-Aguilar, A. et al. 2010. Recapture processes and biological inference in monitoring  
609 burrow-nesting seabirds. — *Journal of Ornithology* 151: 133-146.
- 610 Schaub, M. et al. 2004. Estimating survival and temporary emigration in the multistate capture-  
611 recapture framework. — *Ecology* 85: 2107-2113.
- 612 Stearns, S. C. 1976. Life history tactics: a review of ideas. — *Q. Rev. Biol.* 51: 3-47.
- 613 Tavecchia, G. et al. 2016. Climate-driven vital rates do not always mean climate-driven  
614 population. — *Global Change Biol.* n/a-n/a.

**Ponchon, Aurore; Choquet, Rémi; Tornos, Jérémy; McCoy, Karen D.; Tveraa, Torild;  
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inducing dispersal. *Ecography* 2018 ;Volum 41.

DOI [10.1111/ecoq.03334](https://doi.org/10.1111/ecoq.03334)



615 Taylor, C. M. et al. 2015. Using local dispersal data to reduce bias in annual apparent survival  
616 and mate fidelity. — *The Condor* 117: 598-608.

617 Tyre, A. J. et al. 2003. Improving precision and reducing bias in biological surveys: estimating  
618 false-negative error rates. — *Ecol. Appl.* 13: 1790-1801.

619 Walther, G. R. et al. 2002. Ecological responses to recent climate change. — *Nature* 416: 389-  
620 395.

621 Williams, B. K. et al. (eds.) 2002. Analysis and management of animal populations. —  
622 Academic Press.

623 Zimmerman, G. S. et al. 2007. Finite study areas and vital rates: sampling effects on estimates  
624 of spotted owl survival and population trends. — *J. Appl. Ecol.* 44: 963-971.

625

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626 **Table 1:** Goodness-of-fit tests of the Cormack-Jolly-Seber model for each field-based dataset.

627 Significant chi-square statistics ( $p < 0.05$ ) reflecting model assumption violations are in bold.

628

	Single-site dataset			Multi-site dataset without BA			Multi-site dataset with BA		
	$\chi^2$	$df$	$p$	$\chi^2$	$df$	$p$	$\chi^2$	$df$	$p$
Goodness of fit components									
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	<b>0.0019</b>	421.9	7	<b>&lt;0.001</b>	278.0	7	<b>&lt;0.001</b>
Test 2.CL	0	4	1	17.5	7	<b>0.014</b>	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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631 **Table 2:** Most parsimonious models selected based on QAICc for each of the three datasets.

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

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

634

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

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

638

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

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

645

Design	Model	Number of parameters	Deviance	QAIC	QAICc
Single-site (Multistate with an unobservable state)	<b>s(i)T(i)p(i)</b>	<b>4</b>	<b>812.28</b>	<b>820.28</b>	<b>820.38</b>
	<b>s(slope)T(i)p(i)</b>	<b>5</b>	<b>810.69</b>	<b>820.69</b>	<b>820.84</b>
	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)	<b>s(i), p(i)</b>	<b>2</b>	<b>828.06</b>	<b>832.06</b>	<b>832.09</b>
	<b>s(slope), p(i)</b>	<b>3</b>	<b>826.38</b>	<b>832.38</b>	<b>832.44</b>
	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)	<b>s(slope), p(i)</b>	<b>3</b>	<b>1488.34</b>	<b>1494.33</b>	<b>1494.36</b>
	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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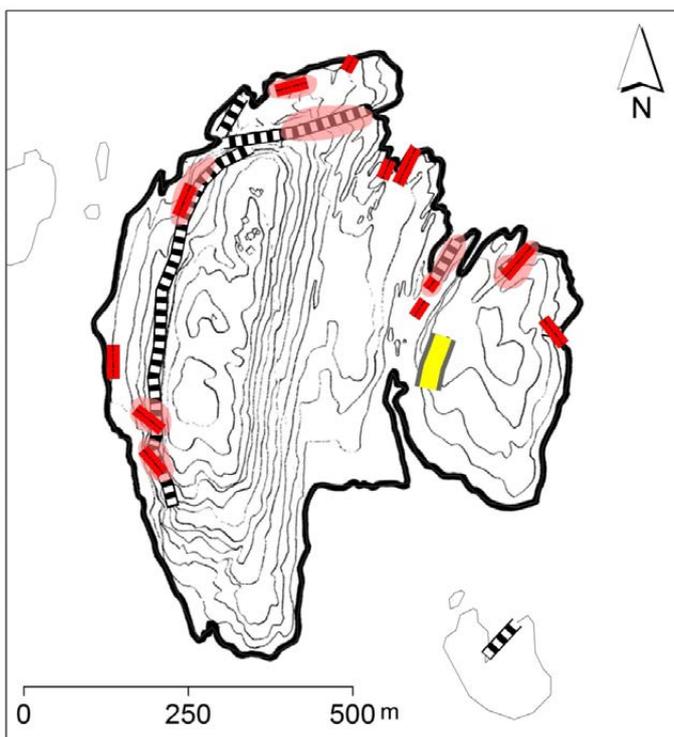
DOI [10.1111/ecoq.03334](https://doi.org/10.1111/ecoq.03334)



