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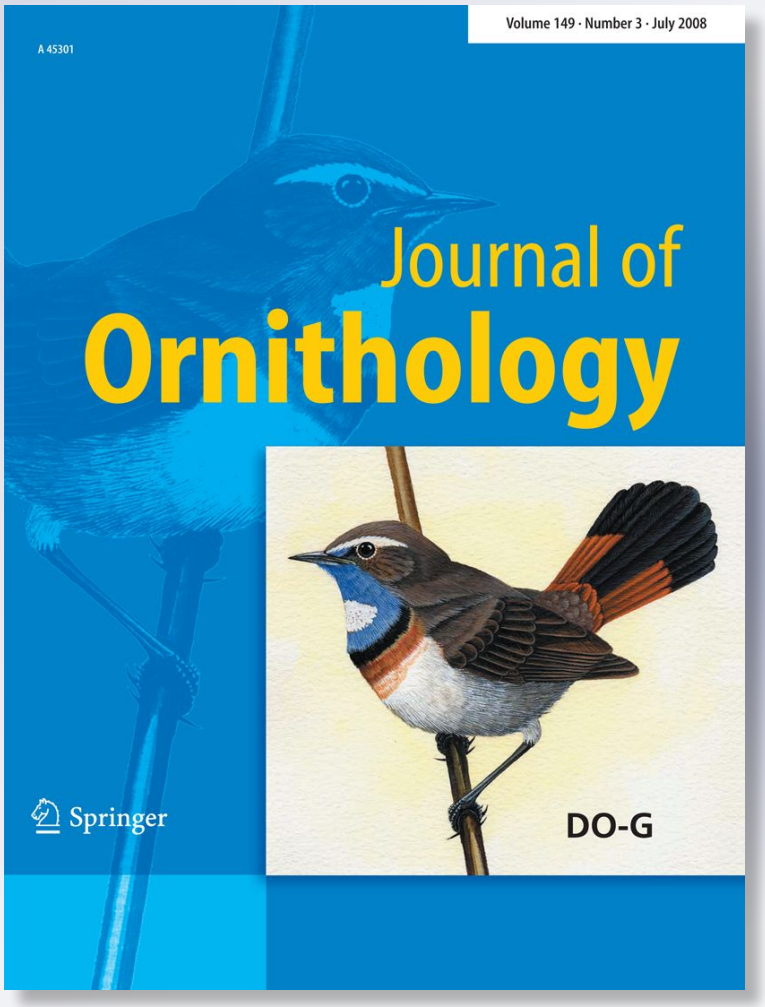

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ORIGINAL ARTICLE

Modelling state uncertainty with photo series data for the estimation of breeding success in a cliff-nesting seabird

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Abstract Breeding success in cliff-nesting seabirds has until now been estimated through repeated nest checks by field workers during the breeding season. The use of automatic cameras offers a method for collecting mark–recapture data that can be modelled in order to estimate productivity without making recurring inspections. This saves expense and work hours in the field and allows for more colonies to be monitored. Capture histories for Brünnich's Guillemot *Uria lomvia* breeding sites in a colony on Svalbard were generated using a series of photos taken by a time-lapse camera during the breeding season. To account for state uncertainty for the offspring when only the adult could be observed on the breeding site, we applied a multievent model. We estimated egg survival, hatching success and chick survival rates by modelling state transitions. Subsequently, the estimates were used to calculate breeding success. In order to assess the performance of the model, we compared the estimates with field observations of productivity. The observed breeding success in the study plot lay within the confidence intervals of the breeding success estimated by our model. We show that automatic cameras can be used to collect data which, by the application of new modelling techniques, will provide reliable estimates of demographic parameters that are vital for research and management of cliff-nesting birds. The method presented is a very good supplement to physical examination or "manual" around-the-clock monitoring of breeding birds.

