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Estimating survival rate in Brünnich's guillemot (*Uria lomvia*) chicks
- a study of mark-recapture methods using photo series data

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Abstract

Obtaining estimates of breeding success in cliff-nesting seabirds demands extensive fieldwork, including repeated colony visits. Automatic time-lapse cameras provide an efficient way of collecting observational data for colonial birds with minimal disturbance levels. In this study three different mark-recapture models were applied to resighting data for Brünnich's guillemot (*Uria lomvia*) chicks obtained from photo series. Performances of the various models as potential tools for estimating chick survival over the breeding season were assessed.

In the photos taken during the course of this study, the Brünnich's guillemot chicks were concealed by the brooding parents most of the time, making direct observations difficult, though the adults could be seen at many breeding-sites throughout the season. Recognizing that an adult bird has some probability of concealing a chick, observations of adults on the breeding-sites were recorded in addition to chick resightings. Pradel's multievent model was applied to the capture histories to estimate state transition probabilities while accounting for the uncertainty of the state of the chick when only the adult was observed. The Cormack-Jolly-Seber (CJS) model and Pollock's robust design were also applied to chick resighting data, and the estimates produced by the models were compared to field observations of breeding success.

All of the models tested underestimated survival rates when the breeding-sites were located on wide and densely populated ledges. Under these conditions violations of model assumptions were most likely to occur. Scarcity of observations of empty breeding-sites and strong site fidelity exhibited by Brünnich's guillemots despite chick loss were two apparent causes of bias in the state transition probabilities estimated by the multievent model. The survival rate estimates that were closest to documented chick survival were produced using the CJS model and Pollock's robust design when heterogeneity in capture probabilities was low or could be modeled.

One limitation in this study was the relatively small sample size. Even though precision of the survival estimates can be maintained if capture probabilities are high, the complexity of the multievent model and Pollock's robust design in particular demand a larger number of capture histories in order to make well-founded inferences. However, this study does provide a good basis for further investigations as it identifies the main challenges facing investigators planning to estimate chick survival in seabirds using resighting data from photo series.

Contents

1 Introduction

Reproductive success is one of the key parameters determining population dynamics of seabirds. For cliff-nesting birds breeding in high densities on inaccessible ledges it is often difficult to identify the breeding pairs and determine the fate of their offspring. Therefore, traditional methods to estimate reproduction call for repeated visitations of marked individuals (see Walsh et al. 1995). This procedure requires large resources in terms of time and qualified personnel. To increase the efficiency of data collection and minimize observer bias it is therefore desirable to develop new methods for estimating reproduction in cliff-nesting birds. The objective of this thesis is to explore the usability of mark-recapture (MR) data collected from successive photos of bird colonies in estimation of chick survival in Brünnich's guillemots (*Uria lomvia*). These colonial breeders hide their chicks well, and most often only the parent can be seen, causing problems in determining whether the chick is alive or dead. By marking each nest and recording all observable events on it, this problem is approached by modeling state transitions with the recently developed multievent model of Pradel (2005).

The Brünnich's guillemot is one of the most numerous seabird species in the northern hemisphere (Anker-Nilssen et al. 2000). It has a circumpolar distribution, breeding in arctic and sub-arctic seas between 46°N and 82°N (Nettleship and Evans 1985). It spends most of the year at sea and comes to land only to breed. The breeding takes place in steep cliffs close to the sea, and breeding pairs form dense colonies of varying size (Harris and Birkhead 1985). Brünnich's guillemots often breed sympatrically with common guillemots (*Uria aalge*) (Anker-Nilssen et al. 2000) and both species show marked mate- and site-fidelity (Gaston and Nettleship 1981, Harris et al. 1996).

Arrival at the colonies and timing of breeding for the Brünnich's guillemot varies with environmental conditions (Nettleship and Evans 1985). In Svalbard, where this study was carried out, the egg-laying starts at the end of May or early June (Strøm 2006). Laying is rather synchronous within "small areas" of the colony (Harris and Birkhead 1985). Each breeding pair produces a single egg which is placed directly on a narrow, rocky ledge or, occasionally, in crevices and caves in the cliff. Breeders often incubate shoulder to shoulder, in physical contact. The pair will defend the spot on which the egg is laid (hereafter termed "breeding-site") throughout the breeding period, and breeders are aggressive both towards neighboring site-holders and non-breeding birds (Gaston and Nettleship 1981). Incubation lasts for about 32 days, and the chicks

jump from the ledges before they are fully fledged, between 16 and 30 days after hatching (Harris and Birkhead 1985). The male parent then accompanies the chick on the swimming migration towards the rearing and wintering areas (Bédard 1985). Eggs, chicks and adult guillemots are subject to predation by arctic fox (*Vulpes lagopus*) and glaucous gulls (*Larus hyperboreus*) during the breeding season in Svalbard (Strøm 2006). Eggs are also lost because they roll off the ledges, get wedged in cracks, crushed or dislodged during intraspecific fighting or they simply do not hatch (Gaston and Nettleship 1981). There is also a risk of chicks falling off the ledges, but chick mortality is generally lower than egg-loss (Gaston and Nettleship 1981).

True breeding success in guillemots is given by the number of chicks that survive the breeding period divided by the number of pairs that attempted breeding (Walsh et al. 1995). A preliminary study in 2006 showed that obtaining these numbers from photos covering more than just a few breeding-sites is not straightforward. The fact that the breeders lay their eggs directly on narrow ledges which are usually crowded with several other breeding and non-breeding birds implies two major challenges: First, locating the breeding-sites and counting the breeders (i.e. the number of pairs that attempted breeding) is difficult. Second, visual detection of chicks is limited once the eggs have hatched. The adults will conceal the chicks with their bodies most of the time, and for a large proportion of the breeding-sites only the adult was observed on the photos although field inspections revealed that there was a chick on the site. In addition, even if a chick has left or is lost from a breeding-site there still might be adults occupying the site. This is probably due to competition for high-quality sites (Birkhead 1985). Female Brünnich's guillemots are known to stay at the breeding-site for up to 20 days after the chick has left the colony (Gaston and Nettleship 1981). Thus, observing an adult on a site where a chick was previously recorded will not tell for certain if the chick is dead or alive. This means that knowing the fate of each individual chick will be impossible. A method for estimating chick-survival based on a limited amount of observations is therefore required, and this method must account for the uncertainty related to observing an adult on the breeding-site without being able to determine if the chick is alive.

This problem can be solved within the framework of mark-recapture methodology (also known as "capture-(mark)-recapture") (Seber 1982, Pollock et al. 1990, Lebreton et al. 1992). A capture history is built for each breeding-site by examining a number of successive photos of the colony and recording every observation of the chick and every failure to observe it. The single-state Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) estimates survival using only capture

histories for individuals detected at least once over the study period. Under this design a chick that goes undetected is either alive and hidden under its parent or dead and gone from the site. However, since an adult guillemot sitting on a breeding-site has some probability of concealing a living chick, observations of adults can contribute information that should be utilized to achieve a more representative estimate of chick survival. By defining "alive" and "dead" as the possible states for the chick one can consider this a multistate mark-recapture (MSMR) problem with uncertainty of state assignment when an adult is observed. This way capture histories consisting solely of observations of adults can also be included in the data set.

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 thesis the performance of Pradel's (2005) multievent model is explored as a means to estimate probability of hatching and survival for Brünnich's guillemot chicks. For the purpose of increasing data extraction efficiency, it is also interesting to assess whether qualitatively good estimates of survival rates can be obtained using capture histories that include at least one certain observation of a chick. Therefore, the output of the CJS model and Pollock's (1982) robust design with these data is also examined. The estimates produced by the models using MR data from photo series from two different colonies in Svalbard are compared with field observations of breeding success. First, a brief outline of the general framework of MR methodology will be given, including single-state, multistate and multievent modeling. It will also be explained how these models can be applied to resighting histories for Brünnich's guillemot chicks obtained from photos.

2 Methodological framework

Although the main focus of this work is the exploration of the performance of the multievent model, this section will present the different modeling designs under investigation in developmental order, starting with the Cormack-Jolly-Seber model. This order of presentation will be followed throughout the remainder of the thesis.

2.1 Mark-recapture methodology – the CJS model

To estimate survival in the field under natural conditions one must follow marked individuals through time (Lebreton et al. 1992), which is the concept of MR methodology. MR studies usually consist of $K > 2$ distinct sampling occasions at which animals are captured or observed (Pollock et al. 1990). On each occasion previously unmarked individuals are marked with unique identifiers and released back into the population. Subsequent recaptures can be implemented either via observation (resighting) or by physical capture. For previously marked animals the identification codes are recorded. Repeated sampling results in individual capture histories – the basic data units of the study. Each capture history consists of K elements, the values of which depend on whether the animal was captured or not on the sampling occasions. Capture is indicated by the value 1, while a 0 means the individual was not captured. For a study involving 5 sampling occasions the capture history (01010) tells that the animal was first captured on sampling occasion 2, then recaptured or seen again on occasion 4. On occasions 3 and 5 the animal was not recorded, either because it was in the sampled population, but escaped recapture, or because it left the sampling area prior to sampling. For occasion 5 there is also the possibility that the animal died after it was recaptured on occasion 4. The task in survival estimation is to develop probability models for the biological processes giving rise to the capture history data (Williams et al. 2002).

A milestone in estimating survival using MR methods was the common approach by Cormack (1964), Jolly (1965) and Seber (1965) which considered time-dependent survival and recapture rates for a single group of individuals ("single" here refers to a population that covers an area with certain boundaries within which the individuals are free to move and mix with other individuals of their kind, but the area is "single" with respect to the parameters being estimated (Jolly 1965)). The CJS model uses a multinomial distribution to model captures and recaptures for a population consisting of animals of the same age (single-age), and for which losses and gains can occur between sampling occasions (open population) (Williams et al. 2002). When time

between sampling occasions is too short for gains and losses the population is termed "closed".

Assumptions underlying the CJS model are (Seber 1965, 1982, Lebreton et al. 1992):

1) Every animal present in the population at sampling period i has the same probability p_i of being captured or resighted in this period.
2) Every marked animal present in the population immediately following the sampling in period i has the same probability φ_i of survival until sampling period $i+1$.
3) Marks are neither lost nor overlooked, and are recorded correctly.
4) Sampling periods are instantaneous and recaptured animals are released immediately.
5) All emigration from the sampled area is permanent.
6) The fate of each animal with respect to capture and survival probability is independent of the fate of any other animal.