648 **Figures**

649 **Figure 1:** Map of the different areas included in the single-site (thick yellow line) and multi-  
650 site (red lines) designs. All kittiwake nesting cliffs are represented by striped black and white  
651 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.  
 660

	Full dataset	Reduced dataset	
<b>Scenario 1:</b> Constant survival and dispersal rates tested	Single-site + BA design 	Single-site design 	
<b>Scenario 2:</b> Constant survival; different local and regional dispersal rates tested	Three sites design 	Single-site + BA design 	Single-site design 
<b>Scenario 3:</b> Decreasing survival and constant local dispersal rate tested	Single-site + BA design 	Single-site design 	

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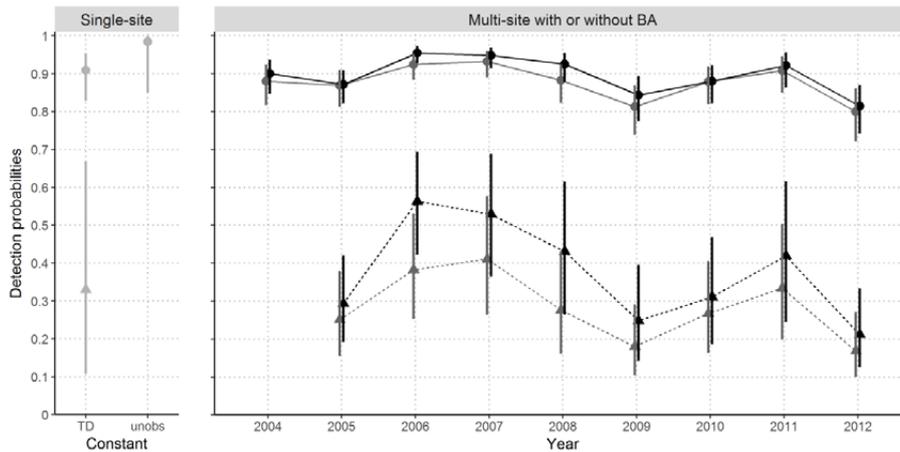
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662 **Figure 3:** Detection probabilities and associated 95% confidence intervals estimated from the  
 663 best selected models for the single-site field-based dataset analyzed with a trap-dependent  
 664 model (TD) and a multistate model with an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



