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Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival.

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ABSTRACT

1. Long-term monitoring programs often involve substantial input of skilled staff time. In mark-recapture studies, considerable effort is usually devoted to both marking and recapturing/resighting individuals. Given increasing budgetary constraints, it is essential to streamline field protocols to minimize data redundancy while still achieving targets such as detecting trends or ecological effects.
2. We evaluated different levels of field effort investment in marking and resighting individuals by resampling existing mark-recapture-recovery data to construct plausible scenarios of changes in field protocols. We demonstrate the method with 26 years data from a common guillemot *Uria aalge* monitoring programme at a major North Sea colony. We also assess the impact of stopping the ringing of chicks on our ability to study population demography using integrated population models (IPM) fitted to data, including information on breeding adults. Different datasets were removed artificially to explore the ability to compensate for missing data.
3. Current ringing effort at this colony appears adequate but resighting effort could be halved while still maintaining the capacity to monitor first-year survival and detect the effect of hatch date on survival prospects.
4. The IPM appears robust for estimating survival, productivity or abundance of the breeding population, but has limited capacity to recover year-specific first-year survival when chick data are omitted. If productivity was not monitored, the inclusion of chick data would be essential to estimate it, albeit imprecisely.
5. *Synthesis and applications.* Post-study evaluation can help streamline existing long-term environmental monitoring programs. To our knowledge, this study is the first use of data thinning of existing mark-recapture-recovery data to identify potential field effort reductions. We also highlight how alternative monitoring scenarios can be evaluated with IPMs when data are collected on different aspects of demography and abundance. When effort reduction is necessary, both approaches provide decision-support tools for adjusting field protocols to collect demographic

data. The framework has broad applicability to other taxa and demographic parameters, provided suitable long-term data are available, and we discuss its use in different contexts.

Keywords: data thinning, hidden parameters, individual covariates, integrated population model, juvenile survival, long-term monitoring, mark-recapture-recovery, productivity, survey design, *Uria aalge*.

INTRODUCTION

Long-term population monitoring is critical for many ecological studies and conservation programmes in a rapidly changing world, but often involves significant skilled staff time. This is particularly true for intensively monitored populations in which several aspects of a species' demography may be studied alongside population abundance. However, the continuity of many, perhaps even most, long-term studies is continually being challenged by the problem of maintaining uninterrupted funding (Clutton-Brock & Sheldon 2010). As monitoring programs and long-term individual-based studies come under increasing pressure to save money, it becomes imperative to optimise the use of resources to make them as cost-effective as possible. However, it is also necessary to minimise the risks of programmes failing to achieve their primary aims such as detecting population trends, identifying environmental drivers or pin-pointing which life stages are most vulnerable. In addition, one of the most valuable aspects of such studies is to discover previously unsuspected effects (Wintle, Runge & Bekessy 2010) and this often depends on having spare capacity.

The relevance of study design to ecological studies is widely recognised but often disregarded (Yoccoz, Nichols & Boulinier 2001). In the context of mark-recapture ('MR') studies, design considerations include a range of issues that can affect estimator bias and/or precision (Lindberg 2012). In this paper we focus on one particular design aspect, namely the implications of varying field effort, in terms of marking and recapturing individuals, in order to meet the objectives of a MR-based monitoring programme. Sample-size recommendations are typically based on simplistic model

structures (e.g. Burnham *et al.* 1987). For more complex and targeted structures, two different approaches have been suggested: (i) computer-intensive Monte Carlo simulations, where many datasets are generated and analysed (e.g. Chambert *et al.* 2012), and (ii) a less commonly used method based on a single dataset of expected values (Burnham *et al.* 1987) that is valid under large sample approximations (e.g. Devineau, Choquet & Lebreton 2006).

Here we resample an extensive mark-resight-recovery (MRR) dataset for common guillemot *Uria aalge* (Pontoppidan, 1763) (hereafter guillemot) chicks ringed at the Isle of May, south-east Scotland (56°11'N, 2°34'W) between 1983 and 2009, to simulate the effect of varying field effort on our ability to estimate survival over the chicks' first winter and investigate individual-level covariates. Monitoring the guillemot population on the Isle of May, one of the four 'Key Site' seabird colonies in the UK's Seabird Monitoring Programme (Mavor *et al.* 2008), involves annual assessments of (i) the total breeding population, (ii) breeding success, (iii) survival of breeding adults and (iv) the survival of chicks after they leave the colony. The last is particularly important since guillemot chicks go to sea when only a quarter of their adult size and are then fed for several weeks by the male parent while completing their growth (Harris, Webb & Tasker 1991). However, estimating chick survival is time-consuming, involving (i) a team of ringers to maintain a marked population (about 10 person-days year⁻¹) and (ii) a skilled observer to search cliffs and sea-rocks regularly and record ringed individuals returning to the colony (an annual average of 58 daily searches of 2–3 hours). Is all this effort essential or can input be reduced without losing the ability to detect within and among year variation in survival?

Although the effectiveness of some aspects of monitoring on the Isle of May has been assessed (e.g. detecting abundance trends, Sims *et al.* 2006), no such evaluation has been conducted for the MRR sampling. Our study assessed whether variations in first-year survival and relationships with individual-level covariates could have been detected had field effort been reduced, following two strategies: (i) reducing the time spent looking for ringed guillemots; (ii) reducing the number of chicks ringed. We constructed and analysed scenarios where field effort was progressively reduced by

resampling the chick mark-resight-recovery data already collected. We also investigated an extreme scenario that involved stopping ringing chicks altogether, thus losing the direct source of information on immature survival. As breeding adults were also monitored on the Isle of May (resightings of ringed birds, productivity data and population counts), we examined the usefulness of an integrated population model (IPM) to monitor the population. IPMs model simultaneously abundance and the demographic parameters that drive its fluctuations (Besbeas *et al.* 2002). This strategy of combining datasets may allow the estimation of demographic parameters for which no direct data are available (e.g. productivity in Besbeas *et al.* 2002; productivity and proportion of females in Tavecchia *et al.* 2009), so we investigated whether we could recover first-year survival from the adult-related datasets alone. Conversely, we explored whether the omission of juvenile survival data degraded the estimation of adult survival and abundance that could be achieved with an IPM. Finally, we considered a hypothetical scenario, in which productivity data, that can also be time-consuming to obtain, were not collected either. Fig.1 provides a summary of the analyses conducted.