Survival and capture probabilities frequently differ between individuals as a function of attributes such as e.g. sex, body mass and age (Williams et al. 2002). If there are any such attributes that are not controlled by the investigator, assumptions 1 and 2 are not met, i.e. there is heterogeneity in the parameters p_i and φ_i underlying the capture history data. Aspects of the study design can also lead to heterogeneity. Sampling methods used to obtain recapture or resighting data should therefore cover the entire population as homogeneously as possible, and effects of capture and handling (trap response) should be minimized (Seber 1982). For a procedure that is relying on obtaining the capture histories from photos physical marking of the individuals will not be possible. Seeing that Brünnich's guillemot chicks are difficult to distinguish by visual characteristics like color and size they must instead be marked by their positions in the colony. This approach rests on the assumption that the chicks don't move away from their breeding-sites over the course of the study. The advantage of photo-"captures" is that capture and survival heterogeneity as a result of handling will not be an issue.

Meeting the assumption that marks are neither lost nor overlooked is important to ensure homogeneity of recapture probability. A systematic and accurate photo-processing procedure is necessary to make sure that resightings are linked to the correct breeding-sites. This in turn also relies on the assumption that chicks don't move around on the ledges. Long sampling periods can cause heterogeneity of survival among

released animals, hence the reason for the assumption of instantaneous sampling. A photo certainly represents an instantaneous form of resighting, so concerns regarding immediate release are redundant. However, if resightings from a series of photos are pooled to form a single sampling session the time between the first and last photo can not be long enough to allow gains or losses to occur in the sampled population.

If one can not assume that all emigration from the population is permanent (i.e. if animals can leave temporarily to return later) p_i will not reflect capture probability alone. It will instead be a product of the probability of being in the population and the probability of being captured or observed, and this can result in biased estimates of capture probability and in turn survival probability (Kendall et al. 1997).

Whether fates of the individuals are independent (assumption 6) largely depends on the characteristics of the animals under investigation. Dependence of fates violates the assumptions of the multinomial distribution underlying the CJS model (Lebreton et al. 1992), which will lead to biased estimates of variance for the point estimates of p_i and φ_i (Williams et al. 2002).

For all MR models the probability distribution of the capture history data is conditional on the new releases in each period and the cell probabilities associated with each capture history. Estimation of the model parameters is based on the number of animals exhibiting each of the observable capture histories. Estimates are obtained by maximum likelihood estimation (MLE) (Williams et al. 2002). The capture probability p_i is estimated by conditioning on all animals caught before and after period i, and then asking what proportion of these animals were actually captured at i. For the CJS model with fully time-specific survival and capture-probability the estimable parameters are $\varphi_1,...,\varphi_{K-2}$ and $p_2,...,p_{K-1}$. The parameters φ_{K-1} and p_K can be estimated only as the product $\varphi_{K-1}p_K$, but not separately.

2.2 Pollock's robust design

Pollock (1982) presented a modeling-design that allowed analysis of demographic parameters using a combination of methodology from closed and open population models. Sampling occurs over K primary periods each consisting of l secondary periods. The latter are close enough in time that the population size is assumed to be constant within each primary sampling period. One can thus view this modeling approach as a series of short-term studies of closed populations put together to form a long-term study of an open population (Williams et al. 2002). The advantage of this design is that the secondary sampling periods provide the information needed to

model the probability p_i^* of being detected at least once within every primary sampling session. With the probability of being captured during primary session 1 available one can also estimate population size N_1 and in turn recruitment rate B_1. In addition, the survival probability estimate $\hat{S}_{K-1}$ can be separated from the product $\hat{S}_{K-1}\hat{p}_K^*$, making N_K and B_{K-1} estimable as well (Williams et al. 2002). Thus, the robust design opens for estimation of parameters not otherwise estimable in closed or open models considered separately, and it provides more robust estimation of capture probability, survival and abundance.

Apart from the parameters mentioned, modeling under the robust design produces estimates of the probability p_{ij} of first capture and the probability c_{ij} of recapture for each primary session (where j indexes the number of secondary occasions within the session) (Kendall et al. 1995). For the intervals between primary sessions the probability γ_i'' of emigration from the study area and the probability γ_i' of remaining outside the study area given that the animal has previously left the area are also estimated.

Assumptions underlying the models under the robust design include those for both the closed and open models (Williams et al. 2002). For the closed capture modeling of samples within each primary session it is assumed that

1) the population is closed to gains and losses throughout the whole session,
2) marks are neither lost nor incorrectly recorded,
3) capture probability over the secondary periods varies according to specifications dictated by the structure of the selected closed-population model,
4) the fate of each animal is independent of the fates of all other animals with respect to capture and survival probability.

Additionally, under the likelihood-based approach to the robust design an animal must be missed (not captured) in each of the secondary occasions of primary period i in order to be missed in primary period i (Kendall et al. 1995). Assumptions underlying the modeling of primary period data are given in the previous section. Like the CJS model the robust design can only use capture histories that include at least one capture of each individual during the study.

2.3 Multistate and multievent modeling

Multistate models represent a generalization of the single-state CJS model permitting for the individuals to move stochastically among a finite set of states over a finite number of sampling occasions (Schwarz et al. 1993). "State" may refer to phenotypic state (e.g. egg, chick) or geographic location or both (Williams et al. 2002). As for single-state models a 0 in the capture history denotes that the animal was not captured. Captures, however, are now indicated with different codes according to which state the animal was captured in. For a two-state system with states "1" and "2" the capture history (01022) describes an animal that was first captured and released in state 1 on the second occasion, not seen on occasion 3, and recaptured in state 2 on both occasions 4 and 5. Thus, some time between occasion 2 and occasion 4 the individual made a transition from state 1 to state 2. Parameters are now state-dependent, and additionally, the survival probabilities incorporate the probabilities of transition from one state to another. The assumptions underlying single-state modeling also apply to the multistate model, but the first two assumptions are modified to (Schwarz et al. 1993, Williams et al. 2002)

1) every marked animal present in state r at sampling period i has the same probability p_i^r of being captured or resighted; and
2) every marked animal in state r immediately following the sampling in period i has the same probability φ_i^{rs} of surviving until sampling period $i+1$ and moving to state s by period $i+1$.

Additionally, it is assumed that state transition probabilities reflect a first-order Markov process, "first-order" meaning that the state at time $i+1$ depend only on the state at time i, not on periods prior to i (Schwarz et al. 1993).

The survival-transition parameter φ_i^{rs} can be decomposed into separate parameters for survival and transition. Under the assumption that survival between two sampling periods depends only on the state at the first period, φ_i^{rs} can be written as

$$\varphi_i^{rs} = S_i^r \psi_i^{rs},$$

where S_i^r is the probability that an animal in state r at sampling period i survives and remains in the population to period $i+1$, and ψ_i^{rs} is the probability that an animal is in state s at sampling period $i+1$ given that it was in state r at period i (Williams et al. 2002). The transition probabilities ψ_i^{rs} are conditional on survival.

The time-dependent multievent model of Pradel (2005) is an extension to multistate mark-recapture modeling which estimates transition probabilities between states while accounting for uncertainty in state assignment. The objects of interest are still assumed to move independently over a finite set N of states through a finite number K of sampling occasions. However, the states are not observed directly. Instead, at each occasion the investigator observes and records an event that is expected to reflect the underlying state to some extent. Following Pradel's notation the set of states occupied by an animal is $E = (e_1,\ldots,e_N)$, and the state "dead" is always included in E. A finite set Ω of L possible events $(v_1,\ldots,v_L)$ must be defined, and the codes in the capture histories represent the observed events for the animals. Considering the states of interest for the Brünnich's guillemot chicks in the chick-rearing period as $e_1 =$ "alive" and $e_2 =$ "dead" an estimate of survival will be given by the probability of not making the transition from state "alive" to state "dead", i.e. the probability of transition from "alive" to "alive".

Observing a 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 state "dead". One can also observe an adult without being able to tell whether it has a chick or not. This gives the following set of possible events for the breeding-site: $v_1 =$ "adult", $v_2 =$ "chick" and $v_3 =$ "no chick". The multievent model uses a set of parameters to write out 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,
- $b_{uj,i}$, the probability of event v_u for an animal in state e_j at time t,
- $b_{uj,t}^0$, the probability of event v_u for an animal in state e_j at time t, which is then detected, i.e., $Pr(v_u | e_j$ and "detected").

To avoid confusion with the notation of survival probability in the CJS model, $\psi_{ij,t}$ will be used here in stead of $\varphi_{ij,t}$ to indicate transition probability.

Table 1 shows how the defined states for the Brünnich's guillemot chicks are linked to the observed events for the breeding-sites through the parameter $b_{uj,t}$. Reasonable constraints should be applied, e.g. the state of the chick can not be "alive" when the breeding-site is observed with no chick.

Table 1: The relations between two states (e_1 and e_2) and three possible events (v_1, v_2 and v_3) for Brünnich's guillemot chicks in the chick-rearing period under Pradel's multievent model presented in a matrix pattern. b_{uj} denotes that the probability of observing event v_u for an animal in state e_j is less than 1. "0" denotes event probabilities constrained to zero. For any column with more than one b_{uj}, state assignment is uncertain for the observed event. Columns sum to 1.

	v_1 Adult on site	v_2 Chick on site	v_3 No chick on site
e_1 Alive	b_{11}	$(1 - b_{11})$	0
e_2 Dead	b_{12}	0	$(1 - b_{12})$

If in addition the egg-stage can be added as a separate state one can also estimate hatching success, i.e. the probability of transition from state "egg" to state "alive". Breeding success will in turn be given by the product of hatching success and chick survival.

For the multievent model it is assumed that the event observed on occasion t depends only on the unobserved underlying state of the animal at the moment (Pradel 2005). Successive states are also assumed to obey a Markov chain, which is a stationary countable Markov process with equal time steps (Williams et al. 2002).

3 Methods

3.1 Field methods and data

During the breeding season of 2007, capture histories of Brünnich's guillemot chicks were collected from two colonies on Spitsbergen, the largest island of the Svalbard archipelago in the Barents Sea. One colony (79°10'N, 11°52'E) is on the eastern shore of Krossfjorden, 2.6 km NW of the mountain top of Amfifjellet. It has no official name, and will here be called the Amfifjell colony (Figure 1). It is situated in a north-oriented cliff that stretches approximately 20 meters upwards and 20 meters inwards from the beach and has a slight overhang. The lowest ledges are 6-7 meters above the high-water mark. This is a relatively small colony, consisting of approximately 100 pairs of Brünnich's guillemots (E. Lorentzen, pers. obs.). The cliff was photographed from the edge of a morainal plateau on the opposite side of a hollow

Figure 1: Map of Svalbard with the positions of the Brünnich's guillemot colonies at Amfifjellet and Ossian Sarsfjellet marked by red dots.

in the terrain. The other colony is located at the west-oriented cliffs of Ossian Sarsfjellet in Kongsfjorden, and will be referred to as the Ossian Sars colony (78°56'N, 12°27'E). Approximately 1100 pairs of Brünnich's guillemots and 1000 pairs of Kittiwakes (*Rissa tridactyla*) are nesting in the nearly horizontal rock walls between 30 and 100 meters above the beach (SCRIB 2007). The ledges on one side of a ravine in the cliff were selected to be studied as they could be photographed from the top of the other side of the ravine (Figure 2).

