1 ESTIMATING RECRUITMENT AND SURVIVAL IN PARTIALLY-MONITORED POPULATIONS

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18 Running title: Estimating vital rates with partial monitoring

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Summary

1. In evolutionary and ecological studies, demographic parameters are commonly derived from detailed information collected on a limited number of individuals or in a confined sector of the breeding area. This partial monitoring is expected to underestimate survival and recruitment processes because individuals marked in a monitored location may move to or recruit in an unobservable site.

2. We formulate a multi-event capture–recapture model using E-SURGE software which incorporates additional information on breeding dispersal and the proportion of monitored sites to obtain unbiased estimates of survival and recruitment rates. Using simulated data we assessed the biases in recruitment, survival and population growth rate when monitoring 10% to 90% of the whole population in a short and a long-lived species with low breeding dispersal. Finally, we illustrate the approach using real data from a long-term monitoring program of a colony of Scopoli's shearwaters *Calonectris diomedea.*

3. We found that demographic parameters estimated without considering the proportion of the area monitored were generally underestimated. These biases caused a substantial error in the estimated population growth rate, especially when a low proportion of breeding individuals were monitored.

4. The proposed capture–recapture model successfully corrected for partial monitoring and provided robust demographic estimates.

5. *Synthesis and applications*. In many cases, animal breeding populations can only be monitored partially. Consequently, recruitment and immature survival are underestimated, but the extent of these biases depends on the proportion of the area that remains undetected and the degree of breeding dispersal. We present a new method to obtain robust and unbiased measures of survival and recruitment processes from

capture–recapture data. The method can be applied to any monitored population

regardless of the type of nests (e.g. artificial or natural) or breeding system (e.g. colonial

or territorial animals) and it only relies on an estimate of the proportion of the

monitored area. The unbiased estimates obtained by this method can be used to improve

the reliability of predictions of demographic population models for species'

conservation and management.

Key-words: *Calonectris diomedea*, Scopoli's shearwater, demography, capture–

recapture, multi-event, experimental design, vital rates, dispersal, population modelling,

partial monitoring

Introduction

Population ecologists use mathematical models of animal populations to describe the

current population status and forecast future trajectories (Caswell 2001; Morris & Doak

2002). Population models require precise, robust and unbiased estimates of

demographic parameters (Morris & Doak 2002; Williams, Nichols & Conroy 2002;

Zabel & Levin 2002), which in most ecological studies are estimated by monitoring

only a portion of the population (Fig. 1) (Yoccoz, Nichols & Boulinier 2001). Partial

monitoring is inevitable because, in addition to problems inherent to species distribution

and monitoring effort, animals may recruit in inaccessible/unobservable sites. A

common case, for example, is monitoring programs conducted at artificial breeding sites

(e.g. nest boxes), in which individuals breeding in natural places remain undetected (see

examples in Tavecchia *et al.* 2002; Pilastro, Tavecchia & Marin 2003; Cannell *et al.*

2011). Similarly individuals may breed in inaccessible sectors of the breeding areas

(Jenouvrier *et al.* 2008; Sanz-Aguilar *et al.* 2010; Fig. 1).

Capture–recapture techniques provide an analytical approach to obtain robust estimates

of many demographic parameters from detailed life-history data of marked animals

(Lebreton *et al.* 1992; Williams, Nichols & Conroy 2002; Thomson, Cooch & Conroy

2009). The appeal of capture–recapture techniques is that detection failures can be

incorporated into the model and demographic parameters can be estimated together with

detection probabilities. Detection failures can result from imperfect detection or a

temporary emigration from the study area, such as delayed recruitment or intermittent

breeding (Jenouvrier *et al.* 2008; Sanz-Aguilar *et al.* 2011). Capture–recapture models

with unobservable states/sites ('ghost' states/sites) can be used to incorporate temporary

movements and they have been applied for the study of recruitment processes and

reproductive skipping (e.g. Jenouvrier *et al.* 2008; Kendall, Nichols & Hines 1997;

Sanz-Aguilar *et al.* 2011). A limitation of capture–recapture models, however, is that

permanent, as opposed to temporary, emigration is generally confounded with mortality

(unless information on dead recoveries or auxiliary sightings are available, Burnham

1993; Barker 1997). Thus, animals that recruit and permanently breed into unobservable

areas are assumed to be dead and parameters refer to animals in monitored sites only

(e.g. local survival, Lebreton *et al.* 1992).

Parameters derived from the monitored areas/nests are then typically assumed to be

representative of the whole population. However, Lambrechts, Visser & Verboven

(2000) pointed out the risks associated with monitoring a limited area or number of

breeding places when studying recruitment. Indeed, individuals born in monitored nests

will remain undetected if they recruit in unobservable locations, negatively biasing the

measure of lifetime recruitment and individual fitness (Lambrechts, Visser & Verboven

2000). The problem of underestimating recruitment is not confined to evolutionary

studies. Population models require non-biased demographic estimates for obtaining

95   robust projections and reliable conservation diagnoses. In many animals, adult dispersal

96   distances between breeding seasons are relatively short or even non-existent, but

97   juveniles typically perform natal dispersal, i.e. they depart permanently from their natal

98   site and/or area looking for their first breeding site (Gaines & McClenaghan 1980;

99   Greenwood 1980; Greenwood & Harvey 1982). Consequently, in addition to

100   recruitment, immature survival derived locally may also be underestimated when

101   breeders tend to be faithful to their breeding site (see for example Ballerini *et al.* 2015).