MATERIALS AND METHODS

Reference MRR analysis

Data and field methods

Details of the field methods are given in Harris, Frederiksen & Wanless (2007). A total of 6665 guillemot chicks were ringed between 1983 and 2009 (96–325 annually), with a colour ring on one leg (inscribed with an individual code) and a numbered metal ring on the other. Two areas were used: a 400-m length of cliff ('area A') that was readily visible from the cliff top and a nearby skerry where visibility was restricted ('area B'; only until 1997). From 1984 to 2010, regular searches were made for ringed birds that had returned to the colony, resulting in 11152 individual resightings. These translated into 4021 detections (over complete seasons) in the MR history, because birds were often resighted more than once per season. In addition, 242 ringed birds were reported dead away from the Isle of May by members of the public (BTO Ringing Scheme, unpublished data).

Chicks were weighed ($\pm 1\text{g}$) at ringing and the length of the bent wing was measured ($\pm 1\text{mm}$) to give two individual-level covariates (details of field methods and equations below in Harris, Halley & Wanless 1992): (i) relative hatch date (RHD), calculated as the chick hatch date (ringing date – estimated age at ringing) minus the annual mean hatch date of all chicks ringed that year. Age at ringing (AR) was estimated for chick i from wing length W_i as: $AR_i(\text{days}) = 0.373 W_i(\text{mm}) - 5.8$. Therefore $RHD_i = (I_i - J) / 0.373(W_i - \bar{W})$, where I_i is the ringing date from the first of June and bars represent average over chicks in the same cohort. (ii) Body condition index (BCI), the raw residual (observed mass – expected mass): $BCI_i = M_i - (\alpha_0 + \alpha_1 W_i^{-1})$, where expected mass was modelled as a linear function of W_i^{-1} , separately for each year. RHD was significantly correlated with AR ($\rho = -0.761, P < 0.001$) but not with BCI.

Reference model and individual-level covariates

We analysed the chick mark-resight-recovery dataset in the frequentist framework with program MARK (White & Burnham 1999), using the ‘combined live-dead encounter’ model which estimates true survival S , fidelity F , resight probability p and recovery probability r ; the inclusion of rings recovered outside the Isle of May enabled us to estimate S and F separately (Burnham 1993).

We restricted the analysis to the first 9 years of life for each cohort; after that age most guillemots have started breeding (Harris, Frederiksen & Wanless 2007). We first constructed a reference model with age-dependent survival and resight probabilities, allowing selected variables to have annual variation to account for the marked fluctuations in resighting and recovery rates during the last years of the period. We investigated different plausible structures, conducting model selection based on the Akaike Information Criterion corrected for overdispersion and small sample size, QAICc (Burnham & Anderson 1998). The final structure had year-dependent first-year survival $S_1(t)$, but constant survival separately for four older age classes (S_2, S_3, S_4 and S_{3-9}). Resight probabilities were estimated independently for ringing areas A and B, as guillemots tend to come back to the general area where they were born and different resight probabilities are known for these areas (Harris, Frederiksen

& Wanless 2007). Resight probabilities were year-dependent, separately for 3 age classes ($p_2(t)$, $p_3(t)$ and $p_{4-9}(t)$), but $p_1 = 0$ for age 1 as young guillemots do not return to their natal colony in the first year of life. Fidelity was fixed to unity for younger birds ($F_{1-4} = 1$, as a preliminary exploration revealed boundary estimates of 1 for these probabilities) and was constant for each of age classes '5' and '6' (F_5, F_6 , which are estimable parameters). Once guillemots start breeding they have high site fidelity but individuals may become unidentifiable/unobservable at the colony due to loss of colour rings and recruitment to invisible parts of the colony. The probability of 'retaining a readable ring and continuing to breed at visible location' ('ring retention'; Reynolds *et al.* 2009), denoted ψ , was defined for 7–9 years of life and is equivalent to the parameter F_{7-9} estimated in the model. Ring-recovery probability was fitted as a linear trend with time on the logit scale, common to all ages. Our structure was similar to that used by Harris, Frederiksen & Wanless (2007) for data collected up to 2001, but had a time trend in recovery probability; for the full time period our reference model showed an improvement of 120 QAICc units compared to their structure.

The reference model described above was then used to test for relationships of s_1 with the individual-level covariates (RHD and BCI) described in the previous section. We carried out model selection based on QAICc to compare the reference model (no covariates) to models with additive (including quadratic) and interaction relationships between cohort and the covariates on the logistic scale, considered independently.

Reducing resighting and ringing effort

We used the 27 years (1984–2010) of MRR data to construct plausible scenarios of changes in field protocols. Searches for ringed birds occurred regularly from mid-April to mid-July, with 8–109 (mean=58) search days per year. We created four new MRR datasets to investigate outcomes of survey effort reduction: 1) resightings restricted to those made from 1 June onwards (dataset 'DJune'), when most immature age-classes are visiting the colony (Halley, Harris & Wanless 1995); 2) resightings drawn from 50% ('D50%'), 25% ('D25%') and 10% ('D10%') of the calendar days each season,

selected at random; Of the original 11152 individual resightings, the reduced datasets had 6095/5585/2809/1054 records respectively (approximate field effort reduction of 45%, 50%, 75% and 90%). The actual number of '1's in the MR history reduced from 4021 to 2796/2695/1669/811 respectively (effective reductions of 30%, 33%, 58% and 80%). Ring-recovery data came from members of the public independently of our field effort and were left unchanged.

We analysed the reduced datasets with models $S_1(t)$ and $S_1(t + RHD)$. We kept the reference model structure for comparison purposes, although we note that model selection might favour simpler model structures (e.g. fewer immature age-classes) when data are reduced. We compared the estimates with those obtained from the analysis of the full dataset and verified whether we could still detect the effect of RHD.