At the end of the incubation period a CamTrakker® automatic time-lapse camera system (CamTrak South, Inc., Watkinsville) was placed facing each colony from a favorable angle as to optimize the probability of seeing the chicks in the photos. The system consisted of a Sony® DHC-H5 digital camera (7.2 mega pixels and 12 times optical zoom), a time-lapse control unit and a battery that were built into a waterproof box. The distance from the camera to the cliff was 89 and 28 meters at the Amfifjell and Ossian Sars colony, respectively (measured with Leica range finding binoculars). The camera zoom was set for the photos to include as many sites as possible, and at the same time allow adult and juvenile birds to be distinguishable. The photographed areas of the two colonies will here be termed "plots". From 20th June to 27th July the plots were photographed in 4-hour intervals, resulting in 6 photos per plot per day.

The study plots were selected mainly because they could be photographed from a favorable angle, but at the same time they represented two different types of ledges that are frequently used by Brünnich's guillemots. The plot in the Amfifjell colony included a fairly wide ledge with birds sitting in 3-4 rows from the inner wall to the edge, in addition to one long ledge made by a horizontal crack in the cliff. The wide ledge held the majority of the birds within this plot. In the plot at the Ossian Sars colony the breeders were more spread out than at the Amfifjell. Very few of the ledges within the Ossian Sars plot had room for more than a single row of birds, and the number of birds sitting closely together on a ledge ranged from 1 to approximately 15, with single birds or pairs of close neighbours being the most common.

In order to obtain the real number and positions of the chicks the ledges were searched at the closest range possible on 5 separate days in the second half of the chick-rearing period. At the Amfifjell colony this implied rappelling down the cliff and removing the adults to see whether chicks were present and mark their positions. The ledges at Ossian Sars were not accessible this way, but the breeding-sites could be viewed at a short distance from the other side of the narrow ravine. This approach is

assumed to have given a slightly low biased number of chicks for the Ossian Sars colony. The positions of the chicks were marked on a photo copy of the plot.

Brünnich's guillemot chicks most commonly rest between the flank and wing of the parent (Gaston and Nettleship 1981). This makes the parent assume a characteristic pose with one wing trailing on the ground. Adults brooding like this were assumed to have a chick, and each chick hidden this way was counted even if the chick itself could not be seen. This is a commonly used, although not 100% reliable, way of telling if adult guillemots have chicks (H. Strøm pers. comm.).

3.2 Obtaining capture histories from photos

Gaston and Nettleship (1981) found that from the beginning of egg-laying to the start of fledging most of the Brünnich's guillemot breeding-sites were permanently occupied by at least one member of each breeding pair. Therefore, all resting-positions that were occupied by an adult on every photo over a 5-day interval at the end of the incubation period (27th June – 1st July) were assumed to be breeding-sites containing eggs and representing the number of breeding-attempts. The breeding-sites were marked in the photos using digital overlay-technique (Figure 2). All photo-processing was done with Adobe Illustrator®.

Figure 2: The study plot at the Ossian Sars colony with the mounted time-lapse camera in the foreground (left) and a segment of the plot with Brünnich's guillemot breeding-sites marked by circles (right).

The start of chick-rearing was set to be 10th July, as field observations revealed that a majority of eggs were hatched by this date. Survival of older chicks is generally high, and since they are able to leave the colony after 15 days, chicks aged 15 days and older are normally considered survivors (Gaston and Nettleship 1981, Walsh et al. 1995). The first observed fledging took place on 25th July, and to avoid mistaking fledged survivors for lost chicks no resightings were made later than 23rd July. Photos from 5 days (10th, 13th, 15th, 20th and 23rd July) of the chick-rearing period were analyzed. 6 photos from each day were examined, resulting in a capture history with 30 capture occasions for each breeding-site. One of the following events was recorded on each occasion:

1 = adult (might be hiding a chick)
2 = chick [the chick is directly visible or otherwise indicated (see previous section)]
3 = empty site OR adult only (no egg and no chick)

The capture histories were grouped by colony. Table 2 presents an example of capture histories for three breeding-sites produced by the photo-analysis.

Table 2: Example of mark-recapture data for Brünnich's guillemot (*Uria lomvia*) chicks collected by resightings of breeding-sites on photos taken in a 4-hour interval on 5 discrete days in the chick-rearing period. Notation: 1 = adult bird is observed and state of chick is uncertain; 2 = chick is observed; 3 = no chick on site (certain observation).

Site ID	Date				
	10th July	13th July	15th July	20th July	23rd July
1	111111	111212	111111	111222	113113
2	121111	111111	111221	221211	111313
3	111111	111111	111111	333131	111313

Survival estimation with the CJS and multievent models uses data with a single recording for each discrete sampling occasion. For every capture history the 6 captures per day were therefore pooled, resulting in one recorded event for each of the 5 days. Event 2 was recorded if the chick was observed on at least one of the photos within a day, and likewise at least one observation of the site being empty would lead to event 3 being recorded for the day. In the capture histories used under the CJS model and robust

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design the sightings of chicks were treated as captures and indicated by 1s, while all other observations were noted 0. Following the example given in Table 2 the capture history of site 1 would be translated into "01010" to fit the data structure of the CJS model. For multievent modeling the same site would have the capture history "12123".

3.3 Single-state modeling

The CJS model and Pollock's robust design were applied to estimate survival and capture probability using only capture histories from breeding-sites that had at least one sighting of a chick during the chick-rearing period.

3.3.1 CJS model

Survival and capture probabilities for the Brünnich's guillemot chicks under the CJS model were estimated in program MARK ver. 5.0 (White and Burnham 1999). To allow for separate modeling of survival and capture rates of the two colonies the CJS model was generalized into a multiple-group single-age model (Williams et al. 2002). For simplicity it will be referred to as the CJS model here. Goodness of fit (GOF) for the global model (φ_{g*t}, p_{g*t}) including time- and colony-specific survival and capture probabilities was tested by a bootstrap procedure with 2000 simulations in program MARK. The bootstrap procedure was chosen because it is developed for use with small sample sizes (Williams et al. 2002). The variance inflation factor c was estimated by dividing the observed deviance by the mean of the simulated deviances from the bootstrap procedure (White et al. 2001). If the estimate of c was larger than 1 overdispersion was adjusted for by multiplying the estimated variances and covariances by $\hat{c}$ prior to model selection (Burnham and Anderson 2002).

Examination of the estimated β-values revealed that when additive effects between variables were included in the model the number of estimable parameters was frequently miscalculated. The cause of this is that the logit-link function is used for models with additive effects, allowing the parameter values to asymptotically approach the boundaries of the [0, 1] interval (White and Burnham 1999). For model parameterizations including additive effects the number of parameters was therefore adjusted to account for miscalculation of estimable parameters.

Estimates produced by both the CJS model and robust design are presented with standard errors (SE) as measures of variation. Overall survival probability for known chicks over the period from 10th to 23rd July under the CJS model was calculated by

$$\hat{\phi}_g = \prod_{i=1}^{K-1} \left(\hat{\varphi}_{i,g}\right)^d,$$ (1)

where i refers to capture occasion, g denotes colony and d represents the number of days between i and $i+1$. When daily survival rate is constant over the whole period an estimate of variance for this overall survival rate estimate is

$$\text{var}(\hat{\phi}_g) = \left[D\left(\hat{\varphi}_g\right)^{D-1}\right]^2 \text{var}(\hat{\varphi}_g),$$ (2)

where D denotes the total number of days in the period.

3.3.2 Robust design

When modeling survival and capture under the robust design the same closed capture model should be used for all primary sampling periods unless there are apparent reasons for doing otherwise (Williams et al. 2002). Following recommendations by Pollock (1982), program CAPTURE developed by Otis et al. (1978) was applied to find the most appropriate closed-population model. The test revealed that model M_0 (no variation in capture probability among chicks or among secondary sampling occasions) was probably the best choice for 4 of the 5 primary periods. Model M_0 was therefore initially used for all of the primary sampling sessions under the robust design modeled in program MARK (White and Burnham 1999). However, during the course of the study heterogeneity in capture probabilities was suspected among the chicks. Menkens and Anderson (1988) found that the model selection procedure in program CAPTURE frequently fail to select the appropriate model when population sizes are small. The closed-population model M_h, allowing heterogeneity in the capture probabilities, was therefore also tested. Results of both these alternative modeling procedures will be presented. To obtain these models, probability p_{ij} of first capture was set equal to probability c_{ij} of recapture, ruling out behavioral response to captures. As the chicks could not emigrate from the plot the emigration parameters γ''_i and γ'_i were set to 0. Through different model parameterizations the capture probability p^*_i was tested for variation between primary sampling sessions, and at each primary session p^*_i was tested for differences between colonies. The abundance parameter N was set to differ between colonies and between primary periods. Due to scarcity of data, it was assumed that it would not be advisable in terms of precision to model more than two particular mixtures of capture probabilities among the chicks under the heterogeneity model. The probability π of a particular mixture was set to be constant over time and different for

the colonies, under the assumption that the different physical characteristics of the two plots would be the main factor causing any heterogeneity.

Seeing that estimation of the variance inflation factor c is not available for the robust design in MARK, potential overdispersion could not be adjusted for. Overall chick survival rate from 10th to 23rd July was calculated in the same manner as with the CJS model [Eq. (1)], with $\hat{S}$ replacing $\hat{\varphi}$ in the equation.