102   This bias may be important in ecological and conservation studies of short-lived species

103   (Sæther & Bakke 2000) and in species with deferred breeding in which the pre-

104   breeders' survival and recruitment probabilities are often responsible for the observed

105   population fluctuations (Gaillard *et al.* 2000; Votier *et al.* 2008; Sergio *et al.* 2011;

106   Servanty *et al.* 2011) and may play an important role in future population dynamics

107   (Sergio *et al.* 2011).

108   Here we propose a method to obtain unbiased estimates of recruitment and survival in

109   partially monitored populations; a very common situation in natural populations. This

110   analytical approach allows the estimation of immature survival and age-dependent

111   recruitment probabilities taking into account the recruitment of those animals that breed

112   in unobservable locations. In this respect, our approach corrects the biases reported by

113   Lambrechts, Visser & Verboven (2000) and provides unbiased estimates of recruitment

114   processes. The method joins classical capture–recapture models based on individual

115   encounter histories with additional information on breeding dispersal and the proportion

116   of the monitored population in a multi-event framework (Pradel 2005). We validate our

117   modelling approach and explore the consequences of estimating demographic

118   parameters through partial monitoring of breeding sites using simulated data on two

119   hypothetical species: a short-lived species breeding in their first year of life, and a long-

120   lived species with deferred breeding. Finally, we illustrate our approach using a long-

121   term data set from a monitored population of Scopoli's shearwaters *Calonectris*

122   *diomedea*. As occur in many other shearwaters and petrels, the hypogeous nesting habit

123   of the species makes it difficult to locate and access nests, and consequently only a

124   portion of the population was monitored. This monitoring scheme is expected to

125   underestimate immature survival and recruitment probability as some new breeders born

126   in the colony may recruit in unobservable or inaccessible nests, leading to incomplete

127   records of age-related recruitment processes. Our modelling approach successfully

128   estimates vital rates in the presence of incomplete monitoring of breeding sites, which

129   would otherwise be underestimated by classical capture–recapture methods. We show

130   that population viability analyses, highly relevant in conservation biology and for

131   species management, predict biased population trajectories when the demographic

132   parameters are estimated without the proposed correction for partial monitoring.

133   **Materials and methods**

134   *Estimating demographic parameters in the presence of uncertainty*

135   When only a portion of the breeding area is monitored, marked individuals can recruit

136   in unobservable or inaccessible breeding places. Newly developed multi-event models

137   (Pradel 2005) distinguish what can be observed in the field, i.e. the events coded in the

138   individual encounter history, from the underlying individual states (Pradel 2005). This

139   allows for the possibility that individuals recruit at unobservable breeding locations. For

140   the sake of simplicity, we denote locations in which breeding animals can be seen or

141   caught as 'observable nests' and those in which animals breed undetected as

142   'unobservable nests'. We consider six biological states in which an animal can be at a

143   given time: pre-breeder (PB), first-time breeder in an observable nest (FTBo), first-time

144   breeder in an unobservable nest (FTBu), experienced breeder in an observable nest

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145 (EBo), experienced breeder in an unobservable nest (EBu) and dead (D; Fig. 2). Note

146 that an intermediate state (first-time breeder, noted 'B') was included to model

147 recruitment, independently from where the recruitment occurs (observable/unobservable

148 nests; Fig. 2). This intermediate state is necessary to model and estimate separately the

149 age-dependent recruitment. What we observed, i.e. the events, are simply the marking at

150 birth (event coded '1') and the following recaptures as a breeder (event coded '2'). The

151 event for unobserved individuals on a particular occasion is coded as '0'. We describe

152 the probability associated with the state-dependent observations using the following

153 probabilities:

154   $\phi_{i,j}^{s}$ = the probability of surviving in state s for an individual of class j between time i

155   and $i+1$. Note that j denotes a general grouping factor (e.g. sex or age).

156   $\pi_{i,j}^{PB-B}$ = the recruitment probability for an individual of class j, i.e. the probability of

157   moving from a pre-breeding state to a breeding state between time i and $i+1$.

158   β_{i} = the probability, conditional to π, to recruit into an observable nest between time i

159   and $i+1$. We assume recruitment to occur randomly, thus this probability is

160   equal to the proportion of observable nests in the study area.

161   $\delta_{i,j}$ = the probability of changing nests for an individual of class j after a breeding

162   attempt between time i and $i+1$; assumed to be random and independent of

163   observability status.

164   $p_{i,j}^{S}$ = the probability of observing an individual of class j, in state s at time i.

165 The multi-event model can be built using the above quantities to describe the

166 probability of being in a particular state or moving between states. The first vector in

167 multi-event models should contain the initial state probabilities, corresponding to the

168 probabilities that an encounter history starts from a given state. Here the vector is

7

169   degenerated because all individuals were captured for the first time as PB (i.e. marked at

170   birth) so the probability was 1 for the PB state (vector 1).