A similar approach was used to explore the effect of reducing the numbers of chicks ringed while maintaining the resighting effort at the real level. In these reduced datasets we retained 50% or 25% of the ringed chicks, randomly chosen (datasets 'Ring50%' and 'Ring25%' respectively). The corresponding number of resightings in the MR detection history was reduced from 4021 to 1961 and 1000 respectively (51% and 75% reduction). The number of recoveries declined from 242 to 122 and 72 respectively (50% and 70% reduction). These datasets were then analysed with the reference model and the model with additive RHD effect, as described above.

Stopping fieldwork on immature guillemots

To explore the consequences of stopping the ringing of guillemot chicks (and thus being unable to estimate immature survival directly) we extended an integrated population model (IPM) using mark-resight data from guillemots ringed as breeding adults at the Isle of May, annual counts of breeding pairs and data on annual breeding success previously developed for this guillemot colony (Reynolds *et al.* 2009). In total, five IPM models were fitted to various components of the dataset (Table 1; see also Fig.C1, Appendix S3 in Supporting Information). When MRR data were omitted we estimated apparent survival ' ϕ ' instead of true survival ' S '.

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When no information is collected for individual chicks, we cannot study the effect of individual covariates on survival. Instead we compared the estimates of $S_1(t)$ obtained from an IPM that included the chick MRR dataset (model 'IPM1', equivalent to our reference model) with those from an IPM without the chick MRR dataset (model 'IPM2', which had $\phi_1(t)$ but a combined immature survival and fidelity for the rest of age classes: $\phi_{2+} = \phi_2 \phi_3 \phi_4 \phi_5 F_3 F_6$).

We further investigated the potential gain for the estimation of adult survival, productivity and population abundance when direct information on juvenile survival was incorporated into an IPM, as the integration of independent datasets may bring higher precision than independent analyses (Besbeas, Lebreton & Morgan 2003). Thus, we compared adult-related estimates from IPM models with ('IPM1') and without ('IPM3') the chick MRR dataset; the latter model had constant combined juvenile survival $\phi_{1+} = \phi_1 \phi_2 \phi_3 \phi_4 \phi_5 F_3 F_6$.

Finally, in a hypothetical scenario where no breeding data were collected, we explored whether our ability to recover information on productivity $\rho(t)$ using an IPM improved when the chick MRR dataset was incorporated. For this we compared the estimates of productivity obtained when breeding success data were available ('IPM1') as a reference, to models in which such data were not incorporated, and either included ('IPM4') or omitted ('IPM5') chick MRR data. In these cases, productivity became a hidden parameter and its estimation rested upon its effect on population abundance.

IPM model structure

An IPM jointly models different likelihood components related to the different datasets, assuming independence. Breeding success data consisted of a series of yearly counts of guillemot chicks $C(t)$ that fledged from a number of monitored adult pairs that made a breeding attempt. As guillemots lay a single egg, data was modelled as a binomial variable $C(t) \sim \text{Bin}(E(t), \rho(t))$, where $E(t)$ was the

number of eggs laid and $\rho(t)$ was productivity in year t (Lahoz-Monfort *et al.* 2013). Similarly, the number of adult pairs skipping breeding in a particular year was modelled as $B(t) \sim \text{Bin}(M(t), \xi(t))$, where $\xi(t)$ was the probability of breeding and $D(t)$ was the number of pairs that bred out of $M(t)$ monitored pairs.

Adult MR data from the Isle of May (Lahoz-Monfort *et al.* 2011) were modelled according to the standard open-population Cormack-Jolly-Seber model (reviewed in Lebreton *et al.* 1992), assuming no adult emigration and fully time-dependent adult survival $S_a(t)$ and resight probability. We constructed the likelihood corresponding to the chick MRR data based on a computationally efficient multistate approach (McCrea 2012), where immature fidelity was estimated as permanent emigration to an unobserved state that did not contribute to population abundance at the Isle of May (but from which rings could be recovered). Here the full chick MRR dataset was used, including resightings/recoveries for birds > 8 years old and a structure based on the reference model used above in MARK. Adult survival was a common parameter with the adult MR likelihood component. Finally, we modelled a time-series of complete counts of breeding females, $N_a(t)$, using a state-space model with an observation process (counts $n(t)$ were imprecise observations of the true underlying population: $n(t) \sim N(N_a(t), \sigma_n^2)$, with observation error variance σ_n^2) on top of a state process that related true abundance to the demographic rates through a Leslie matrix,

$$\begin{pmatrix} N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \\ N_4(t+1) \\ N_5(t+1) \\ N_a(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & \xi(t)\rho(t) \cdot 0.5 \cdot S_1(t) \\ S_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_5 F_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_a(t) F_a & S_a(t) \end{pmatrix} \cdot \begin{pmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \\ N_4(t) \\ N_5(t) \\ N_a(t) \end{pmatrix} + \begin{pmatrix} \eta_1(t) \\ \eta_2(t) \\ \eta_3(t) \\ \eta_4(t) \\ \eta_5(t) \\ \eta_a(t) \end{pmatrix}$$

where η_x were additive binomial error terms to account for stochasticity. The model assumed that guillemots start breeding at age 6 (median of observations at this colony; Harris, Halley & Swann 1994) and that there was negligible adult emigration and a balanced sex ratio at birth. The “retention of colour rings and recruitment to a visible location” ψ did not appear in the Leslie matrix as, unlike for true emigration, these individuals still contributed to abundance and population growth. Although a

few birds hatched at other colonies are known to recruit into the Isle of May population, our models assumed no immigration as we had insufficient data to estimate it.

The issue of non-independence in IPM has still not been fully resolved. In our analysis, the assumption of independence between datasets was not strictly met as some included information from different life history aspects of the same individuals and these birds were also counted in the census. However, in practice, given that the demographic data were collected on <5% of the total population, we believe the impact of any dependence was likely to be small.