3.4 Multievent modeling

As the breeding-sites were identified on photos taken at the end of the incubation period (27th June-1st July) and the first capture occasion was 9 days later, the egg-state was included in the multievent model to account for mortality in the first 9-day period. Although no direct observations of eggs were made in the photos, all breeding-sites were assumed to have an egg on the 1st July. This was implemented by adding a 1 before the first recording in each capture history, indicating that the actual event was "adult" for every site on this occasion. This approach would allow the modeling of hatching probability. In accordance with the principles of multievent modeling the states for the chicks were defined as $e_1=$ "egg", $e_2=$ "alive" and $e_3=$ "dead", where "alive" corresponds to the chick stage, whereas "dead" is the state of an egg or chick that has been lost. The possible events for the breeding-sites were defined as $v_0=$ "not observed", $v_1=$ "adult", $v_2=$ "chick" and $v_3=$ "no chick". Event v_0 is automatically included to deal with 0s in the capture histories, but would in this case be redundant since each breeding-site was observed on every occasion. In program E-SURGE (Choquet et al. 2008) the capture histories were fitted to a multievent model with the states and events described above. For the general model the initial state was set to egg-state. The transition matrix

$$\Psi_i = \begin{pmatrix} \psi^{egg,egg} & \psi^{egg,alive} & (1-\psi^{egg,egg}-\psi^{egg,alive}) \\ 0 & \psi^{alive,alive} & (1-\psi^{alive,alive}) \\ 0 & 0 & 1 \end{pmatrix}_i$$

at occasion i was applied. The egg can either stay in the egg-state, turn into a living chick or die, as indicated in the top row of the matrix. Once in the alive-state the chick can stay alive or die. The dead-state is an absorbing state, as dead individuals can only stay dead. The event matrix was set to

$$B_i = \begin{pmatrix} 0 & 1 & 0 & 0 \\ 0 & b_{adult|alive} & (1-b_{adult|alive}) & 0 \\ 0 & b_{adult|dead} & 0 & (1-b_{adult|dead}) \end{pmatrix}_i ,$$

where columns and rows refer to events and states, respectively. By this matrix the model will estimate the probabilities of observing an adult given that the site is empty and given that there is a living chick on it. As noted above the egg-state can only have the event "adult".

Goodness of fit for the multievent model could not be evaluated as no GOF-test has been developed for this design yet (R. Choquet, pers. comm.). In the results section the estimated daily transition and event probabilities are presented with standard errors (SE). Overall chick survival for the chick-rearing period under the multievent model was calculated by

$$\hat{\phi}_g = \prod_{i=1}^{K-1} \left(\hat{\psi}_{i,g}^{alive,alive} \right)^d \tag{3}$$

with the same notation as for Eq. (1), but with estimated transition probability $\hat{\psi}^{alive,alive}$ replacing the survival rate estimate $\hat{\varphi}$. Breeding success in the different colonies was calculated by

$$\hat{B}_g = \left(\hat{\psi}_{i,g}^{egg,alive} \right)^9 \prod \left(\hat{\psi}_{i,g}^{alive,alive} \right)^d , \tag{4}$$

with the first term expressing hatching probability over the 9-day interval between the day when the breeding-sites were identified and the first capture occasion.

3.5 Model selection

Testing the importance of time and inter-colonial differences on survival and capture probability while securing precise estimates of these parameters was sought achieved through an appropriate model selection procedure. The models were parameterized to imply only estimation of parameters of relevance for the Brünnich's guillemot chicks from a logical and biological point of view (see sections 3.3 and 3.4 for details). Within this frame all possible combinations of time- and colony-dependence for survival and capture rate, including constant rates, interactions and additive effects of the two variables, were considered for the single-state models. Under the multievent modeling design the approach was simplified due to the high number of

competing models that are possible with the 4 variables *time*, *group*, *from* (state of departure) and *to* (state of arrival) for each of the 2 parameters $\psi_{ij,t}$ and $b_{uj,i}$. First, all combinations of the variables were tested for the state transition parameter while the interaction term ($time \times from \times group$) was kept for the event probability parameter. The models produced were ranked with respect to value of small-sample Akaike's Information Criterion (AIC$_c$), and the model with the lowest value was then selected for further analysis. Next, the parameterization for the state transition probability in this model was kept, while all possible combinations of parameterizations for the event probabilities were tested. These steps were repeated for every parameterization resulting in a high-ranked model until no further progress could be made in terms of obtaining a relatively low AIC$_c$-value.

Models with non-estimable parameters were omitted under all modeling designs, and remaining models were ranked by AIC$_c$-value or by AIC$_c$ adjusted for overdispersion (QAIC$_c$) (Anderson and Burnham 1999). Parameter estimates of daily survival and capture probability were derived from the highest-ranking model in cases where the AIC$_c$-value of the second-best parameterization was more than approximately one unit larger than optimal AIC$_c$, as suggested by Lebreton et al. (1992). If the difference between the best models were smaller, i.e. $\Delta AIC_c < 1$, estimates were computed by model averaging to account for the uncertainty associated with model selection and the variability in the data (Burnham and Anderson 2002). For this procedure the AIC$_c$ or QAIC$_c$ values were used as weights to average the parameter estimates across the models.

Only model parameterizations considered to have substantial support [Δ(Q)AICc < or $\approx$ 2 (Burnham and Anderson 2002)] under each design are presented in the results.

4 Results

47 of the 124 resting-positions used by adult birds within the plot in the Amfifjell colony were defined as breeding-sites. The Ossian Sars colony had 62 identified breeding-sites out of 279 positions used, making a total of 109 sites available for further resightings. 13 of the breeding-sites in the Amfifjell colony were placed so that the adult was occasionally hidden behind other birds or undetectable in the photos due to shadow. In the Ossian Sars colony this was only the case for one site. On 21 of the 47 breeding-sites in the Amfifjell colony the chick was observed at least once. For the Ossian Sars colony the number of known chicks was 36. Thus, a total of 57 capture histories could be used for survival estimates with the single-state Cormack-Jolly-Seber model and Pollock's robust design.

4.1 CJS model

The bootstrap GOF-test for the general model (φ_{g*t}, p_{g*t}) showed that the "known chick" data did not fit the CJS model well (P = 0.0275). This indicates that the assumptions underlying the model were not met and that estimators may be biased (Lebreton et al. 1992, Williams et al. 2002). The estimated variance inflation factor $\hat{c}$ was 1.515, indicating an acceptable model structure, but slight overdispersion in the data (Burnham and Anderson 2002).

After adjusting for overdispersion the two models with the lowest $QAIC_c$ values had constant and colony-specific survival probabilities, respectively (Table 3). The difference in $QAIC_c$ of only 0.03 between these parameterizations implies that under the single-state CJS model it can not be ruled out that daily survival rate for the known chicks differed between the colonies. Probability of capture was time-dependent for the two highest weighted models, whereas model 3 assumed that the colonies had different capture rates changing in a parallel manner over time.

Table 3: Information used in model selection for the 3 best parameterizations under the Cormack-Jolly-Seber model (recaptures only) for resighting-data on Brünnich's guillemot (*Uria lomvia*) chicks collected from photo series for two colonies in Svalbard, 2007. Capture histories are grouped by colony. The number of capture histories $n = 57$.

Model	# parameters	QDeviance	QAIC$_c$	QAIC$_c$ Weight
(1) $(\varphi_{.}, p_t)$	5	32.316	138.146	0.294
(2) (φ_g, p_t)	6	30.124	138.176	0.290
(3) (φ_g, p_{g+t})	7	29.932	140.246	0.103

Estimates of survival and capture probability under the CJS model were produced by model averaging due to the small difference in QAIC$_c$ between the best models. For the Amfifjell colony the daily survival estimates ranged between 0.959 and 0.962 ± 0.026 (Table 4), which is 1-2 % lower and less accurate than what was estimated for the Ossian Sars colony. In both colonies the estimated survival rate was highest between capture occasions 2 and 3, and lowest in the last time interval. With these daily survival rates chick survival over the season was estimated at 0.591 and 0.749 for the Amfifjell and Ossian Sars colony, respectively.

Table 4: Estimates of daily survival and capture probabilities for Brünnich's guillemot (*Uria lomvia*) chicks in two colonies in Svalbard under the Cormack-Jolly-Seber model (recaptures only), given for 4 time intervals in the chick-rearing period of 2007. Estimates are derived from averaging of 20 models, and SE accounts for an estimated overdispersion factor $\hat{c} = 1.515$. The number of capture histories $n = 57$.

Capture occasion[a]	Amfifjell colony				Ossian Sars colony			
	$\hat{\varphi}$	$SE(\hat{\varphi})$	$\hat{p}$	$SE(\hat{p})$	$\hat{\varphi}$	$SE(\hat{\varphi})$	$\hat{p}$	$SE(\hat{p})$
1	0.960	0.026	-	-	0.978	0.015	-	-
2	0.962	0.026	0.720	0.139	0.980	0.014	0.694	0.119
3	0.961	0.025	0.550	30.128	0.978	0.014	0.542	0.115
4	0.959	[b]	0.914	0.118	0.976	[b]	0.923	0.105
5	-	-	0.729	[b]	-	-	0.719	[b]

[a] For daily survival rate φ the estimated probability covers the time interval from the given capture occasion to the next. $\hat{p}$ is the estimated probability of being captured at the given capture occasion.

[b] SE was not estimable due to a failure of program MARK to estimate SE for $\hat{\varphi}_{K-1}$ and $\hat{p}_K$ in model parameterizations including both time-dependent survival and capture probability.

Under the CJS model the detection probabilities for the two colonies were approximately equal and exhibited the same trajectory over time. The particularly low capture probability on occasion 3 (15th July) can be related to weather conditions. On this date the colonies were exposed to direct sunlight creating shadow on a large part of the ledges. With the exception of some of the photos on 10th July all other photos examined were taken in periods with cloudy weather. On occasion 4 (20th July) the capture probability reached a peak in both colonies before it decreased again on the last sampling occasion.

4.2 Robust design

4.2.1 Closed-population model M_0

When model M_0 was used for the closed-population modeling under the robust design, the 5 models with the lowest AIC_c-values included time-specificity in survival rates. Capture probability was colony-specific only in sampling sessions 4 and 5 for these models. This indicates that chick-survival varied over the chick-rearing period and that capture probability seemed to differ between the colonies most considerably towards the end of the season. An overview of model selection information for the 4 best models is presented in Table 5. All these models assume that the colony-specific resighting probabilities do not differ between primary periods 4 and 5.

Table 5: Information used in model selection for the 3 best parameterizations under the robust design with closed-population model M_0 (no heterogeneity in capture probabilities) for resighting data on Brünnich's guillemot (*Uria lomvia*) chicks at two colonies in Svalbard, 2007. Capture histories are grouped by colony. The number of capture histories $n = 57$.

Model[a]	# parameters	Deviance	AIC_c	AIC_c Weight
(1) $(S_t, p_.^1 = p_.^2 = p_.^3, p_g^4 = p_g^5, N_{t*g})$	15	967.633	781.851	0.270
(2) $(S_t, p_.^1, p_.^2 = p_.^3, p_g^4 = p_g^5, N_{t*g})$	16	967.086	783.514	0.118
(3) $(S_t, p_.^1 = p_.^2, p_.^3, p_g^4 = p_g^5, N_{t*g})$	16	967.137	783.565	0.115
(4) $(S_t, p_g^1 = p_{g.}^2 = p_{g.}^3, p_g^4 = p_g^5, N_{t*g})$	16	967.279	783.707	0.107

[a] S denotes daily survival, p^t refers to the probability of being captured at least once in primary period t, and N is the abundance parameter. Emigration parameters γ_i'' and γ_i' are fixed at 0. Abundance N is set to differ between groups and between primary sampling sessions in all models.