171
$$IS = \begin{array}{ccccc} PB & FTBo & FTBu & EBo & EBu \\ (1 & 0 & 0 & 0 & 0) \end{array} \quad \text{vector 1}$$

172   The multi-event model uses a series of matrices with departure states in rows and arrival

173   states in columns to describe the conditional processes considered (Pradel 2005;

174   Choquet, Rouan & Pradel 2009). For the sake of simplicity, subscripts of the parameters

175   are omitted, but note that each parameter can be modelled as a function of time, class

176   and/or state. The first matrix considered (matrix 1) contains the state-dependent survival

177   (ϕ).

178
$$Survival = \begin{array}{c} \\ PB \\ FTBo \\ FTBu \\ EBo \\ EBu \\ D \end{array} \begin{array}{c} \begin{array}{cccccc} PB & FTBo & FTBu & EBo & EBu & D \end{array} \\ \begin{pmatrix} \phi & 0 & 0 & 0 & 0 & 1-\phi \\ 0 & \phi & 0 & 0 & 0 & 1-\phi \\ 0 & 0 & \phi & 0 & 0 & 1-\phi \\ 0 & 0 & 0 & \phi & 0 & 1-\phi \\ 0 & 0 & 0 & 0 & \phi & 1-\phi \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{array} \quad \text{matrix 1}$$

179   The second matrix (matrix 2) corresponds to the recruitment probabilities (π) into an

180   intermediate first-breeding state (B). This transition is conditional on survival

181   probabilities and should thus be considered after matrix 1.

182
$$Recruitment = \begin{array}{c} \\ PB \\ FTBo \\ FTBu \\ EBo \\ EBu \\ D \end{array} \begin{array}{c} \begin{array}{ccccccc} PB & B & FTBo & FTBu & EBo & EBu & D \end{array} \\ \begin{pmatrix} 1-\pi & \pi & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{array} \quad \text{matrix 2}$$

183   The third matrix (matrix 3) includes the additional information collected by population

184   monitoring (see below) and corrects for partial monitoring and breeding dispersal

185   probability. In particular we include the probability that a first-time breeder recruits in

186   an observable nest, which corresponds to the proportion of observable nests in the study

187   area (β), and the breeding dispersal probability, δ (i.e. the probability of changing nest

188   after the year of recruitment). Assuming random breeding dispersal, the probability to

189   move to an observable nest depends on the proportion of observable nests in the study

190   area (β). Consequently, we combined β and δ parameters and we distinguished the

191   probability α of dispersal into an unobservable nest as $\alpha = \delta(1-\beta)$ and the probability ω

192   of dispersal into an observable nest as $\omega = \delta\beta$. Note that the quantities β, α and ω are

193   fixed (i.e. not estimated by the model).

194

$$Nest\_type = \begin{array}{c} \\ PB \\ B \\ FTBo \\ FTBu \\ EBo \\ EBu \\ D \end{array} \begin{array}{c} \begin{array}{cccccc} PB & FTBo & FTBu & EBo & EBu & D \end{array} \\ \left(\begin{array}{cccccc} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \beta & 1-\beta & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-\alpha & \alpha & 0 \\ 0 & 0 & 0 & \omega & 1-\omega & 0 \\ 0 & 0 & 0 & 1-\alpha & \alpha & 0 \\ 0 & 0 & 0 & \omega & 1-\omega & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{array} \right) \end{array} \text{ matrix 3}$$

195   The product of the three previous matrices defined the Markovian process between the

196   states. The last matrix considered is the events matrix (matrix 4), corresponding to the

197   resighting or recapture probabilities (p). Resighting or recapture probability of

198   individuals breeding in unobservable nests is zero. We consider that pre-breeders (PB)

199   have an initial capture probability of 1 and their resighting or recapture probability is

200   fixed at zero (i.e. only breeders are resighted or recaptured).

201

$$Recapture = \begin{array}{c} \\ PB \\ FTBo \\ FTBu \\ EBo \\ EBu \\ D \end{array} \begin{array}{c} \begin{array}{ccc} 0 & 1 & 2 \end{array} \\ \left(\begin{array}{ccc} 1-p & p & 0 \\ 1-p & 0 & p \\ 1 & 0 & 0 \\ 1-p & 0 & p \\ 1 & 0 & 0 \\ 1 & 0 & 0 \end{array} \right) \end{array} \text{ matrix 4}$$

202   A test to assess the goodness-of-fit (GOF) of multi-event models is not available at

203   present. As an approximation, we assessed the GOF of the Arnason-Schwarz model

204   (state- and time-dependent) using program U-CARE 2.3.2 (Choquet *et al.* 2009).

Model validation and consequences of imperfect monitoring on derived population

parameters

When β is wrongly assumed to be 1 (i.e. all nests are observable) we expect immature

survival and recruitment processes to be negatively biased. However, the importance of

this bias may depend on the value of β and the importance of breeding dispersal

processes in the studied species.