We fitted the IPM in a Bayesian framework, where the assumptions of normality and linearity required for a frequentist analysis of the IPM could be relaxed (Brooks, King & Morgan 2004). We used Markov chain Monte Carlo (MCMC) methods implemented in program JAGS v2.2.0 (Plummer 2003); see Appendix S4 for JAGS code and data files. Convergence was assessed with the Gelman-Rubin statistic (Gelman & Rubin 1992) using the R package CODA (Plummer *et al.* 2006) based on 2 overdispersed chains for all variables. The statistic showed no evidence of lack of convergence after 200000 MCMC iterations ($R_{max} = 1.05$, with most values less than 1.02). Consequently 400000 MCMC iterations were discarded in all analyses as burn-in, with a further 400000 iterations kept for analysis. The analysis took 34 hours (PC with 3.4GHz processor). Uninformative priors were used for all parameters ($\sigma_w \sim U(0,5000)$, $U(0,1)$ for probabilities, $U(-5,5)$ for regression parameters), reflecting a lack of prior knowledge. We checked that the priors did not limit the posterior distributions.

RESULTS

Reference model and individual-level covariates

In the reference model, first-year survival estimates showed considerable year-to-year variation, with a steady decline from the late 1990s to extremely low levels in the last five years (Fig.2), which coincided with a drop in adult survival (Lahoz-Monfort *et al.* 2011) and productivity (Lahoz-Monfort *et al.* 2013). For all age classes, resighting probabilities (Fig.2) showed increasing values until 1991 (reflecting a gradual increase in field effort; Harris, Frederiksen & Wanless 2007) followed by a

sustained decline for ages 2 and 3 which appeared to have genuine ecological foundation, given that effort has since remained relatively constant. These downward trends may reflect a long-term change in prospecting behaviour of immature guillemots on the Isle of May (discussion in Appendix S1). Estimates for other model parameters are shown in Table A1 (Appendix S1).

Model selection comparing the reference model (no covariates) to models with additive (including quadratic) and interaction relationships between cohort and covariates on the logistic scale, considered independently, indicated that RHD explained individual variation in S_1 much better than BCI (Table A2, Appendix S1). The top ranking model had an additive effect of RHD, with an estimated negative slope of -0.029 ($-0.053, -0.005$): early hatched chicks had higher chances of survival compared to late chicks (Fig.A2, Appendix S1).

Although penalised by the larger number of parameters, estimates from the full interaction model 't*RHD' had lower deviance and the model was selected over 't+RHD' in a likelihood-ratio test ($\chi^2_{1,df} = 40.1, P = 0.021$). While in many years there was no clear evidence of a year-specific relationship, in others the slope was far from zero and CIs did not include it (Fig.A3, Appendix S1). Estimated relationships (Fig.A4 in Appendix S1) indicate that during years of low S_1 (e.g. 2004–2008) the effect of hatching early was very pronounced (except 2006–2007 when survival was practically zero). In 2005 for example (average survival 0.044) only very early chicks had more than a 20% chance of surviving their first winter. In the years with higher average survival, survival was high except for the very latest hatching chicks.

Impact of reduced survey effort

For the simpler models without covariates, the estimates of S_1 appeared robust to the decrease in resighting effort (Fig.3a). The general pattern was reflected even in the D10% dataset, where a model with constant S_1 had much poorer fit (91 QAICc units) than one having year-variation, probably driven by the extreme changes in first-year survival. The associated uncertainty nevertheless increased with

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data sparseness (larger SD and more boundary estimates; Figs.B1&B2, Appendix S2). As an overall measure of precision, we calculated the generalised variance (the determinant of the estimated variance–covariance matrix) for the regression coefficients corresponding to the estimates of β_1 of each dataset (excluding years with boundary estimates), which increased from $5 \cdot 10^{-23}$ to $6 \cdot 10^{-16}$ as datasets became sparser. Reductions in the number of ringed chicks had a much greater effect; even a 50% decrease in ringing effort brought more boundary estimates in β_1 (Fig.3b) and a noticeable decrease in precision (Fig.B3, Appendix S2).

Survival estimates for older immatures had an increasing uncertainty and bias as the amount of resighting or ringing effort decreased (Fig.B4, Appendix S2). Reducing resighting effort appeared to induce negative bias; the effect is less clear when reducing ringing effort. We expected a reduction in the probability of resighting as less time was spent searching for birds. In contrast, resight probabilities should remain unaffected by a reduction in ringing effort. Both effects were apparent in all age classes (Figs.B5–B7, Appendix S2). A reduction in precision of resight probability estimates was nevertheless likely to follow the lower number of ringed birds. The recovery probability estimates should be relatively unaffected by a reduction in resighting effort, but less precise when fewer chicks are ringed; the precision of slope and intercept estimates supported this expectation (Fig.B8, Appendix S2).

For the models with RHD as individual covariate for β_1 , the inference was relatively robust to decrease in survey effort: only when resight data were retained for 10% of the days was the effect of RHD no longer statistically significant ($\alpha=0.05$; Fig.B9, Appendix S2). The decrease in QAICc when including RHD went from 3.73 in the full dataset, to 4.13/3.42/4.03 respectively for datasets DJune/D50%/D25%. For D10%, QAICc increased by 0.95 units, which was consistent with the 95% CI of its corresponding regression coefficient including zero. Thus if resighting effort had been reduced by 90% we would not have been able to detect a statistically significant effect of RHD on first-year survival. When the reduction was in ringing effort, the decrease in QAICc was 0.86/1.20

units for datasets Ring50%/Ring25% respectively, and the 95% CIs of the RHD regression coefficient included zero: we might have not been able to detect a significant effect of RHD had the ringing effort been halved.

Impact of not ringing chicks

When we attempted the estimation of $\phi_1(t)$ without data on juveniles (IPM2), the model was not able to recover it properly (Fig.4): credible intervals were very wide and medians were not close to those estimated when chick MRR data were included (IPM1). This inability did not affect the estimation of other parameters, largely driven by their respective datasets (e.g. productivity, Fig.C2, Appendix S3). First-year survival could not be estimated for the last 6 years of the period (no information in the adult-related datasets to inform this parameter as the corresponding immatures would not have recruited yet). Removing the chick MRR data from a model that did not attempt to estimate time-dependent first-year survival (IPM3) had a rather small effect on the estimation of adult survival for most years (Fig.C3, Appendix S3), indicating that its estimation was strongly driven by the adult MR dataset. Again, estimates of productivity were not affected (Fig.C4, Appendix S3).