Keywords Mark–recapture · *Uria lomvia* · Survival · Time-lapse photography · Reproduction

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Introduction

Seabird population dynamics are highly sensitive to the annual survival rate of breeders, but breeding success is an equally important component of seabird monitoring programs because it can be highly variable in space and time, and because it can be readily measured by repeated surveys of land-based colonies. Breeding success is generally defined as the number of chicks surviving to fledging age divided by the number of eggs initially laid (Walsh et al. 1995). In populations breeding in high densities on inaccessible cliff ledges, conventional methods to estimate breeding success imply long-lasting nest checks in the colony every other day during the breeding season. This is a tedious task which requires rather large amounts of resources in terms of work-hours, lodging and support elements, especially in remote colonies. Automatic cameras offer an alternative way to monitor bird colonies and obtain data for demographic studies. A camera can be mounted on almost any spot from which a field worker would otherwise observe the colony or a segment of it. By examining a range of successive photos, it is possible to follow the development on the nests in the study plot throughout the breeding season. Hence, the photos represent capture occasions, and individual capture histories can be formed from the observations made for each nest. Demographic parameters can thereby be estimated within the framework of mark–recapture (MR) modelling. If one

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is able to observe absence and presence of eggs and chicks, hatching success and chick survival rate can be estimated as state transitions by using multistate modelling (Arnason 1973; Schwarz et al. 1993). However, a photo will not necessarily reveal the true state of the egg or chick in a nest. This is the case for the Brünnich's Guillemot *Uria lomvia* (Linnaeus), a colonial seabird breeding on narrow ledges in steep cliffs between 46 and 82°N (Nettleship and Evans 1985). Guillemot pairs do not build nests, but place their single egg directly on a chosen spot (hereafter termed "breeding site") on the ledge. They brood the offspring almost continuously and always stand between it and the edge of the ledge. Adult birds will also frequently continue to occupy the breeding site even after the egg or chick is lost. Therefore, it is often uncertain whether the egg has hatched and, if so, whether the chick is alive or dead. We model this state uncertainty by applying the recently developed multievent model (Pradel 2005) to MR data for Brünnich's Guillemot breeding sites.

The baseline for modelling survival and state transition parameters is the creation of individual capture histories by marking and recapturing or resighting animals through time (Lebreton et al. 1992). Multistate mark–recapture models allow us to estimate the probability of transition between states, provided that we are able to assign the study objects to a state whenever they are detected (Arnason 1973; Schwarz et al. 1993). In the case of the Brünnich's Guillemots, the state is unknown every time the adult prevents us from seeing if the breeding site is empty or if it holds an egg or a chick. Several approaches to address uncertainty about an animal's state upon detection have been developed over the recent years (e.g. Kendall et al. 2003; Pradel 2005; Nichols et al. 2007). In this study, we consider the general framework of Pradel's (2005) multievent model, which is the most adequate model to address our problem because it allows us to follow the breeding site rather than the individual. Note that as, in our case, any breeding site starts at the first occasion, this framework is equivalent to the framework of multistate occupancy models with imperfect detection (MacKenzie et al. 2009). Under the multievent model design, the objects of interest—the breeding sites—are assumed to move independently over a finite set N of states through a finite number K of sampling occasions. However, the state of the object is not necessarily observed directly. Instead, at each occasion, the investigator records an event that is expected to reflect the underlying state to some extent. Observing a Brünnich's Guillemot chick on a breeding site will always imply that the chick is alive. If the site is completely empty, or if one can see an adult which clearly has no chick, the chick has certainly died, so both these observations are directly consistent with the offspring being lost. And finally, one can also observe an adult without being able to tell whether it has a chick or not. By including observations of adults in the data, we contribute information that can be utilised in the modelling process. This way, even capture histories consisting solely of observations of adults can be included in the dataset. State transition estimates will thereby become more precise and representative of the study plot. Additionally, including the egg-stage in the dataset will allow the direct estimation of egg-survival and hatching success.

We present parameter estimates of egg survival, hatching success and chick survival produced by the multievent model using photo series data from a Brünnich's Guillemot colony on Svalbard. As a by-product, we calculate the probability of breeding success and compare the result with field observations of productivity for the study plot.

Methods

Photo sampling and data preparation

During the breeding season of 2007, we captured a series of photos of a segment (plot) of the Ossian Sarsfjell colony (78°56′N, 12°27′E) on Spitsbergen, the largest island of the Svalbard archipelago in the Barents Sea. A CamTrakker® automatic time-lapse camera system (CamTrak South, Watkinsville, USA) was used to take one photo every 4 h from the end of the incubation period to the start of fledging. The camera was fixed facing the study plot from the other side of a ravine in the cliff. From this point, the ledges could be viewed from above and slightly from the side, and the distance from the camera to the centre of the study plot was 28 m. The camera zoom was set for the photos to include as many breeding sites as possible, and at the same time allow a reasonable chance of any chick to be distinguished.