To investigate these points, we generated data considering two sets of parameters, one

typical of a short-lived species (pre-breeder survival: 0.20; adult survival: 0.40; full

recruitment at age 1; fecundity: 3 females produced per breeding female; see examples

in small mammals and passerines in Schaub & Vaterlaus-Schlegel 2001; Ernest 2003;

Payevsky 2006) and one of a long-lived species (pre-breeder survival: 0.80; adult

survival: 0.9; first reproduction at age 5; progressive recruitment: 0.5; and fecundity: 0.3

females per breeding female; see examples in large mammals and seabirds in Sæther &

Bakke 2000; Ernest 2003; Jenouvrier *et al.* 2008). All the scenarios assumed a recapture

probability of 1 to consider an optimal situation in which all observable nests are

monitored exhaustively. The first set of simulated data sets considered a breeding site

fidelity of 1 (i.e. δ=0) and 10 increasing values of β (from 0.1 to 1; see Appendix S2 in

Supporting Information). Additionally, to investigate the effect of breeding dispersal on

parameter estimation, we considered nine additional scenarios for each of the two

hypothetical species: combining β values of 0.25, 0.5 and 0.75 with values of breeding

dispersal δ of 0.1, 0.2 and 0.3 (see Appendix S2). For each set of parameters we

simulated 1000 capture–recapture histories.

For each of these 38 simulated data sets, we ran: i) a classical multistate capture–

recapture model, which did not take into account recruitment into unobservable sites, ii)

a multistate model with an unobservable state (i.e. ghost site) but no supplemental data

230 and iii) the new multi-event model described above. Models were built and fit to the

231 data using E-SURGE 1.6.3 (Choquet, Rouan & Pradel 2009).

232 In a second step, to investigate the demographic consequences of not accounting for

233 recruitment into unobservable nests, we used the estimates obtained by classical

234 multistate modelling and their respective standard errors (SE) to calculate the expected

235 stochastic population growth rate (λ) through an age- and stage-structured population

236 model (see Appendix S3) (Caswell 2001; Morris & Doak 2002; Cooch, Cam & Caswell

237 2012). Demographic analyses were carried out with the package Popbio in software R

238 (Team 2005; Stubben & Milligan 2007) (Appendix S3). The variance of survival and

239 recruitment parameters estimated from capture–recapture was incorporated into the

240 model by randomly selecting parameter values from a beta-distribution (Morris & Doak

241 2002). We ran 10 000 stochastic population model simulations and calculated the mean

242 stochastic population rates and their SE (Appendix S3).

243 *Recruitment and immature survival of Scopoli's shearwater*

244 To illustrate the modelling approach with real data, we used field data from a long-term

245 monitoring program of a colony of Scopoli's shearwaters in a small islet off Mallorca,

246 Balearic archipelago, Spain. Shearwaters breed in burrows, mainly located under

247 boulders and vegetation, where a single egg is laid in May and incubated by both

248 parents until June. Newborns leave the colony in October for their first trans-equatorial

249 migration and come back to breed at 4–7 years old (Jenouvrier *et al.* 2008). Each year

250 we monitored about 160 accessible nests. Every year a small number of new accessible

251 nests is found and added to the monitoring scheme. Similarly some nests are lost every

252 year due to vegetation cover or the occasional erosion of the rocky slopes, forcing

253 individuals to change nests (Sanz-Aguilar *et al.* 2011). We used data on 1298

254 individuals ringed as chicks (event '1') since 2001 and their recaptures as breeding

255   adults in the monitored nests until 2014 (event '2'). Survival probability was modelled

256   following previous results of the same population (Sanz-Aguilar *et al.* 2011; Pradel &

257   Sanz-Aguilar 2012; Genovart *et al.* 2013; Tenan *et al.* 2014). In particular, we

258   considered a constant survival parameter, no age effects in pre-breeder survival, a

259   minimum age at first reproduction of 5 years and a time-dependent recapture probability

260   of breeders. Models were built and fit to the data using E-SURGE 1.6.3 (Choquet,

261   Rouan & Pradel 2009). Additional information was used to obtain a measure of β (see

262   Appendix S1). In particular, we obtained an estimate of the annual proportion of

263   monitored nests, β, using a two-session capture–recapture protocol on marked

264   fledglings (mean β =0.585, Table S1.1, Appendix S1). In addition, Sanz-Aguilar *et al.*

265   (2011) estimated breeding dispersal probability in our population, δ, as 0.04. This

266   estimate was used to calculate the annual α and ω parameters of the third matrix

267   described above (Table S1.2, Appendix S1).

268   Model selection was based on Akaike's Information Criterion adjusted for the effective

269   sample size, AICc (Burnham & Anderson 2002). During model selection we first

270   modelled the effect of age (from 5 to age 8+) on survival of breeders and subsequently

271   the effect of age on recruitment probability (from 5 to age 11+). We built final models

272   by combining the retained structures of survival and recruitment parameters (models

273   differing ≤ 2 AICc points). For each final model *j*, we calculated the Akaike weight, w_j,

274   as an index of its relative plausibility (Burnham & Anderson 2002). Estimates were

275   obtained by model averaging, where final models contributed to the final estimate

276   according to their w_j (Burnham & Anderson 2002). In order to study the robustness of

277   parameter estimates taking into account parameter uncertainty of the proportion of

278   monitored nests, β, and breeding dispersal probabilities, δ, we ran once again those final

279   models considering nine combinations of the mean value and lower and upper 95%

280   confidence interval of β and δ (Table S1.1–4, Appendix S1) and we calculated model-

281   averaged estimates for each combination.

282   Finally, we ran again the final models but considering the hypothetical full monitoring

283   of the breeding population (β=1) to obtain the estimates of parameters that will be

284   obtained without corrections of β.