Estimates of daily survival and capture probabilities derived from model 1, which proved to be the clearly best-fitted model, are given in Table 6. Daily survival probability increased over the first three time intervals, and then dropped in the last period. The estimates produced resulted in an overall chick survival of 0.539.

Detection probability was low for both colonies over the first three primary sampling sessions. For the remaining two sessions the colonies developed differently, with the Amfifjell colony maintaining approximately the same resighting probability as before, while in the Ossian Sars colony probability of detection was more than doubled. Variation around the estimated detection probability was highest in the two last sampling sessions and larger for the Amfifjell colony than at Ossian Sars.

Table 6: Estimates of daily survival and capture probabilities for Brünnich's guillemot (*Uria lomvia*) chicks in two colonies in Svalbard under Pollock's robust design, given for 4 time intervals in the chick-rearing period of 2007. Estimates are derived from model $(S_t, p_.^1 = p_.^2 = p_.^3, p_g^4 = p_g^5, N_{t*g})$ (no heterogeneity in capture probabilities). The number of capture histories $n = 57$.

Primary sampling session[a]	$\hat{S}$	SE $(\hat{S})$	Amfifjell colony		Ossian Sars colony	
			$\hat{p}^*$	SE $(\hat{p}^*)$	$\hat{p}^*$	SE $(\hat{p}^*)$
1	0.966	0.024	0.211	0.019	0.211	0.019
2	0.968	0.026	0.211	0.019	0.211	0.019
3	0.985	0.014	0.211	0.019	0.211	0.019
4	0.884	0.034	0.210	0.040	0.499	0.028
5	…	…	0.210	0.040	0.499	0.028

[a] For daily survival rate S the estimated probability covers the time interval from the given primary sampling session to the next. $\hat{p}^*$ is the estimated probability of being captured at least once within the given primary sampling session.

Estimates of chick abundance $(\hat{N})$ were produced for both colonies on each session. The number of chicks estimated for the last sampling occasion was 15 ($\pm$ 3) and 22 ($\pm$ 0) in the Amfifjell and Ossian Sars plot, respectively. These estimates are compared to the actual number of surviving chicks in Table 11 in section 4.4.2.

It should be noted that with all parameterizations there appeared to be difficulties in estimating all abundance parameters. In particular, $\hat{N}$ seemed not to be correctly calculated for sampling period 5, and sometimes for period 4, in the Ossian Sars colony.

4.2.2 Closed-population model M_h

The model parameterizations that proved to be best when heterogeneity was allowed in the primary sampling sessions under the robust design all suggested that survival-rates were colony-specific (Table 7). Apart from this difference the best parameterizations were similar to those seen when model M_0 was used. The best model was, however, different in that capture probability was not assumed to be equal for the last two sampling periods. Capture probabilities for the first three sessions were modeled as constant over time and equal for the two colonies.

Table 7: Information used in model selection for the 3 best parameterizations under the robust design with closed-population model M_h (allowing heterogeneity in capture probabilities) for resighting data on Brünnich's guillemot (*Uria lomvia*) chicks at two colonies in Svalbard, 2007. Capture histories are grouped by colony. The number of capture histories $n = 57$.

Model[a]	# parameters	Deviance	AICc	AICc Weight
$(1)\,(S_g, \pi_g, p_.^1 = p_.^2 = p_.^3, p_g^4, p_g^5, N_{t*g})$	24	911.846	746.470	0.365
$(2)\,(S_g, \pi_g, p_.^1 = p_.^2 = p_.^3, p_g^4 = p_g^5, N_{t*g})$	20	921.893	747.302	0.241
$(3)\,(S_g, \pi_g, p_.^1, p_.^2 = p_.^3, p_g^4 = p_g^5, N_{t*g})$	22	917.466	747.452	0.224

[a] S denotes daily survival, π denotes probability of a particular mixture, p^t refers to the probability of being captured at least once in primary period t, N is the abundance parameter. Emigration parameters γ_i'' and γ_i' are fixed at 0. Abundance N is set to differ between groups and between primary sampling sessions in all models.

Under model 1 the estimated probability of a particular mixture of capture probabilities was 0.146 ± 0.066 for the Amfifjell plot and 0.274 ± 0.066 at Ossian Sars. The interpretation of these estimates is that modeling with two different capture probabilities among the chicks seem to fit slightly better for the Ossian Sars colony than for the Amfifjell. The two proportions of chicks with different capture probabilities are denoted X and Y, respectively. Throughout the first three sampling sessions proportion X of the chicks were estimated to have a detection probability of 0.489 ± 0.072 in both colonies, while proportion Y had a capture probability of 0.100 ± 0.021. For the two last primary sessions the picture is more complex (Figure 3). At the Amfifjell plot the detection probability of proportion X increased in session 4 and then decreased in session 5. At Ossian Sars the development was the completely opposite for this

proportion. For proportion *Y* in the Ossian Sars colony the capture probability increased abruptly to 0.557 ± 0.069 in session 4, but fell to 0.180 ± 0.053 in the last session. The trajectories of the proportions may indicate that the heterogeneity in capture probabilities for the Brünnich's guillemot chicks is strongest early in the chick-rearing period, and less pronounced as they grow larger.

Model 1 estimated that the daily survival rate of the chicks in the Amfifjell colony was 0.960 ± 0.022. For the Ossian Sars plot the survival rate was estimated to be higher (0.982 ± 0.010). Estimated chick abundance in the last sampling session was 17 ± 4 and 28 ± 4 for Amfifjell and Ossian Sars, respectively.
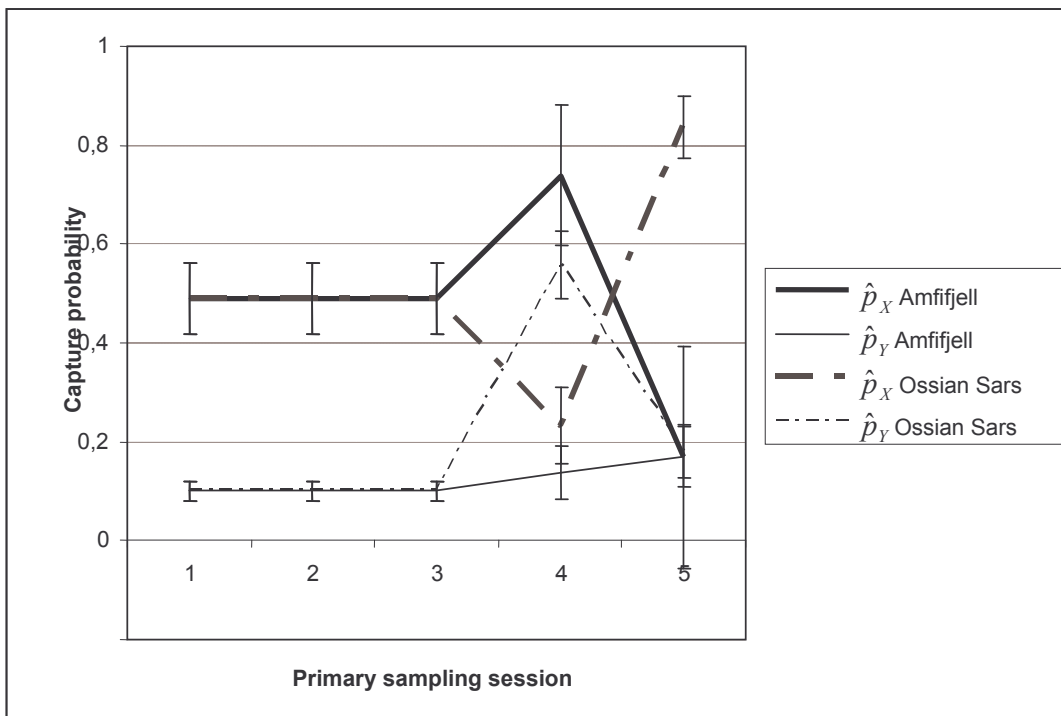
Figure 3: Estimated probability p_i^* of at least one capture within the primary sampling session for Brünnich's guillemot (*Uria lomvia*) chicks in photos from two study plots over 5 discrete sampling sessions modeled with Pollock's robust design. Closed-population model M_h assuming two mixtures *X* and *Y* of capture probabilities is used for all primary sampling periods. Error bars are $\pm$ SE. The number of capture histories = 57.

4.3 Multievent model

The multievent model with the lowest AIC_c value was model $(\pi_{.},\psi_{to+group},b_{from*group+time})$ (Table 8). This model assumes that the transition probabilities varied only with respect to state of arrival, and that this variation was parallel between the two colonies. Thus, the chance of hatching successfully for an egg (given by the transition probability $\psi^{egg,alive}$) was equal to the probability $\psi^{alive,alive}$ of staying alive for a chick under this parameterization. The probability of event "adult" differed with the underlying state of the chick. The model also states that the probability of observing an adult on a site was different for the colonies and changing in a parallel manner over time. The second-best model, which had a ΔAIC_c of 1.375, differs only from model 1 by assuming that hatching probability was not equal to survival probability for a chick.

Table 8: Information used in model selection for the three best parameterizations under the multievent model for mark-resighting data of Brünnich's guillemot (*Uria lomvia*) chicks collected from photo series for two study plots in Svalbard, 2007. Capture histories are grouped by colony. The number of capture histories $n = 109$.

Model[a]	# parameters	Deviance	AIC_c
(1) $(\pi_{.},\psi_{to+g},b_{f*g+t})$	11	718.450	740.862
(2) $(\pi_{.},\psi_{to+f*g},b_{f*g+t})$	13	715.669	742.237
(3) $(\pi_{.},\psi_{to*g},b_{f*g+t})$	12	718.451	742.938

[a] *to* denotes state of arrival, *f* denotes state of departure, *g* denotes group (colony) and *t* denotes time.

The difference in AIC_c between the two best models under the multievent design was more than one unit, which supports the choice of model 1 as the model describing these MR data best (Lebreton et al. 1992). Estimates of daily transition probabilities for the two colonies derived from model 1 are presented in Table 9. The daily probability of surviving and/or hatching successfully (transition from state "egg" or "alive" to state "alive") was estimated to be 4 % lower for individuals in the Amfifjell plot than at Ossian Sars. For both colonies the estimated probability $\hat{\psi}^{egg,egg}$ of an egg not hatching *and* not being lost was close to zero. Hence, the estimated daily probability of egg loss was approximately the compliment of daily hatching probability ($\hat{\psi}^{egg,alive}$).