Following the method used by Gaston et al. (1994), we assumed that all resting-positions that were occupied by a sitting adult on every photo over a 5-day interval (30 occasions) at the end of the incubation period (27 June–1 July) were active breeding sites. "Sitting" here refers to the position a Guillemot needs to keep in order to hold an egg in place underneath it. A total of 62 active sites were identified, representing the number of pairs that attempted breeding and containing one egg each at 1 July. This date was therefore the first sampling session, for which we fixed the state of all the 62 breeding sites to "egg" in the modelling process. Since egg loss may clearly occur in the early stages of the incubation period, some of these sites may potentially have been held by breeders that had lost their first egg, but still continued to occupy their breeding sites. Consequently, we might have included empty sites

among those we assumed to have an egg, the implications of which will be discussed later. Five more sampling sessions were chosen (10, 13, 15, 20 and 23 July). Based on field observations, we expected most eggs to be hatched by 10 July, in other words between the first two sampling sessions. The mean duration of the chick-rearing period for Brünnich's Guillemots is 21 days, and the main bulk of the chicks fledge within a period of 3–6 days (Gaston and Nettleship 1981; Strøm 2006). Very few chicks were therefore expected to have departed by the last session, which was 13 days after most eggs were assumed to have hatched.

In order to increase detection probability, six photos from each of the 5 days were thoroughly examined and later pooled to give one observation per session. For each breeding site, one of the following events was recorded:

1 = adult (presence of egg or chick is uncertain),
2 = chick (certain observation that the chick is present),
3 = empty (certain observation that egg or chick is absent).

Since we assumed that there was an egg on each breeding site at the beginning of the study, although no egg was directly observed, we implemented the egg-state on the first session by entering a "1" as the first recording in each capture history. To account for individual heterogeneity in detection probability, the breeding sites were separated into two groups according to expected degree of chick visibility. Twelve breeding sites that were partly hidden in crevices or behind rocks or neighbouring birds constituted the "low-visibility sites", whereas the rest (50) were treated as "high-visibility sites".

In order to obtain a measure of breeding success comparable to the output from the multievent model, we checked the contents of the 62 active breeding sites on the last sampling session. The ledges were observed through binoculars at a distance of 12–14 m from the other side of the narrow ravine while a rope was lowered down to the breeding sites from the top of the cliff to make the brooding parents move and reveal any chicks. This approach is assumed to have given a slightly low biased number of remaining chicks, seeing that some chicks might have been missed during the search. The observed breeding success given in the results should therefore be regarded as a minimum.

Multievent modelling

The multievent model uses a set of parameters to calculate the probabilities of any encounter history (Pradel 2005):

- $\varphi_{ij,t}$, the probability of being in state e_j at time $t+1$ if in state e_i at time t,
- $\pi_{i,t}$, the probability of being in state e_i when first detected at time t,
- $b_{uj,t}$, the probability of event v_u for an animal in state e_j at time t,
- $b^0_{uj,t}$, the probability of event v_u given the state e_j at time t for an animal encountered for the first time at t, i.e. $Pr(v_u|e_j$ and "first encountered at t").

The matrices ϕ and B are associated with parameters of transitions and events, respectively.

To estimate hatching and survival rates for the Brünnich's Guillemot chicks, we considered the three states "egg", "chick" and "dead". An estimate of hatching success would then be given by the probability of moving from the egg-state to the chick-state, whereas survival rate would be consistent with the probability of staying in state "chick". In order to estimate hatching success conditional on survival, we decomposed state transitions into two steps. The "step one" transition matrix

$$\varphi^S = \begin{pmatrix} \varphi^{\text{egg,egg}} & 0 & (1-\varphi^{\text{egg,egg}}) \\ 0 & \varphi^{\text{chick,chick}} & (1-\varphi^{\text{chick,chick}}) \\ 0 & 0 & 1 \end{pmatrix}$$

models survival of eggs and chicks between two occasions. Rows correspond to states of departure, and columns represent states of arrival, both in the order "egg", "chick" and "dead". The "step two" transition matrix

$$\varphi^H = \begin{pmatrix} (1-\varphi^{\text{egg,chick}}) & \varphi^{\text{egg,chick}} & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

models the hatching probability. The event matrix was set to

$$B = \begin{pmatrix} 0 & 1 & 0 & 0 \\ 0 & (1-b_{\text{chick|chick}}) & b_{\text{chick|chick}} & 0 \\ 0 & (1-b_{\text{dead|empty}}) & 0 & b_{\text{dead|empty}} \end{pmatrix},$$