285   **Results**

286   *Simulated data, capture–recapture and population models*

287   Pre-breeder survival was underestimated for both the short-lived and long-lived

288   simulated data sets without breeding dispersal (δ=0) when the possibility of recruitment

289   in unobservable nests was not considered in the analyses (Fig. 3A & 3C). Recruitment

290   probabilities were correctly estimated for short-lived species (Fig. 3C) but

291   underestimated for long-lived species when β≤0.5 (Fig. 3A). In contrast, breeder

292   survival was correctly estimated for all simulated data sets (Fig. 3A & 3C). In multistate

293   models, considering an unobservable site (i.e. ghost site), but in which β was not fixed,

294   only survival of breeders was estimated correctly (results not shown).When β value

295   used in simulations was fixed in the multi-event model, all parameters were correctly

296   estimated (Fig. 3B & 3D). The population growth rate calculated assuming β=1 was

297   negatively biased by its effects on immature survival and recruitment estimates. This

298   effect was more pronounced for the short-lived than for the long-lived species, and

299   under small values of β (Fig. 4).

300   In long-lived and short-lived simulated data sets with partial monitoring (β) of 0.25, 0.5

301   and 0.75 and low to moderate dispersal values (0<δ≤0.3), pre-breeder survival was

302   correctly estimated using the classical multistate model (assuming β=1) (Fig. S4.2 &

303   S4.5 respectively, Appendix S4). Recruitment probabilities were underestimated,

304   especially under low values of β and high values of δ (Fig. S4.1 & S4.4, Appendix S4).

305   Breeder survival was correctly estimated for short-lived species but underestimated for

306   long-lived species (Fig. S4.3 & S4.6, Appendix S4). Multistate models considering an

307   unobservable site provided better recruitment estimates than classical multistate models

308   but they showed very large parameter uncertainty, especially for short-lived species

309   (Fig. S4.1–S4.6, Appendix S4) with additional problems of parameter identifiability

310   (Appendix S4). By fixing the correct β, α and ω values used in data simulations, the

311   multi-event models correctly estimated all parameters (Fig. S4.1–S4.6, Appendix S4).

312   Despite contrasting results on parameter estimates with those obtained with $\delta=0$, the

313   population growth rate calculated assuming $\beta=1$ was similarly negatively biased for

314   both short-lived and long-lived species, especially under small values of β (Fig. S4.7,

315   Appendix S4).

316   *Real case study: the Scopoli's shearwater*

317   The GOF test indicated that the general model assuming time- and state-dependent

318   parameters explained the data adequately (χ^2 =11.732, d.f.=11, *P*=0.384).

319   We began model selection considering the mean values of β and δ (Tables S1.1 and

320   S1.2, Appendix 1) and eliminating non-significant effects from the general structure of

321   the survival parameters (model s1, Table 1), which considered differences between pre-

322   breeders and breeders aged 5, 6, 7 and $\geq$8 and differences in recruitment probabilities

323   between individuals aged 5 to 10 and $\geq$11. The model with the lowest AICc value

324   indicates differences in survival between breeders aged 5 and $\geq$6 (model s6, Table 1),

325   although a model including survival differences among breeders aged 5, 6 and $\geq$7 was

326   also highly supported (ΔAICc=1.17, model s3, Table 1). We selected the survival

327   structure of model s6 to model recruitment probabilities (Table 1). The retained models

328   (ΔAICc=0.10, Table 1) included recruitment differences for birds aged 5, 6 and $\geq$7

329   (model r5, Table 1) and aged 5, 6, 7 and $\geq$8 (model r6, Table 1). Finally, we used these

330   retained structures (models s3, s6, r4 and r5) to build the final models (models C1–C4,

331   Table 1) and obtain the model-averaged estimates of survival and recruitment

332   probabilities (Table 2). We ran again models C1–C4 fixing different combinations of β,

333   α and ω parameters (considering mean values and lower and upper 95% confidence

334   intervals of β and δ; Table S1.5, Appendix 1). All models showed similar estimates of

335   survival and recruitment (Table S1.5, Appendix 1) to those obtained when using only

336   the mean values (Table 2), confirming the robustness of parameter estimates. In our

337   case study of Scopoli's shearwaters, by considering a hypothetical total monitoring of

338   the breeding area (β=1) with the classical multistate modelling approach, pre-breeder

339   survival and recruitment parameters were underestimated, but adult survival estimates

340   were the same (Table 2). The difference in cumulative survival until age of first

341   breeding (age 5) by considering the real proportion of nests monitored or unreal full

342   monitoring (β=1) was ~6% (0.35 and 0.29, respectively).