Table 9: Estimates of daily transition probabilities for Brünnich's guillemot (*Uria lomvia*) chicks in two colonies in Svalbard, 2007, under the multievent model $(\pi_{.}, \psi_{to+g}, b_{f\bullet g+t})$. The number of capture histories $n = 109$.

Parameter	Amfifjell colony		Ossian Sars colony	
	Estimate	SE	Estimate	SE
$\hat{\psi}^{egg,egg}$	<< 0.001	<< 0.001	<< 0.001	<< 0.001
$\hat{\psi}^{egg,alive}$ and $\hat{\psi}^{alive,alive}$	0.948	0.010	0.988	0.003

Overall chick survival estimated with model 1 was 0.499 ± 0.070 for the Amfifjell colony and 0.851 ± 0.037 for the Ossian Sars colony. Breeding success (the product of hatching success and overall chick survival) was calculated to be 0.308 ± 0.074 in the Amfifjell colony and 0.761 ± 0.076 in the Ossian Sars colony.

The probability of observing an adult on a breeding-site clearly depended on whether there was a living chick on the site or not, as indicated by the three best-fitting models. Estimates from model 1 show that for a site that held a chick the probability of recording the event "adult" decreased gradually for both colonies from approximately 0.75 to 0.40 over the breeding season, disrupted only by a rise on capture occasion 4 (15th July) (Figure 4). For the Ossian Sars colony the same pattern of change is displayed if the chick is dead, but the probability of recording an adult on the site was estimated slightly lower in this case, ranging from 0.50 to 0.18. For the Amfifjell colony, on the other hand, the probability of seeing an adult on an empty site was estimated to be close to 1 throughout the whole period.
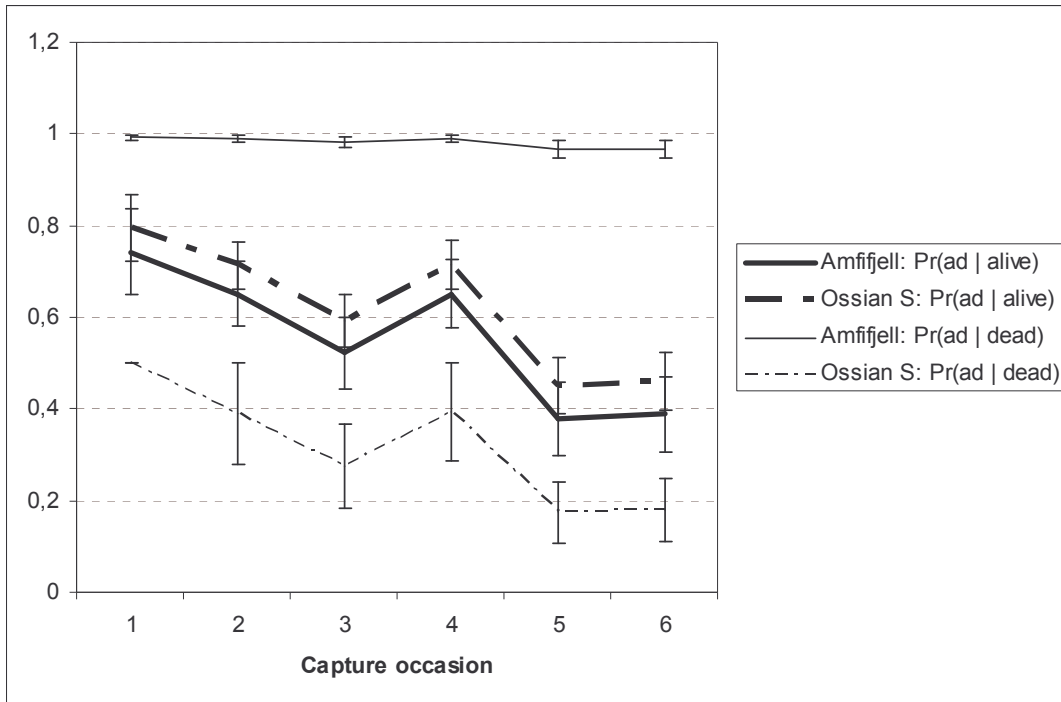
Figure 4: Estimated probability of event "adult" (ad) given that the chick is alive and dead, respectively, on Brünnich's guillemot (*Uria lomvia*) breeding-sites in two colonies in Svalbard over 6 capture occasions in 2007. Estimates are derived from the multievent model $(\pi_{.}, \psi_{to+g}, b_{f*g+t})$. Error bars are ± SE, and time between the capture occasions is 9, 3, 2, 5 and 3 days, respectively. The number of capture histories *n* = 109.

Since a living chick on a breeding-site can only produce the event "adult" or "chick" under this model, the probability of observing a chick on the site is the complement of the probability of recording the adult only. Thus, the chance of observing a chick was estimated to increase over the period in both colonies.

4.4 Model estimates and reality compared

4.4.1 Breeding success

The close-range investigations of the ledges in both colonies on the last capture occasion (23rd July) revealed that 32 of the 47 breeding-sites identified on photos of the Amfifjell colony had a living chick. In the Ossian Sars colony there were at least 28 surviving chicks out of the 62 breeding-sites on the same date. This yields what will here be termed a "true breeding success" of 0.681 and 0.452 for the Amfifjell and Ossian Sars colony, respectively. For the latter the estimate is a minimum, keeping in

mind that the ledges could not be investigated as thoroughly as in the Amfifjell colony. Assigning the surviving chicks to their respective breeding-sites on the Amfifjell plot proved to be a difficult task, as some chicks that could be found under the close-range searches might have belonged to breeding-sites that could not be seen in the photos due to camera angle and characteristics of the ledges. Chicks belonging to breeding-sites that were not among the 109 sites defined at the start of the study were disregarded to the extent possible. Biases of unknown direction can, however, not be ruled out for the breeding success observed at the Amfifjell colony. Comparing the true breeding success with the estimates derived from the multievent model reveals a lack of accordance between reality and model estimates (Table 10). The multievent model underestimated breeding success for the Amfifjell plot with more than 37 %, whereas for the Ossian Sars colony the estimate was nearly 31 % higher than true breeding success.

Table 10: True breeding success for two Brünnich's guillemot (*Uria lomvia*) study plots in Svalbard, 2007, compared with estimated breeding success derived by multievent modeling of mark-resighting data from photo series. The number of breeding-attempts is 109.

Method for estimating breeding success B	Amfifjell colony		Ossian Sars colony	
	$\hat{B}$	SE$(\hat{B})$	$\hat{B}$	SE$(\hat{B})$
Field inspections	0.681		0.452	
Multievent modeling	0.308	0.074	0.761	0.056

4.4.2 Chick survival

Of the 21 breeding-sites that were known to have hatched a chick within the plot at the Amfifjell colony there were 17 that had a chick on the last capture occasion, which gives a true chick survival rate of 0.810 between 10th and 23rd July. In the Ossian Sars colony there were 27 chicks left of the 36 that had hatched successfully, resulting in a true chick survival of 0.750. As noted for breeding success, a more thorough search method would probably have given a somewhat higher survival rate at Ossian Sars. In Table 11 these rates are compared with the overall survival probability estimates deduced from the single-state models. The CJS model produced an estimate of overall chick survival for the Amfifjell colony that was 21.9 % lower than the true survival rate. The estimate for the Ossian Sars colony, however, was very close to true survival. Chick survival was underestimated for both colonies under the robust design using

model M_0 for the primary periods. When modeling individual heterogeneity in capture probabilities the estimates were greatly improved, especially for the Ossian Sars colony. Overall chick survival estimated by the multievent model is also presented in Table 11 for comparison, although the reader should keep in mind that the multievent model estimators are based on a larger data set than the single-state estimators. Like breeding success, chick survival is underestimated for the Amfifjell colony and overestimated for the Ossian Sars colony by the multievent model.

Table 11: True chick survival rate over the chick-rearing period for two Brünnich's guillemot (*Uria lomvia*) study plots in Svalbard, 2007, compared with estimated chick survival derived from different approaches for modeling survival with mark-resighting data from photo series.

Method for estimating overall chick survival rate ϕ	Amfifjell colony		Ossian Sars colony	
	$\hat{\phi}$	SE $(\hat{\phi})$	$\hat{\phi}$	SE $(\hat{\phi})$
Field inspections[a]	0.810		0.750	
Single-state CJS model[a]	0.591	[c]	0.749	[c]
Robust design, no heterogeneity[a]	0.539	[c]	0.539	[c]
Robust design, heterogeneity[a]	0.586	0.178	0.790	0.103
Multievent model[b]	0.499	0.070	0.851	0.037

[a] Field inspections and capture histories producing the model estimates follow the same 57 individuals.

[b] The data set for the multievent model also includes capture histories with no resightings of chicks (*n* = 109).

[c] SE was not calculated due to the complexity of the procedure when time intervals of unequal lengths have different survival estimates.

Chick abundance $(\hat{N})$ estimated for the last sampling session under the robust design with closed-population model M_0 was lower than the true number of surviving chicks found in both colonies on this date (Table 12). The difference was most pronounced in the Ossian Sars plot. Including heterogeneity in the model produced abundance estimates that were closer to the true number of chicks, though the variance was larger.

Table 12: True number of surviving Brünnich's guillemot (*Uria lomvia*) chicks in two study plots in Svalbard at the end of chick-rearing in 2007 compared with estimated chick abundance derived from Pollock's robust design using two alternative closed-population models. Field inspections and capture histories producing the model estimates follow the same 57 individuals.

Method for estimating chick abundance N before fledging	Amfifjell colony		Ossian Sars colony	
	$\hat{N}$	SE $(\hat{N})$	$\hat{N}$	SE $(\hat{N})$
Field inspections	17		27	
Pollock's robust design, no heterogeneity[a]	15	3	22	0
Pollock's robust design, heterogeneity	17	4	28	4

[a] Point estimate and standard error for the Ossian Sars colony appeared not to have been correctly computed due to unreasonably high beta estimates.

5 Discussion

The three different modeling designs that were applied to mark-resighting data for Brünnich's guillemot chicks generated ambiguous survival estimates. Averaged estimates for competing parameterizations under the Cormack-Jolly-Seber model produced an estimate of chick survival for the Ossian Sars colony that was in accordance with field investigations. Pollock's robust design underestimated survival for the same plot when individual heterogeneity in capture probabilities was not allowed in the model. The multievent model, accounting for uncertainty of state for breeding-sites by utilizing observations of adults, overestimated chick survival for the Ossian Sars colony. Survival probability for the Amfifjell colony was underestimated by all models.