where rows correspond to states as before, and columns represent events. The event "not observed" is always included in the matrix (column 1), but it is redundant here since all breeding sites were always checked. Columns 2, 3 and 4 correspond to the events "adult", "chick" and "empty", respectively. By applying this matrix, one will estimate the probability of observing a chick given it is on the site ($b_{\text{chick|chick}}$ = chick detection probability), and the probability of observing that a site is empty, meaning that the chick is certainly dead ($b_{\text{dead|empty}}$). As noted above, the egg-state can only have the event "adult". Since all the breeding sites contained an egg at the first encounter, only the parameters $\pi_{i,1}$ and $b^0_{uj,1}$ are present in the likelihood, and the probability of being in the egg-state at first encounter ($\pi_{\text{egg},1}$) was set to 1. In order to get estimates of daily hatching and survival rates, the lengths of the time

intervals were specified. All modelling was performed with program E-SURGE (Choquet et al. 2009).

Model selection

Instead of testing a variety of competing models, we chose to run the relatively simple model ($\varphi^{S}_{f\cdot t[1,2345]}$, $\varphi^{H}_{t[1,2345]}$, $b_{f\cdot[g+t(234,56)]}$) with parameterisations based mainly on the conclusions from Gaston and Nettleship's (1981) thorough studies of Brünnich's Guillemots at Prince Leopold Island. They found that the rate of egg loss decreased over most of the incubation period. Since the first time interval in our dataset covered the end of incubation and the start of chick-rearing for most breeding sites, we found it reasonable to allow egg survival to differ between time intervals 1 and 2, and to estimate a constant survival rate thereafter. Chick mortality can be expected to be higher in the first couple of days after hatching than in the rest of the chick-rearing period. We did not expect this difference to be detectable in our study, because only the estimates of daily chick survival for time intervals 2 through 5 would be used for the purpose of breeding success estimation (see "Appendix"). By interval two, we assumed that chick survival rates would have stabilised on a level that remain roughly constant for the rest of the chick-rearing period. Consequently, we did not model temporal change in survival rates after time interval 1. Hatching success was set to differ between time interval 1 and the rest of the study period on the basis that most eggs were expected to hatch during the first time interval.

It was reasonable to assume that the chicks would become gradually more visible as they grew older. However, in order to keep the model simple, we did not allow full time-dependence in detection rates. At sessions 2 through 4, the event probability was kept constant. A difference was modelled between sessions 4 and 5, after which it was constant for sessions 5 and 6. We presumed that this temporal change in detection probability would be equal for the two groups of sites. Thus, an additive effect between group and time was modelled.

With the parameter estimates from the model, we were able to compute an estimate of breeding success by applying the equations presented in "Appendix". The variance of the estimated breeding success was approximated by using the delta method (Williams et al. 2002). All estimates are presented with confidence intervals (CI) as measures of variation.

Results

As expected, the probability of detecting a chick ($\hat{b}_{\text{chick|chick}}$) was estimated to be low on the first sampling sessions and higher towards the end of the chick-rearing period (Fig. 1). For the group of sites where chick detection rate was expected to be lower, the estimated probability of observing an empty nest appeared to have hit the upper boundary [$\hat{b}_{\text{dead|empty}} = 0.999$, CI = (0.000, 1.000)]. The estimated daily egg survival rate (transition $\hat{\varphi}^{\text{egg,egg}}$) in the first time interval was 0.988 [CI = (0.971, 0.995)], and this rate did not change after sampling session 2, which was also according to expectations (Fig. 2). Hatching probability ($\hat{\varphi}^{\text{egg,chick}}$) was significantly higher in the first time interval than in the remainder of the period. The estimated daily chick survival rate ($\hat{\varphi}^{\text{chick,chick}}$) from 10 to 23 July was 0.994 [CI = (0.976, 0.998)] (Fig. 2). Using the estimated egg survival, hatching success and chick survival for the different time intervals, we estimated breeding success to be 0.552 [CI = (0.435, 0.669)].