343   **Discussion**

344   *Model advantages*

345   The estimation of precise age-dependent recruitment and survival probabilities is

346   fundamental to infer population dynamics and viability (Morris & Doak 2002;

347   Williams, Nichols & Conroy 2002; Cooch, Cam & Caswell 2012; Oro 2013). For a long

348   time, different statistical methodologies based on capture–recapture data have been

349   developed and improved to properly and simultaneously estimate survival and

350   recruitment parameters (e.g. Clobert *et al.* 1994; Pradel 1996; Pradel & Lebreton 1999;

351   Schwarz & Arnason 2000; Kendall & Nichols 2002; Lebreton *et al.* 2003; Desprez *et al.*

352   2013). Unfortunately, most capture–recapture methods using live recapture data

353   estimate local parameters, i.e. they are not able to deal with permanent emigration,

354   confounded with mortality (but see models including dead recoveries, Burnham 1993;

355   Barker 1997). Recruitment in unmonitored/unobservable breeding sites represents a

356   special case of "permanent emigration" when breeding dispersal is null. Here we

357   provide a new capture–recapture methodology based on incorporating additional

358   information collected in the field to account for the possibility of recruitment in non-

359   monitored sites and to correctly estimate demographic parameters and test biological

360   hypotheses simultaneously.

361   We show here that adult survival for both short and long-lived species is correctly

362   estimated without corrections when the breeding population is only partially monitored

363   and there is no breeding dispersal (simulated data) or occurs in very low proportions

364   (0.04, real data). However, juvenile survival for both short- and long-lived species and

365   recruitment for long-lived species are underestimated. In contrast, when breeding

366   dispersal occurs at low to medium probability (0.1–0.3) juvenile survival is correctly

367   estimated without further corrections but recruitment for both short- and long-lived

368   species and adult survival for long-lived species are underestimated. These biases may

369   cause a substantial error not only in the estimated vital rates but also in the estimated

370   population growth rate, especially when low proportions of breeding individuals are

371   monitored (Fig. 4 and Fig. S4.7).

372   Numerous long-lived animals (including birds and mammals) are territorial, and

373   breeders exhibit high site fidelity to breeding sites, and even among short-lived species,

374   juveniles disperse in higher proportions than adults (Gaines & McClenaghan 1980;

375   Greenwood 1980; Greenwood & Harvey 1982).

376   Natural populations may cover areas too large to be sampled by capture–recapture or

377   they can include inaccessible sites to researchers. For example, Jenouvrier *et al.* (2008)

378   used mark–recapture data collected on a subsample of about 30% of the nests in a

379   Scopoli's shearwater colony to estimate survival and recruitment probabilities. This

380   partial monitoring of individuals breeding in accessible nests has also been used for

381   estimating demographic parameters for other hypogeous seabird species, e.g. storm

382   petrels *Hydrobates pelagicus* (Sanz-Aguilar *et al.* 2009). The survival and recruitment

383   estimates obtained from these studies may be underestimated, because the proportion of

384   breeding sites monitored is lower than 50% as we have found here for such a case. In

385   fact, population models for a storm petrel study population predict a colony decline

386   (Sanz-Aguilar *et al.* 2009), whereas different dynamics (stability or even growth) have

387   been found (Libois *et al.* 2012; Tenan *et al.* 2014) suggesting that demographic

388   estimates used in population projections might be underestimated.

389   The methodological approach presented here could also benefit from additional

390   advantages of multi-event models such as the inclusion of uncertainty in breeder state

391   assignment (Desprez *et al.* 2013). However, we should note that although the estimate

392   of recruitment probability obtained by the proposed model was unbiased, it applies at a

393   population level and is not suitable for the study of individual lifetime recruitment

394   (Lambrechts, Visser & Verboven 2000).

395   *Model limitations*

396   The first limitation of the method proposed here is that it requires information on the

397   proportion of monitored nests (β) and the probability of breeding dispersal (δ).

398   However, this type of information can be obtained or estimated by other methods

399   alternative to the individual capture–mark–recapture programs on fixed breeding sites

400   (Williams, Nichols & Conroy 2002; Thomas *et al.* 2010). For example, Cannell *et al.*

401   (2011) combined count at beaches and capture– mark–recapture to estimate the

402   population size of little penguins *Eudyptula minor*; a distance sampling procedure was

403   used to estimate the number of breeding pairs at the world' largest colony of Scopoli's

404   shearwater (Thomas *et al.* 2010; Defos du Rau *et al.* 2015); and here we estimate

population size of shearwaters by capture–recapture of chicks in and outside nests (see

details in Appendix S1). Our approach to estimate proportion of monitored nests (β) can

be used in other species in which fledglings/juveniles wander far from their nests (e.g.

storm petrels), flock together in communal crèches (e.g. slender-billed gulls

Chroicocephalus genei) or use communal roosting sites (e.g. Egyptian vultures

Neophron percnopterus). Moreover, we believe that most field ecologists can estimate

the proportion of monitored nests (β) or can make an informed guess as to how large β

is in their study site (e.g. Jenouvrier *et al.* 2008; Sanz-Aguilar *et al.* 2009). On the

contrary, breeding dispersal (δ) may be more difficult to estimate. Sanz-Aguilar *et al.*

(2011) estimated nest dispersal in Scopoli's shearwaters using a multi-event approach,

although this estimate may be slightly underestimated as only observable nests were

considered in the model. Other methods to obtain breeding dispersal estimates, such as

radio tracking, could also be used. However, for many species showing high breeding

site fidelity this parameter can probably be neglected. A second limitation of our

method is that it cannot include uncertainty in β or δ and consequently parameter

variances are underestimated. We acknowledge that state–space models in a Bayesian

framework would be more adequate to incorporate uncertainty (Gimenez *et al.* 2007;