Finally, we attempted to estimate productivity when no direct data on breeding success were incorporated (Fig.C5, Appendix S3). When such estimation was carried out without chick MRR data (IPM5), the estimates were completely unreasonable (no significant correlation with accurate estimates from model IPM1: $r=0.14$, $P=0.54$). By incorporating chick MRR data (IPM4), productivity could be estimated with some success ($r=0.75$, $P=0.0001$), although imprecisely.

The models described above in which it was not possible to estimate a fully time-dependent hidden parameter ($\phi_1(t)$ in IPM2 and $p(t)$ in IPM5) were associated with overfitting in the estimation of the female breeding population (Fig.5). The model structure was too flexible and hidden parameters were estimated so that the abundance estimates could match the observed counts closely; the estimated observation error was consequently small ($\sigma_N=606$ and 533 respectively). Model IPM4, despite an

imprecise estimation of productivity, followed the estimates of IPM1 closely. This effect, linked to the estimation of fully time-dependent hidden parameters, has been observed by Tavecchia *et al.* (2009).

DISCUSSION

Despite an almost universal acceptance of their importance to understanding the ecological consequences of rapid changes in the environment, long-term studies are continually under threats to their funding (Clutton-Brock & Sheldon 2010). Research programmes are coming under increasing pressure to make the collection of field data more streamlined and cost effective, the ‘more-for-less’ ethos. When forced to reduce field activities, it is best to make informed decisions by considering whether any part of fieldwork can potentially be scaled down or even stopped, without compromising the quality or usefulness of the results. Here we provide a decision-support statistical framework for how such exploration can be carried out in the context of mark-recapture-recovery studies, using an existing dataset to construct artificial scenarios of reduced field effort that allow us to explore alternative monitoring scenarios and assess the benefits of data integration through integrated population models.

Guillemot juvenile survival

Our study extended a previous analysis of first-year survival conducted up to 2001 (Harris, Frederiksen & Wanless 2007) and included a series of years when first-year survival was extremely low, notably 2004–2008. These poor survival rates followed on from unusually poor breeding success (Lahoz-Monfort *et al.* 2013) and chicks fledging in poorer body condition compared to the long-term average (unpublished data). We found that hatch date was an important factor affecting first-year survival, with early chicks surviving better than later ones (also observed e.g. in European shags *Phalacrocorax aristotelis*; Harris *et al.* 1994). In contrast, the body condition index (BCI), a measure of actual weight relative to that expected for a chick of that size, was non-significant. These results support those from the previous Isle of May study (Harris, Frederiksen & Wanless 2007) and findings in the Baltic (e.g. Hedgren 1981). The importance of hatch date but not body condition is probably associated with the

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guillemot's fledging strategy whereby the chick leaves the colony, accompanied by the male parent, when only partially grown and completes its development at sea (Harris, Webb & Tasker 1991). Thus chicks that maximise time at sea before the onset of autumn storms are likely to be at an advantage, while feeding conditions when chicks become independent many weeks after leaving the colony may be unrelated to those during the breeding season. We nevertheless found some evidence suggesting that BCI may have some effect in years of extremely poor overall first-year survival ($\Delta\text{QAICc}=4.24$ for the model with BCI compared to 8.43 in Harris, Frederiksen & Wanless 2007).

Reducing field effort and future design of this monitoring programme

For the Isle of May guillemot study, the estimates of first-year survival were robust with respect to decreasing the resighting effort, with the quality of the estimation starting to fail before 90% effort reduction. Thus, a substantial part of the current effort went into making resightings that were redundant in terms of estimating first-year survival. For each marked bird, a resighting in a particular year was not directly relevant to the estimation of first-year survival if the animal was seen in another year; the critical piece of information, i.e. survival over its first winter, was still contained in the history. This was less important when estimating survival for older age classes, suggesting that inference for early-age parameters required less resighting effort.

Our results also suggested that little precision in survival estimates would be lost either by reducing the number of checks from 60 (the historical yearly average over the study period) to 29 checks dispersed either throughout the whole breeding season or commencing on or after 1 June. Given that researchers have to be present during June to ring chicks, from a practical point of view there is much to recommend searching for returning birds from 1 June onwards. Resighting effort could also be reduced without losing the capacity to detect the effect of hatch date. Thus, effort could be reduced by around a half while still attaining the current aims of this monitoring programme to estimate first-year survival and assess the effect of hatch date. In contrast, reducing the numbers of ringed chicks had a more direct impact on resightings, indicating that in this study first-year survival

estimates were less robust to a decrease in ringing effort. Maintaining ringing effort at the current level of 250–300 chicks per annum is therefore necessary to attain the aims of the programme. In terms of individual-level covariates, chick phenology appeared to be consistently more important for determining first-year survival. Thus estimating chick hatch date based on measuring wing length should be prioritised over weighing chicks to calculate a BCI. In practice this might allow the size of the ringing team to be reduced from 5–6 to 4–5.

Integrated population models

Our IPM had limited capacity to recover year-specific first-year survival when chick MRR data were omitted, although the joint modelling of the adult-related datasets allowed the estimation of a constant probability that combined survival from the chick stage until recruiting age. This is of relatively limited value if the primary interest of a monitoring programme lies in estimating first-year survival or identifying individual-level covariates (as no direct information on the fate of individual chicks is available). An IPM could potentially be considered for investigating cohort-level covariates, a case not addressed in this study. Also, site fidelity cannot be studied if ring-recovery data are not included. However, when the primary interest is monitoring survival and productivity, or abundance of the breeding population, an IPM appears quite robust to the absence of chick MRR data. Finally, the IPM framework allows the exploration of a further hypothetical change in the monitoring scheme: in an artificial scenario of breeding success not being monitored, the inclusion of chick MRR data was essential in order to obtain productivity estimates, albeit imprecise ones. Any decision to stop fieldwork on guillemot chicks ultimately depends on the specific objectives of monitoring, particularly the importance attached to estimating year-dependent first-year survival and making ecological inferences regarding this demographic parameter.