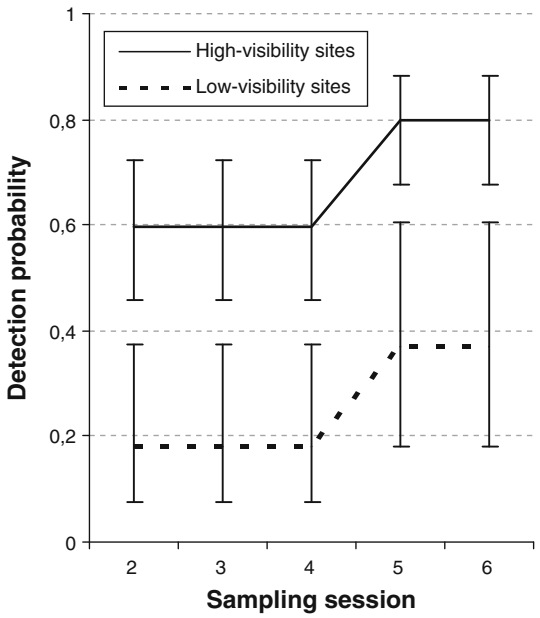

Fig. 1 Estimated probabilities of detecting a chick on high- and low-visibility Brünnich's Guillemot *Uria lomvia* breeding sites in a Svalbard colony over 5 sampling sessions in 2007. Estimates are derived from multievent model ($\varphi^{S}_{f\cdot t(1,2345)}$, $\varphi^{H}_{t(1,2345)}$, $b_{f\cdot[g+t(234,56)]}$). *Error bars* are 95% confidence intervals, and time between the sampling sessions is 3, 2, 5 and 3 days, respectively. The number of capture histories $n = 62$

Close-range inspections of the study plot on the last capture occasion revealed that of all 62 breeding sites identified there were 27 that had a living chick. This yields a breeding success of 0.435, which is at the lower limit of the confidence interval of the estimators from the multievent model. Considering that the chick counts in the field on the last sampling session might have been incomplete, meaning that in reality the breeding success was likely somewhat higher than 0.435, this is a very encouraging result.

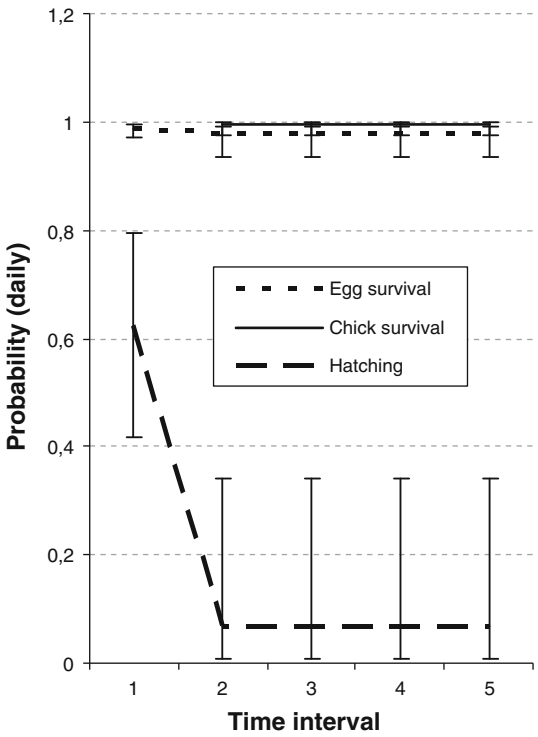

Fig. 2 Estimated daily probabilities of egg survival, chick survival and hatching for Brünnich's Guillemots *Uria lomvia* in a Svalbard colony over 5 time intervals from 1 to 23 July in the 2007 breeding season. Estimates are derived from multievent model ($\varphi^{S}_{f\cdot t[1,2345]}$, $\varphi^{H}_{t[1,2345]}$, $b_{f\cdot[g+t(2345,6)]}$). *Error bars* are 95% confidence intervals, and time intervals are 9, 3, 2, 5 and 3 days long, respectively. The number of capture histories $n = 62$

Discussion

By applying a multievent model to estimate state transition probabilities while accounting for uncertainty of state for Brünnich's Guillemot breeding sites, we were able to produce an estimate of breeding success that corresponded with the breeding success observed for the study plot.

The point estimate derived from the model output was slightly above the observed productivity. We modelled chick survival rate as constant over all time intervals covering the chick-rearing period, whereas Gaston and Nettleship (1981) show that chick deaths are clearly more likely to occur during the first 2 days after hatching. Immediate post-hatching deaths might have occurred early in the first time interval without being represented as chick mortality in the output. Decreasing the time gap between the first and second sampling session should make any such variation in chick survival between the first time intervals visible.