King 2012) but would limit the use of model information theory to test biological

hypotheses on parameter variation. Bayesian model selection is complex,

computationally challenging and no consensus has emerged in the literature on a single

approach (see discussion in Tenan *et al.* 2014). On the contrary, the analytical

framework we propose here allows researchers using the available tools of model

selection in a more user-friendly environment. Model averaging using AICc can be

easily carried out for considering uncertainty in model selection (Burnham & Anderson

2002). Moreover, we show that the parameter robustness of the model can be assessed

430   by fixing different values of β and/or δ and when uncertainty of β and/or δ is small,

431   model parameters are highly robust (see Appendix S1). Finally, another possible

432   limitation of our approach is that it assumes random movements in breeding dispersal

433   and random recruitment in observable and unobservable sites, which cannot be true in

434   some situations (see for example Igual *et al.* 2007). However, this assumption may be

435   true for many monitoring schemes (e.g. Fig. 1A) and additional constraints in β

436   modelling (e.g. different β values for groups of individuals born or breeding in different

437   sectors of the breeding area as central vs. peripheral areas, Figs. 1B & 1C) could be

438   included in the model when information on dispersal processes (e.g. distribution of

439   dispersal distances) is available.

440   *Synthesis and applications*

441   When monitoring a breeding population, animals in unobserved areas are assumed to be

442   dead, an assumption that inevitably leads to underestimation of recruitment and

443   immature survival. This bias is implicitly assumed to be small, and parameters

444   estimated at the monitored areas are taken as a representative of the whole population.

445   However, we show here that this assumption is not always correct and the extent of the

446   bias depends on several features of the study, such as the species' degree of breeding

447   dispersal and the proportion of monitored area. We illustrate how to combine

448   information at the population and individual level to correctly estimate age-dependent

449   survival and recruitment. This approach can be applied to any system in which

450   individuals can breed undetected. A typical case would be either birds or small

451   mammals breeding in artificial nest boxes in which natural breeding sites cannot be

452   monitored (e.g. Pilastro, Tavecchia & Marin 2003; Cannell *et al.* 2011). A similar case

453   would be colonial waterbirds or territorial raptors, in which monitoring is conducted

454   only in accessible nests and territories (e.g. Jenouvrier *et al.* 2008; Sanz-Aguilar *et al.*

455 2009; Zabala & Zuberogoitia 2014). Correct estimates of demographic parameters are

456 essential to predict unbiased population trajectories through population models

457 (Coulson *et al.* 2001; Williams, Nichols & Conroy 2002). We recommend the use of the

458 proposed method when data are collected on partially monitored populations of species

459 with moderate to high breeding site fidelity.

Acknowledgements

466 **Data Accessibility**

467 - R scripts: uploaded as online supporting information (Appendix S2 & S3)

468 - Capture–recapture histories of simulated data and real data on recruitment of Scopoli's

469 shearwater are available at: http://cedai.imedea.uib-

470 csic.es/geonetwork/srv/es/main.home?uuid=5a8efd41-82e8-49f6-b902-b8efd8ddd917.

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627

628 **Supporting Information**

629 Additional Supporting Information may be found in the online version of this article:

630   Appendix S1. Estimation of the annual proportion of nests where breeding adults can be

631   captured (β) and probabilities of nest dispersal (α, ω).

632   Appendix S2. Example of r code for data simulation.

633   Appendix S3. Population models.

634   Appendix S4. Additional tables and figures.

635

636 **Table 1.** Modelling of survival and recruitment probabilities of Scopoli's shearwaters at

637 Pantaleu Islet. Notation: np: number of parameters; Dev: relative deviance; AICc:

638 Akaike information criterion corrected for sample size; ΔAICc: the AICc difference

639 between the current model and the one with the lowest AICc value; AICw: Akaike's

640 weight. Model notation: PB: pre-breeder; B: breeder; "=" means no differences between

641 stages considered; "/" means differences; numbers indicate the age classes considered.

642 Note that all models considered temporal recapture probabilities. Models with the

643 lowest AICc are in bold

Model	Survival	Recruitment	np	Dev	AICc	ΔAICc	AICw
s1	PB/ B(5,6,7≥8)	5,6,7,8,9,10≥11	21	768.17	810.82	2.99	
s2	PB/ B(5,6=7≥8)	5,6,7,8,9,10≥11	20	769.25	809.85	2.02	
s3	PB/ B(5,6 ≥7)	5,6,7,8,9,10≥11	20	768.40	809.00	1.17	
s4	PB/ B(5=6=7≥8)	5,6,7,8,9,10≥11	19	775.06	813.60	5.77	
s5	PB/ B(5=6≥7)	5,6,7,8,9,10≥11	19	772.26	810.79	2.97	
s6	**PB/ B(5≥6)**	**5,6,7,8,9,10≥11**	**19**	**769.29**	**807.83**	**0.00**	
s7	PB/ B	5,6,7,8,9,10≥11	18	776.13	812.62	4.79	
s8	PB=B	5,6,7,8,9,10≥11	17	776.95	811.38	3.55	
r1	PB/ B(5≥6)	5,6,7,8,9,10≥11	19	769.29	807.83	5.23	
r2	PB/ B(5≥6)	5,6,7,8,9≥10	18	770.18	806.67	4.07	
r3	PB/ B(5≥6)	5,6,7,8≥9	17	770.29	804.72	2.13	
r4	PB/ B(5≥6)	5,6,7≥8	16	770.31	802.69	0.10	
r5	**PB/ B(5≥6)**	**5,6≥7**	**15**	**15.00**	**802.59**	**0.00**	
r6	PB/ B(5≥6)	5≥6	14	778.93	807.23	4.64	
C1	PB/ B(5≥6)	5,6≥7	15	772.51	802.8	0.16	0.30