IPMs can be very useful tools in ecological and conservation studies as they can bring improved precision and the possibility to estimate hidden parameters for which no direct data are available (Schaub & Abadi 2011). Furthermore, they allow the evaluation of alternative monitoring scenarios for intensively monitored populations where individual-level data are collected on different

aspects of demography and abundance. As shown here, this can be achieved by artificially removing datasets from the analysis, exploring the impact in our ability to study parameters of interest. Such exploration can be important in monitoring programs for planning or revising the collection of field data related to specific aspects of demography, particularly when such individual-based data are difficult or expensive to gather. To date, this type of IPM-based exploration is still uncommon (with a notable exception in Tavecchia *et al.* 2009).

Wider applicability of the approach

Here we use monitoring protocols, resighting histories and demographic data for common guillemots to illustrate our approach. However, the framework is not specific to seabirds or even MRR data but is applicable to a wide range of situations where there is a need to assess the consequences of reducing survey effort on attaining specified aims and objectives. This is a very different exercise to evaluating study design before starting a new programme. Researchers normally strive to obtain high quality estimates and maximise capacity to find ecological relationships (included unexpected effects; Wintle, Runge & Bekessy 2010). Thus the driver for changing protocols is usually external decisions to reduce funding, although internal changes in research priorities can also result in a need to reallocate staff resources. Irrespective of the motivation, a prerequisite for any reduction in effort is that the dataset must be large. Where the focus is on estimating relationships over time, duration is a key factor (Frederiksen *et al. in press*) and therefore the approach applies best to long-term monitoring programs.

Assessing whether effort could be reduced is particularly valuable where logistics for fieldwork are costly (e.g. in remote places such as the Arctic or offshore islands) or where data collection is extremely time consuming (e.g. needing daily checks of multiple sites). Using IPMs to explore more extreme strategies involving stopping a particular aspect of the work is more data-demanding, requiring censuses and possibly datasets to estimate other demographic components. Finally, other considerations (e.g. timing and synergies with other activities) may create opportunities or impose constraints that need to be factored into the final decision.

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Time series data equivalent to the ones used in our case study are generally more common for vertebrates than invertebrates (Clutton-Brock & Sheldon 2010; but see Catchpole *et al.* 2001). We were principally interested in estimating juvenile survival from MRR but the approach would be equally applicable if the aim was to explore changing effort in adult resighting or if dead recoveries rather than live recaptures/resightings were available.

Our approach is not limited to estimating juvenile survival from MRR data and is equally applicable when marking adult individuals, or when only live-recaptures/resightings or dead-recoveries are available. Although we did not consider changes in 'dead-recovery effort' since our recoveries came from the general public, such exploration may be relevant when it is a dedicated effort carried out by the same project. The concept of re-sampling existing datasets can also be extended to other demographic parameters like emigration or in spatial contexts (e.g. tracking-based home-range area estimation; Soanes *et al.* 2013).

To our knowledge, this study represents the first use of artificially simplifying existing datasets to explore the effect of field effort in mark-recapture studies. Post-study evaluation is no substitute for initial study design, but when there are pressures to reduce costs and ideally get 'more for less', it can help streamline an existing programme, by exploring specific relationships that could otherwise not have been predicted (and therefore simulated) beforehand.

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Service (Ireland) and the ringers themselves. We thank the associate editor and two anonymous referees for comments on an earlier version of the paper.

Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1: Reference model and individual-level covariates.

Appendix S2: Effect of survey effort.

Appendix S3: Integrated Population Models.

Appendix S4: JAGS code and raw data.

Table 1. Integrated Population Models fitted for investigating the effect of not ringing chicks. Different datasets are included (✓) or excluded (×) from the models. ‘MRR_C’: chick mark-resight-recovery data; ‘prod_A’: adult productivity data. Hidden parameters (without direct information): estimated from the rest of the data through the population model. $\phi_1(t)$: year-dependent first-year survival; ϕ_{2+} : constant immature survival (age ≥ 2); ϕ_{1+} : constant immature survival (all ages), equal to $\phi_1 \phi_{2+}$; $\rho(t)$: year-dependent productivity.

Model	MRR _C	prod _A	Hidden parameters
IPM1 (reference)	✓	✓	--
IPM2	×	✓	$\phi_1(t), \phi_{2+}$
IPM3	×	✓	ϕ_{1+}
IPM4	✓	×	$\rho(t)$
IPM5	×	×	$\rho(t), \phi_{1+}$

Fig.1. Analysis steps carried out to investigate reducing fieldwork effort.

Fig.2. Estimates from the reference model without covariates: a) first-year survival (with 95% CIs) for cohorts ringed 1983–2008 (the 2009 estimate, not shown, is imprecise); b) resighting probabilities (CIs)

shown in Fig.A5 in Appendix S1 for clarity) of immatures aged 2 (black), 3 (dashed) and 4–8 (grey) years, ringed in area A. Estimates of 0 for 2-year-old resight probability represent boundary estimates. The 2009 estimate for age 3 was also boundary estimate (1), probably due to the smaller amount of resightings at the end of the period. Similar patterns noticeable in area B (Fig.B6, Appendix S2).

Fig.3. First-year survival probabilities estimated from datasets with increasingly reduced resighting (a) or ringing (b) effort. ‘Full’: complete dataset; ‘DJune’: only resightings June onwards; ‘D50%/25%/10%’: keeping only the resightings of 50%/25%/10% of calendar dates; ‘Ring50%/25%’: using only 50%/25% of ringed chicks (colour version and plots of uncertainty in Figs.B1&B2, Appendix S2).

Fig.4. Comparison of first-year survival estimates from Integrated Population Model IPM2 (no chick MRR data; solid circles and line, with 95% CI) and reference model IPM1 (with chick MRR data; white squares, CIs not shown for clarity).