The model seemed to have difficulties estimating two of the event probabilities for the group of breeding sites with expected low detection rates. This indicates that the data material did not offer a sufficient amount of information to the modelling process. Even though our final estimate of breeding success was not affected significantly by this, there is a potential risk that transition rates will be biased as a result of non-estimable parameters or boundary estimates.

Tagging the Brünnich's Guillemot breeding sites instead of the individuals is a necessity when all "capturing" is conducted by cameras. One potential problem with this is that, if the chicks were able to move to positions on the ledges that could not be observed from the camera point, both tag loss and temporary emigration could have occurred. Chick movement cannot be ruled out if the ledges are wide and flat enough for chicks to change positions or if there are crevices and overhangs where they can escape. We are confident that our study plot left very few possibilities for chick movement, seeing that most breeding sites were situated on short and narrow ledges with room for only one or two neighbouring couples. Brünnich's Guillemot chicks sometimes take refuge under the wings of neighbouring parents if their own parents leave the breeding site (Gaston and Nettleship 1981; Lorentzen, personal observation). This might theoretically lead to misclassification. However, the parents rarely leave their eggs or chicks unattended (Kober and Gaston 2003), so the chance of such an event affecting the data is considered small.

It may very well be argued that not every breeding site which is occupied by an adult bird on 30 different occasions during the incubation phase necessarily holds an egg. Failed breeders and non-breeding birds may occupy potential breeding sites for several days, although we feel confident that the latter will reveal their true state over a 5-day period. Therefore, our assumption that there were eggs on all the constantly occupied breeding sites may deserve critique. We do not have empirical data supporting this assumption, and the main reason for this is that attempting to obtain such data would potentially destroy a large number of eggs. A brooding Guillemot would have to be scared away or physically lifted from the ledge for anyone to state if it has an egg or not, since the egg is lying directly on the rock, and not in a nest bowl. Consequently, as soon as a Guillemot egg is unattended, it is in great risk of falling off the ledge or being snatched by Glaucous Gulls *Larus hyperboreus*. The best alternative would be to watch the study plot constantly for several days and log every single egg-laying, but even then one would not be completely certain that all layings would be registered. For a nest-building species, e.g. like the Black-legged Kittiwake *Rissa tridactyla*, the case would be somewhat different, as fresh nest material would in itself be a good indication that the couple is attempting to breed. Assuming that long-term occupation of a breeding site indicated that the occupying bird had an egg was a mere necessity in our case. The consequence of not meeting this assumption will

probably be a low-biased estimate of breeding success, since a bird which is incorrectly identified as a breeder early in the season will most likely reveal its empty breeding site at a later stage and thus appear to have failed. We have, however, no indication that breeding success was biased low in our study. Even though we consider 30 occasions over 5 days in the incubation period to be adequate for the identification of active breeders, it is always possible to come closer to meeting the assumption by investigating more photos taken during the incubation period. One possible option is to establish two sampling sessions in the incubation period and to try to model egg survival between them. This is a challenge that should be considered closely in further development of our method.

The assumption of equal probability of detection for all the study objects on any given sampling occasion is vital in mark–recapture studies (Lebreton et al. 1992). One possible cause of heterogeneity is unequal chick size due to differences in timing of egg-laying and hatching between pairs. Although Brünnich's Guillemots are reported to show a certain degree of synchrony in egg-laying within colonies or sections of a colony, there will always be some temporal variation in egg-laying and hatching (Gaston and Nettleship 1981; Harris and Birkhead 1985), which might lead to a violation of the assumption of homogeneous detection probability among individuals. Heterogeneity in detection probability was only accounted for by grouping the breeding sites according to expected degree of chick visibility in our study. A possible way of handling lack of synchrony would be to separate cohorts of individuals by utilising information from the photos, e.g. chick sizes or the appearance of eggshell remains on the breeding sites. Simulation remains to be done to quantify the bias on detection probability induced by a lack of synchrony which is not observed in the field. Alternatively, the model can be generalised by considering frailty models or models with two classes of heterogeneity, both of which can be easily fitted using program E-SURGE (Choquet and Gimenez 2011). The start and duration of egg-laying may also vary considerably between years, e.g. as a result of varying climatic conditions. Simply starting the sampling procedure on the same date every year would thus be inappropriate. Instead, the sampling protocol must be adapted to the timing of reproductive events. The investigator will therefore need information on dates of first hatch, last hatch and first fledging. One should ideally collect these data through repeated visits to each study plot, but applying information obtained from the photos and from neighbouring colonies or study plots would be sufficient.