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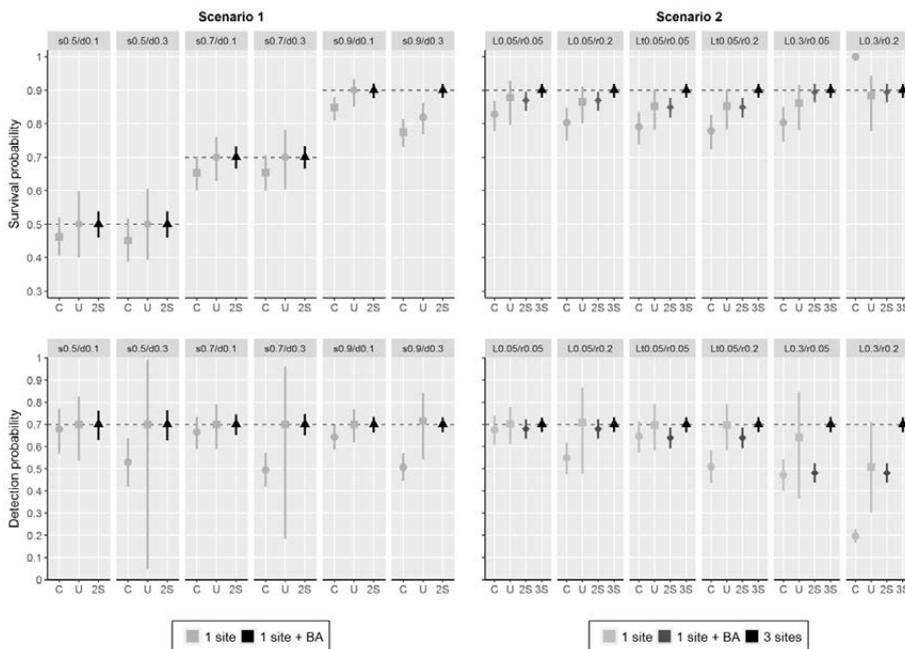
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672 **Figure 4:** Estimates of survival (upper panel) and detection probabilities (lower panel) for a  
 673 combination of survival and dispersal values. In scenario 1 (left panel), we tested how  
 674 different survival ( $s$ ) and dispersal ( $d$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



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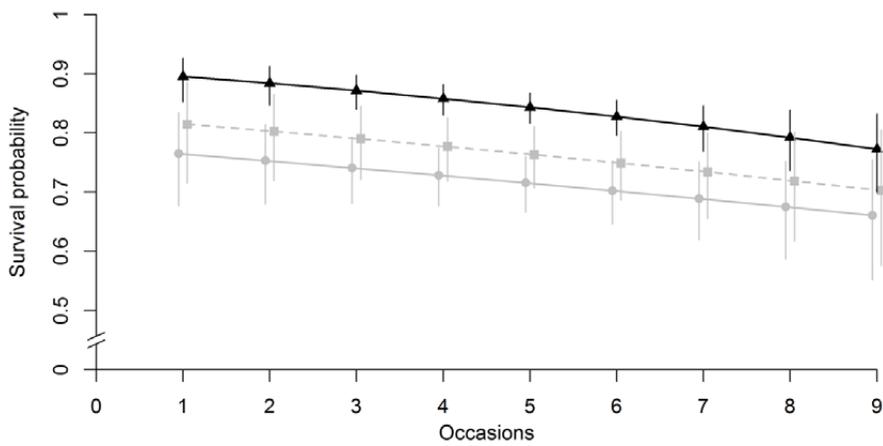
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686 **Figure 5:** Annual survival probabilities estimated from the best ranked-model for Scenario 3,  
 687 implemented with a fixed dispersal rate of 0.3 and a time-dependent survival probability,  
 688 decreasing from 0.9 to 0.75. Light grey points 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
<b>Multi-site+BA</b>	<b>s(i)p(a+t)</b>	<b>12</b>	<b>3980.90</b>	<b>3183.44</b>	<b>3183.50</b>
	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
<b>Trap-dependent model</b>	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
<b>Multi-site without BA</b>	<b>s(i)p(a+t)</b>	<b>12</b>	<b>3925.18</b>	<b>2953.24</b>	<b>2953.30</b>
	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
<b>Trap-dependent model</b>	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
<b>Single-site</b>	<b>s(i)p(a)</b>	<b>4</b>	<b>406.60</b>	<b>414.60</b>	<b>414.67</b>
	s(i)p(a+t)	12	397.61	421.61	422.18
	s(t)p(a)	12	400.73	424.73	425.30
	s(i)p(a.t)	19	391.85	429.85	431.25
<b>Trap-dependent model</b>	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
<b>Single-site</b>	<b>s(i)T(i)p(i)</b>	<b>4</b>	<b>407.62</b>	<b>415.62</b>	<b>415.75</b>
	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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<b>Multistate model with an unobservable state</b>	*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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