The fact that all modeling designs underestimated survival rate for the Amfifjell colony suggests that some colony-specific attribute had decisive influence on the estimators. A suitable approach to unveil which properties may have had this effect is to investigate the assumptions underlying the mark-recapture models and assess to which extent they may have been violated in the two colonies. Model assumptions will therefore be the salient point in this section, and possible causes of the pronounced underestimation of chick survival for the Amfifjell colony will be dealt with first. Seeing that the models produced diverging survival estimates for the Ossian Sars plot, both violation of assumptions and other possible causes of estimator bias are then considered in section 5.2. In his presentation of the multievent model Pradel (2005) does not mention robustness of the estimators to violation of model assumptions. So far, little research has been done regarding consequences of deviations from assumptions for multistate models (Williams et al. 2002). Therefore, the considerations here will be based on what is known for single-state models on this subject.

5.1 Underestimated survival rate for the Amfifjell plot

Low-biased estimates of survival probability under the CJS model can be caused by tag loss, heterogeneous capture probabilities (Lebreton et al. 1992) and temporary emigration (Kendall et al. 1997). Under the robust design both Markovian and random temporary emigration will lead to biased estimates of survival. If marking in itself is negatively affecting the health of the study objects the estimated survival probability will also be biased low (Pollock et al. 1990).

5.1.1 Tag loss and temporary emigration

In this study the chicks were not marked physically. Instead, the breeding-sites were marked, and any observation related to each site was recorded. Negative effects of marking can thus be disregarded. However, both tag loss and temporary emigration could have occurred if the chicks were able to move to positions on the ledges that could not be observed from the camera point. During field visits the chicks were never seen to move around on the ledges, not even when field workers came so close that the parent birds were forced to leave. Some chicks put their heads into nearby cracks or tried to hide between rocks on these occasions, but no movement away from the breeding-sites was recorded. It is therefore unlikely that tag loss and temporary emigration occurred. Still, movement of this kind can not be ruled out completely if the ledges are wide and flat enough for chicks to change positions or if there are crevices and overhangs where they can escape. This type of conditions did apply to some of the breeding-sites within the Amfifjell plot.

5.1.2 Heterogeneous resighting probabilities

The size of the chick can definitely be expected to affect its detection probability. Egg-laying tends to be synchronous, so given that the chicks have approximately equal growth rates, they can also be expected to have equal resighting probabilities at every sampling occasion. Nevertheless, there will always be some temporal spread of egg-laying and hatching (Harris and Birkhead 1985), so the assumption of equal detection probability for all individuals within each capture occasion can not be met in this case.

All three modeling designs suggested that detection probability changed over the course of the study, although they modeled the changes somewhat differently. The distinct increase in resighting probability estimated for both colonies under the multievent model probably reflects the fact that chicks become easier to spot as they grow larger. This is not as evident when looking at the more fluctuating estimates of the CJS model, indicating that the latter failed to capture an expected development detected by the multievent model. Under the robust design an increasing detection probability towards the end of the period was only expressed for the Ossian Sars colony. Despite the growth of the chicks in the Amfifjell colony, their visibility was not increased. This signals that detection probability was independent of chick size in this colony, or that a factor other than chick size was more important in determining visibility of the chicks in the photos.

Through investigations of the data for the wide ledge at the Amfifjell plot it became evident that breeding-sites in the foreground of the photos had more chick resightings than their neighbouring sites further away from the camera. For the sites on the far end of the ledge only the adult could be seen on all sampling occasions. The reason seems to be that adult birds sitting closest to the camera blocked the view enough to reduce the capture probability of chicks located in the middle and on the far side of the ledge. Thus, breeders crowding together on wide ledges appear to cause heterogeneous capture probabilities for the chicks. No pattern of this kind was apparent in the Ossian Sars plot, where the birds were more spread out on a large number of small ledges and the photos were taken from a point overlooking the plot. Even though the survival rate estimator for the CJS model and the robust design is relatively robust to heterogeneous capture rates (Pollock et al. 1990), parameter estimation for the Amfifjell plot obviously suffered under the violation of this assumption.

5.1.3 Lack of data

It seems reasonable to anticipate that underestimated transition probability from "alive" to "alive" under the multievent model can be caused by overestimated probability of state "dead". When calculating the probability that a chick is dead the multievent model accounts for uncertainty of state for chicks that are not known to be dead through Pr(adult | dead), the estimated probability of observing an adult on a breeding-site from which the chick has been lost. Pr(adult | dead) was always high within the plot at the Amfifjell, clearly differing from what was estimated for Ossian Sars. The unreasonably high estimate for the Amfifjell colony is believed to have been caused by lack of observations of empty sites. Only 2 of the 47 capture histories in this plot included the event "no chick". One of these breeding-sites was observed empty on the last two sampling occasions, and the other one was seen empty only on the last occasion. Thus, there was no certain information of empty sites being occupied by adults. In comparison, 14 breeding-sites at Ossian Sars were recorded empty at least once, and, more importantly, on 6 of these sites an adult was observed after the site was known to have lost the chick. Lacking this kind of information for the Amfifjell colony the model calculated the probability Pr(adult | dead) of seeing an adult bird on an empty site by the compliment of the probability of observing that the chick was gone. A low proportion of observations of empty sites rendered a low probability Pr(no chick | dead) of observing that a site was empty. Accordingly, the probability of seeing an adult occupying an empty site was estimated to be high. As more than half of the capture

histories recorded at the Amfifjell colony consisted solely of observations of adult birds, the probability that the chicks were dead was overestimated.

Based on the previous argument it is sensible to believe that the estimated probability of observing an adult on an empty site in the Ossian Sars colony is more reliable than that estimated for the plot at the Amfifjell. In turn the transition probability estimates for Ossian Sars should be less biased, which also appears to be the case. The methodologically important question is then what causes the difference in Pr(adult | dead) between the colonies. Again, the deviation seen at the Amfifjell colony can be related to the width of the most densely populated ledge and the low visual angle for this study plot. The breeders closest to the edge blocked the full view of other breeding-sites, and thus reduced the chance of observing the real state of many of the chicks.

5.2 Diverging survival rates for the Ossian Sars plot

The overall survival rate estimated for the Ossian Sars colony under the multievent model was 10 % higher than the true overall survival rate calculated from field observations. However, for this colony one should keep in mind that the 27 chicks observed on the last day of the study represent the minimum number of surviving chicks. Due to the inadequacy of the search procedure the true survival probability might actually have been higher. If e.g. 2 chicks were missed, and the real number of chicks within the plot was 29, the true survival probability would be only 4.5 % below the multievent model estimator and 5.7 % higher than what was estimated by the CJS model. The estimate derived by the robust design allowing for heterogeneity would in this case be in accordance with reality. Considering this, the models seem to perform equally well when heterogeneity in capture probabilities is not severe. Still, the large difference between true breeding success and the estimate given by the multievent model can not be explained this way, and a lack of accordance between the modeling designs is noticeable. Weaknesses of the study design and other possible causes of estimator bias are therefore considered here.

5.2.1 Methods and sample size

The number of breeding-sites was defined solely by examining photos. Only the 57 capture histories used with the CJS model and robust design were confirmed to have been breeding attempts. Gaston and Nettleship (1981) noted that daily counts of adult Brünnich's guillemots on Prince Leopold Island never fell below the number of

breeding pairs after the median date of egg-laying. However, they also found that non-breeding Brünnich's guillemot pairs may gradually occupy vacant sites in the colony during the incubation period (Gaston and Nettleship 1981). Therefore, assuming that sites that were occupied on every photo over 5 days late in the incubation period had an egg may have led to a positive bias in the number of breeding-sites. This will in turn underestimate breeding success calculated by the number of chicks found on field inspections. As the amount of sites established by non-breeders should not be expected to exceed 5 % (Gaston and Nettleship 1981), the difference would in this case amount to 1 or 2 sites per plot. Particularly popular resting-positions may also have been occupied by non-breeders or off-duty brooders at nearly all times, but these birds would rarely sit down like brooding birds. The effect of "false" breeders on the estimators of the multievent model would probably be an overestimation of egg-loss, as these sites would have a higher probability of revealing that they were in fact empty. Likewise, the estimated probability of event "adult" for a site with no chick could potentially be biased high.

The second-best parameterization of the multievent model assumed that probability of hatching was different from the probability of staying alive for a chick. The better fit of the model that did not distinguish hatching success from chick survival might reflect that hatching had already occurred on a proportion of the breeding-sites before 1st July. After all, the egg-state was an "assumed" state that was never actually observed for any of the breeding-sites on this date. Defining the breeding-attempts on an earlier stage of the incubation period will therefore be appropriate to assure that the parameter $\hat{\psi}^{egg,alive}$ actually reflects hatching success only.

Sample size is above all a determinant for estimator precision, but deserves consideration here even though survival estimates generally appeared to have relatively small variances. The number of capture histories needed to achieve a certain precision in survival rate estimates is closely related to capture and survival probability of the study objects (Williams et al. 2002). Following figures presented by Pollock et al. (1990), who considered a coefficient of variation of 20 % as satisfactory, a capture probability of at least 0.4-0.5 is necessary when sampling a population of 50-100 individuals and survival rate between sampling occasions is 0.9. Resighting probabilities estimated for the CJS model were high enough to meet this requirement, but under the robust design with model M_0 capture rate exceeded 0.4 only in the last two sampling sessions for the Ossian Sars colony. However, the design strategies for the robust design are more complex, as closed and open models are combined (Pollock et

al. 1990). Knowing that small populations require much higher capture probabilities than larger ones, sample size is assumed to have been at a minimum in this case.

Sample size probably also played an important role in the choice of closed-population model for the robust design, seeing that the model selection procedure in program CAPTURE will perform poorly when sample sizes are small (Menkens and Anderson 1988). Due to the small number of chicks observed in this study the program may have been unable to detect patterns of variation in capture probabilities, and defaulted to suggesting model M_0 for the analysis. This would represent a violation of the assumption that capture probability over the secondary periods varies according to specifications dictated by the structure of the selected closed-population model. Using model M_0 when capture probabilities are heterogeneous will result in negative bias in the estimated abundance $\hat{N}$ (Otis et al. 1978), a result seen for both colonies in this study when M_0 was used. Allowing for heterogeneity in capture probabilities within the sampling sessions gave abundance and survival rate estimates that were closer to the true values found through field investigations. Although the probabilities of a particular mixture were not large, all parameters could be estimated under model M_h as opposed to when heterogeneity was not modeled. This further supports the impression that heterogeneity was at work and should be accounted for in the modeling. However, modeling with heterogeneity probably induced a greater uncertainty around the estimates due to the small sample size.

Although the multievent model could make use of nearly twice as many capture histories as the CJS model, a correspondingly higher number of parameters was needed to model all the transition and event probabilities. The multievent model is clearly "data-hungry", and, as discussed above, does not seem to yield correct transition estimates if observations of chicks and empty breeding-sites are not adequately represented in the capture histories.