Seeing that no goodness of fit (GOF) test has yet been developed specifically for the multievent model, we were unable to test GOF for our data in this study. This is certainly a point that needs to be addressed in the further development of the method.

This study shows that resighting data from series of photographs of Brünnich's Guillemot colonies can be used with the multievent model to estimate breeding success in this species. The modelling design handles the problem of state uncertainty for the chicks when a clear view of the breeding site is prevented by the adult. Apart from the data that can be extracted from the photos, information on timing of egg-laying and hatching in the study area should be utilised to improve the accuracy of the estimates. Our way of identifying the number and locations of eggs laid within the study plot is based on an assumption which, in the worst case, may lead to an overestimation of initial breeding attempts. The main caveat regarding our approach is therefore that it produces an estimate of breeding success which is not directly comparable to any measure of reproductive rate calculated as a result of continuous observations of the study plot. Monitoring a colony from one single viewpoint obviously also limits the dataset to mostly include breeding sites which are in the open. Guillemots breeding under overhangs and in caves are known to succeed more often than others (Gaston and Nettleship 1981), and hence our method will not be able to give a representative estimate of breeding success for the colony as a whole. Thus, we strongly emphasise that the method presented here is primarily suited for identification of trends in breeding success in *separate study plots* by inter-annual comparison of estimates. It therefore has value first and foremost as a supplement to manual around-the-clock monitoring, allowing for more study plots to be monitored and freeing human capacities for other tasks. We consider the method especially useful for parts of a seabird colony which cannot be reached physically and for colonies that are located too far away to be visited daily or weekly. Besides Guillemots, we regard our method as applicable for estimating breeding success in most open-nesting colonial seabird species, like, for instance, kittiwakes *Rissa*, albatrosses *Diomedeidae*, petrels *Procellariiformes*, terns *Sternidae* and some gull *Laridae* species, e.g. the Ivory Gull *Pagophila eburnea*. The angle from which the camera is capturing the colony should not be chosen randomly, and for colonies located on more or less flat ground, it will be necessary to elevate the camera to a height from which a suitable number of nests can be viewed. Further development of the method should be conducted to increase the precision of the estimates. Bringing more data into the modelling process should be a main concern in order to minimise variation and reduce the impact of individual heterogeneity of event probabilities. Separating cohorts of individuals and improving the modelling of egg survival will also be important.

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Appendix

The probability to hatch before occasion 2 and survive as a chick until the last occasion K is denoted $h(2)$ and is given by

$$h(2) = \varphi^{\text{egg,egg}} \times \varphi^{\text{egg,chick}}(1) \times \varphi^{\text{chick,chick } K-2},$$

where $\varphi^{\text{egg,egg}}$ is the probability for an egg to survive between two occasions, $\varphi^{\text{egg,chick}}$ is the probability for an egg to hatch between occasions 1 and 2, and $\varphi^{\text{chick,chick}}$ is the probability for a chick to survive between two occasions.

The probability to hatch between occasions 2 and 3 and then survive as a chick until the last occasion K is given by

$$h(3) = \varphi^{\text{egg,egg2}} \times (1 - \varphi^{\text{egg,chick}}(1)) \times \varphi^{\text{egg,chick}}(2) \times \varphi^{\text{chick,chick } K-3},$$

where $\varphi^{\text{egg,chick}}$ is the probability for an egg to hatch between any two occasions after occasion 2.

The probability to hatch at occasion $4 \leq t \leq K-1$ and to survive as a chick until the last occasion is given by

$$h(t) = \varphi^{\text{egg,egg } t-1} \times (1 - \varphi^{\text{egg,chick}}(1)) \times (1 - \varphi^{\text{egg,chick}}(2))^{t-3} \times \varphi^{\text{egg,chick}}(2) \times \varphi^{\text{chick,chick } K-t}.$$

We can estimate the breeding success denoted BS from the sum of probability to hatch:

$$\text{BS} = \sum_{i=2}^{K-1} p(i).$$

This formula can easily be adapted to the case where the probability $\varphi^{\text{chick,chick}}$ and the length of the time interval are not constant.

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