Fig.5. Estimated guillemot female breeding population according to different Integrated Population Models. Panel a) compares the outcome of IPM1 (with chick MRR data; in grey) and IPM2 (no chick MRR data and $\phi_1(t)$ estimated from the rest of the datasets; in black). Panel b) compares two models with no breeding success data (productivity estimated from the rest of the datasets): IPM4 (with chick MRR data; in grey) and IPM5 (no chick MRR data; in black). Annual island-wide counts shown as white squares.

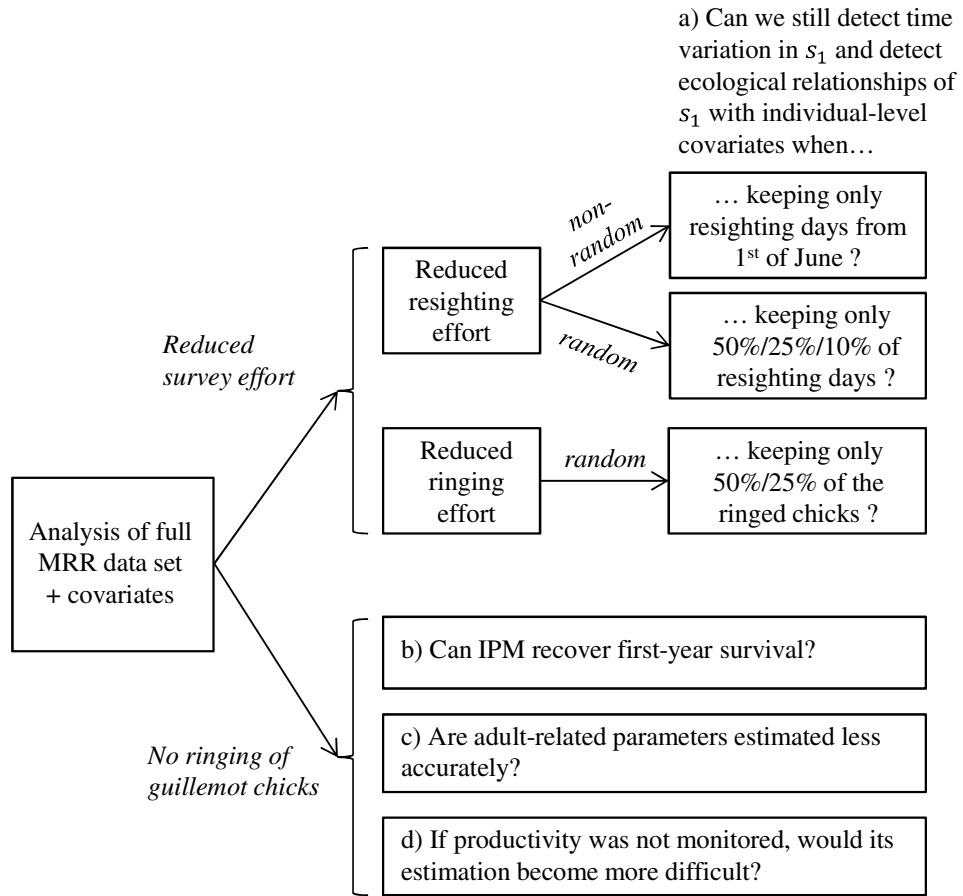


Fig.1

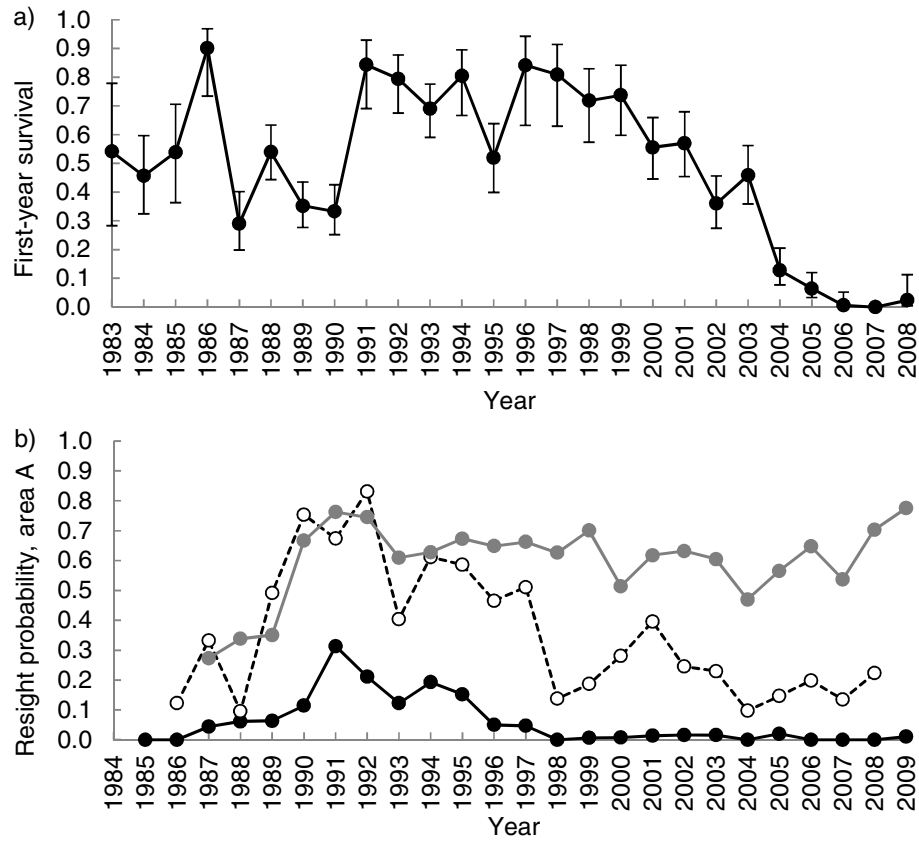


Fig.2

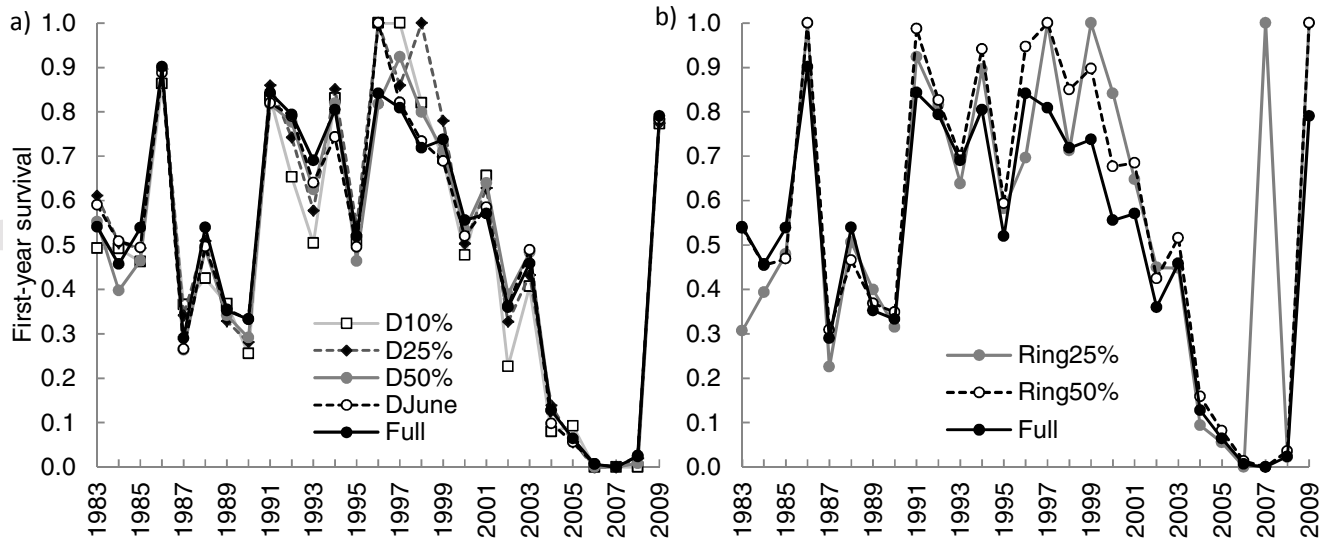


Fig.3

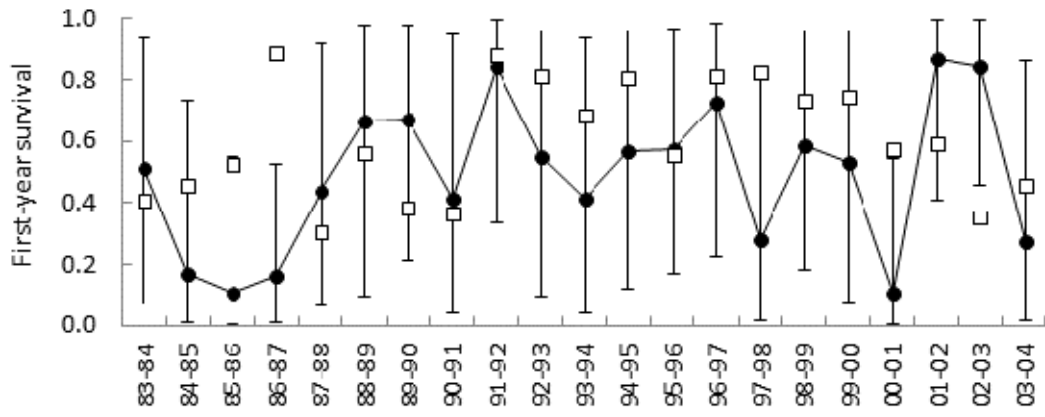


Fig.4

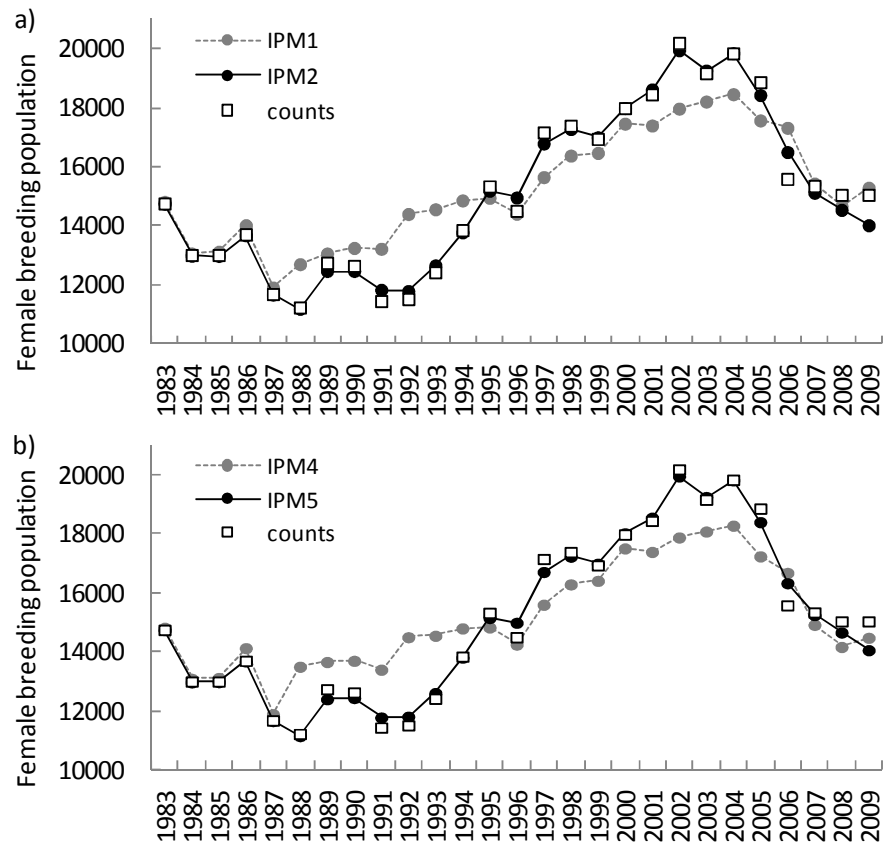


Fig.5

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