Maximizing capture probability and the number of breeding-sites will optimize both estimator precision and reliability of the models. Capture probability can be increased by utilizing more photos. However, it should be stressed that with the methods used in this study, data extraction from the photos was a time-consuming job. Even when the photo processing has become a routine procedure it will not be justifiable in terms of resource use to aim at obtaining more than 30 capture occasions for each plot after all breeding-sites have been identified.

5.2.2 Independence of fates

Gaston and Nettleship (1981) found that breeding success for Brünnich's guillemots on Prince Leopold Island to a certain point increased with the number of close neighbours on the ledges. Adults packed closely together on the ledges can make a strong defense against glaucous gulls, and neighboring breeders could also have some degree of thermal advantage from each other. Breeding success also seemed to be affected by the physical characteristics of the breeding-site on Prince Leopold Island. Effects of these variables were not controlled for in this study. It would be possible to treat the number of neighbours for each breeding-site as an individual covariate in the analyses, but qualitatively good data for the physical characteristics of the ledges would be difficult to extract from photos.

Recognizing that survival probability can depend on the number of close neighbours, the assumption of individually independent survival probabilities should be considered. When a chick dies on the ledge or is taken by predators the adults will very often keep occupying the breeding-site, but probably to a lesser extent than before. This might lead to a thinning of the defensive ranks, making the remaining breeders more vulnerable to attacks. One could therefore argue that the survival probabilities of the chicks are not independent. If so, the dependence should be most pronounced on broad ledges, where e.g. gulls would have enough room to land and molest the breeders. However, guillemots that have lost their chicks have been observed defending the ledges against gulls at least as intensively as parents with chicks (Gaston and Nettleship 1981), so the degree of dependence of survival probabilities in the chick-rearing period is not necessarily of great importance.

5.2.3 Population closure

The six photos (i.e. the secondary sampling occasions) that constituted each primary sampling session under the robust design were always taken within a period of 20 hours. It can very well be argued that this period is too long to rule out any deaths among the chicks. Additionally, even though all chicks were expected to be hatched and in the study area at the beginning of the first sampling session, late hatchers would represent gains to the population that could also occur within any of the primary sessions. The last hatching was in fact observed in the Ossian Sars colony on the 24th July, the day after the last sampling.

Effects of violation of the closure assumption was explored by Kendall (1999), who found that if gains and losses in the study area are completely random they will not

introduce bias to the estimators from closed-population models. In the case of Brünnich's guillemot chicks, mortality is highest immediately after hatching, and then decreases throughout the chick-rearing period (Gaston and Nettleship 1981). The number of hatchings per day exhibits approximately the same pattern after the peak in hatching has been reached. The estimated abundance should therefore not be greatly affected, as the effect of gains would probably be equalized by the effect of losses.

As survival rate estimation is the centre of attention in this thesis, the abundance estimates produced by the robust design have not been focused on. It is nevertheless interesting to notice that by dividing the estimated abundance for the last sampling session by the number of initial breeding-sites one can get approximations of breeding success that are much closer to true breeding success than the estimates produced by the multievent model.

5.2.4 Dependencies of events

The multievent model assumes that the probability of an adult occupying a breeding-site depended only on the state of the egg or chick. A potential violation of this assumption is induced by the territorial behaviour of the Brünnich's guillemot. The fact that the female can stay in the colony to defend the breeding-site for a long time after the chick has fledged will not necessarily be a problem as long as all sampling is done before the fledging starts. However, pairs are also known to have restarted breeding after presumably having lost their chick, which signals that relaying can potentially occur throughout the whole breeding-season. In addition, abandoned sites will probably be visited by non-breeders and neighbouring birds. Hence, adult birds may be occupying breeding-sites at all times regardless of the state of the egg or chick. The event probability estimators of the multievent model can therefore be expected to be biased, which in turn will influence the transition estimates. This is perhaps the chief objection to using the multievent model in this setting. The best way to minimize the potential bias is by sampling from easily surveyed ledges to maximize the number of certain observations of chicks and empty breeding-sites.

6 Conclusions and recommendations

Modelling survival probabilities for Brünnich's guillemot chicks with resighting data from photo series was more successful when using the Cormack-Jolly-Seber model and Pollock's robust design compared to Pradel's multievent model. However, none of the models explored in the study produced convincing survival estimates under all conditions. Wide and densely populated ledges produced complexity in capture probabilities that could not be adequately handled by any of the modelling designs. Individual heterogeneity in capture probabilities probably represented the most severe challenge.

The multievent model does not seem to perform well unless the capture histories include some amount of certain observations of chicks and empty breeding-sites. The apparently complex parameter interactions within this model are not yet fully described, and the assumption that observed events are only dependent on the underlying state of the chick is likely to be violated for Brünnich's guillemots due to their site fidelity even after breeding failure. Too many uncertainties are therefore related to the multievent model for it to be recommended as a means of estimating chick survival in this species at this time.

The CJS model seems to perform better, being simple and producing conservative estimates of chick survival using resighting data that are relatively easily obtained. As Pollock's robust design has the property of allowing heterogeneity to be modelled, it also has the potential of performing well if gains and losses of chicks can be expected to occur at equal rates throughout the chick-rearing period.

The inferences made above are based on a relatively small data set. However, the factors that are most likely to cause bias in estimated survival rates for Brünnich's guillemot chicks when models are applied to resighting data from photos have been identified here. The models evaluated here should be tested further with larger datasets, and avoiding violations of model assumptions will then be essential. Heterogeneity in capture probabilities and dependence of fates for the chicks are minimized if the study plots consist of short, narrow ledges where the breeders have few or no close neighbours. A high camera angle is advisable to provide a full view of all breeding-sites. Both the CJS model and the robust design produce acceptable survival estimates under these conditions. If heterogeneity in capture probabilities can be modelled, the robust design also appears to provide abundance estimates that are close to the true number of chicks, allowing for an alternative approach to estimating breeding success.

7 References

Anderson, D. R., and K. P. Burnham. 1999. Understanding information criteria for selection among capture-recapture or ring recovery models. Bird Study **46**:14-21.

Anker-Nilssen, T., V. Bakken, H. Strøm, A. N. Golovkin, V. V. Bianki, and I. P. Tatarinkova. 2000. The Status of marine birds breeding in the Barents Sea region. Norwegian Polar Institute, Tromsø.

Bédard, J. 1985. Evolution and Characteristics of the Atlantic Alcidae. Pages 1-51 *in* D. N. Nettleship and T. R. Birkhead, editors. The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas. Academic Press, London.

Birkhead, T. R. 1985. Coloniality and Social Behaviour in the Atlantic Alcidae. Pages 355-382 *in* D. N. Nettleship and T. R. Birkhead, editors. The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas. Academic Press, London.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Choquet, R., L. Rouan, and R. Pradel. 2008. Program E-SURGE: A software application for fitting Multievent models. *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling Demographic Processes in Marked Populations. Springer, New York.

Cormack, R. M. 1964. Estimates of Survival from Sighting of Marked Animals. Biometrika **51**:429-438.

Gaston, A. J., and D. N. Nettleship. 1981. The Thick-billed Murres of Prince Leopold Island: a study of the breeding ecology of a colonial high arctic seabird. Canadian Wildlife Service, Ottawa.

Harris, M. P., and T. R. Birkhead. 1985. Breeding Ecology of the Atlantic Alcidae. Pages 155-204 *in* D. N. Nettleship and T. R. Birkhead, editors. The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas. Academic Press, London.

Harris, M. P., S. Wanless, and T. R. Barton. 1996. Site use and fidelity in the common Guillemot Uria aalge. Ibis **138**:399-404.

Jolly, G. M. 1965. Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model. Biometrika **52**:225-247.

Kendall, W. L. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. Ecology **80**:2517-2525.

Kendall, W. L., J. E. Hines, and J. D. Nichols. 2003. Adjusting multistate capture-recapture models for misclassification bias: Manatee breeding proportions. Ecology **84**:1058-1066.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology **78**:563-578.

Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A Likelihood-Based Approach to Capture-Recapture Estimation of Demographic Parameters under the Robust Design. Biometrics **51**:293-308.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling Survival and Testing Biological Hypotheses Using Marked Animals - a Unified Approach with Case-Studies. Ecological Monographs **62**:67-118.

Menkens, G. E., and S. H. Anderson. 1988. Estimation of Small-Mammal Population-Size. Ecology **69**:1952-1959.

Nettleship, D. N., and P. G. H. Evans. 1985. Distribution and Status of the Atlantic Alcidae. Pages 53-154 *in* D. N. Nettleship and T. R. Birkhead, editors. The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Waters. Academic Press, London.

Nichols, J. D., J. E. Hines, D. I. MacKenzie, M. E. Seamans, and R. J. Gutierrez. 2007. Occupancy estimation and modeling with multiple states and state uncertainty. Ecology **88**:1395-1400.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical Inference from Capture Data on Closed Animal Populations. Wildlife Monographs:7-135.

Pollock, K. H. 1982. A Capture-Recapture Design Robust to Unequal Probability of Capture. Journal of Wildlife Management **46**:752-757.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical Inference for Capture-Recapture Experiments. Wildlife Monographs:1-97.

Pradel, R. 2005. Multievent: An extension of multistate capture-recapture models to uncertain states. Biometrics **61**:442-447.

Schwarz, C. J., J. F. Schweigert, and A. N. Arnason. 1993. Estimating Migration Rates Using Tag-Recovery Data. Biometrics **49**:177-193.

SCRIB. 2007. Seabird Colony Registry of the Barents and White Seas. Unpublished database. Norwegian Polar Institute.

Seber, G. A. F. 1965. A Note on Multiple-Recapture Census. Biometrika **52**:249-259.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Charles Griffin, London.

Strøm, H. 2006. Brünnich's Guillemot. Pages 163-166 *in* K. M. Kovacs and C. Lydersen, editors. Birds and mammals of Svalbard. Norwegian Polar Institute, Tromsø.

Walsh, P. M., D. J. Halley, M. P. Harris, A. del Nevo, I. M. W. Sim, and M. L. Tasker. 1995. Seabird monitoring handbook for Britain and Ireland: a compilation of methods for survey and monitoring of breeding birds. Joint Nature Conservation Committee, Peterborough.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46**:120-139.

White, G. C., K. P. Burnham, and D. R. Anderson. 2001. Advanced features of Program MARK. Pages 368–377 *in* R. Field, R. J. Warren, H. Okama, and P. R. Sievert, editors. Wildlife, land, and people: priorities for the 21st century. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland, USA.

Williams, B. K., M. J. Conroy, and J. D. Nichols. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.