| C2 | PB/ B(5≥6) | 5,6,7≥8 | 16 | 770.30 | 802.69 | 0.00 | 0.33 |
| C3 | PB/ B(5,6≥7) | 5,6≥7 | 16 | 771.57 | 803.87 | 1.18 | 0.18 |
| C4 | PB/ B(5,6≥7) | 5,6,7≥8 | 17 | 769.40 | 803.83 | 1.14 | 0.19 |

644

645 **Table 2.** Model-averaged parameter estimates (and SE) of consensual multi-event

646 models including the correction β (Table 1) and considering β=1. Notation: ϕ: survival

647 probabilities; π: recruitment probabilities; PB: pre-breeder; B: breeder

648

| Parameter	Estimates (SE) β correction	Estimates (SE) β=1
ϕ_{PB}	0.81 (0.02)	0.78 (0.03)
ϕ_{B} age 5	0.18 (0.17)	0.18 (0.17)
ϕ_{B} age 6	0.74 (0.08)	0.73 (0.08)
ϕ_{B} age $\geq$7	0.80 (0.04)	0.79 (0.04)
π age 5	0.03 (0.02)	0.03 (0.01)
π age 6	0.10 (0.03)	0.08 (0.03)
π age 7	0.23 (0.08)	0.20 (0.07)
π age $\geq$8	0.32 (0.11)	0.28 (0.11)

649
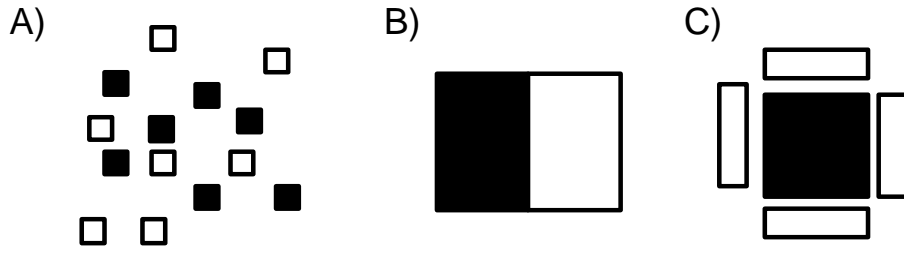
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651

652   **Fig. 1.** In many studies, the sampled individuals (black) represent only a part of the

653   entire breeding population. In the schematic examples above the monitored nests (A),

654   sector (B) or area (C) include 50% of the entire breeding population.

655
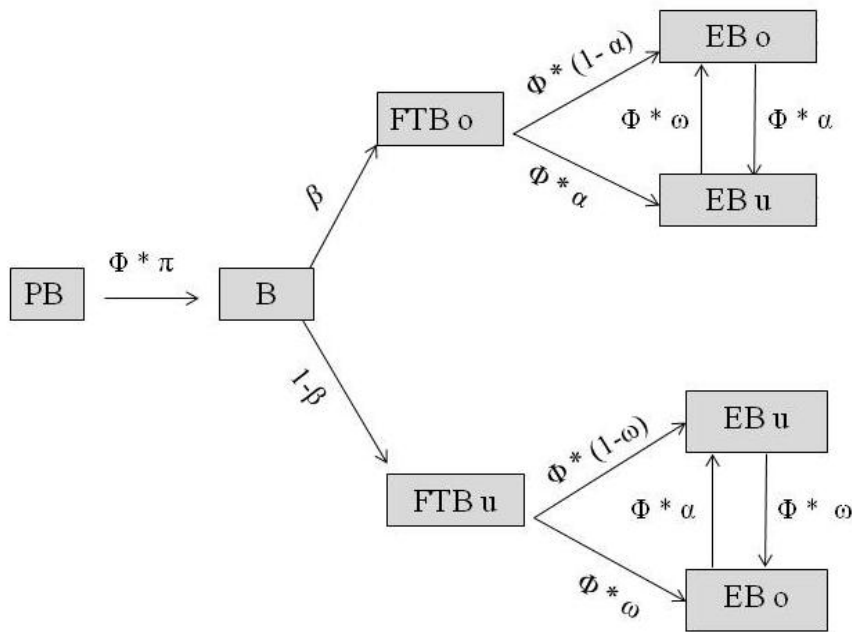
656

657 **Fig. 2.** Schematic representation of the states considered and the probabilities associated

658 with between-states transitions. Notation: PB= pre-breeder, B= first-time breeder,

659 FTBo=first-time breeder in an observable nest, FTBu = first-time breeder in an

660 unobservable nest, EBo=experienced breeder in an observable nest, EBu= experienced

661 breeder in an unobservable nest, Φ=survival probability, π=recruitment probability,

662 β=proportion of observable nests, α probability of moving into an unobservable nest, ω

663 probability of moving into an observable nest. The state 'dead' could be reached from

664 any of the states above and is not represented.

665
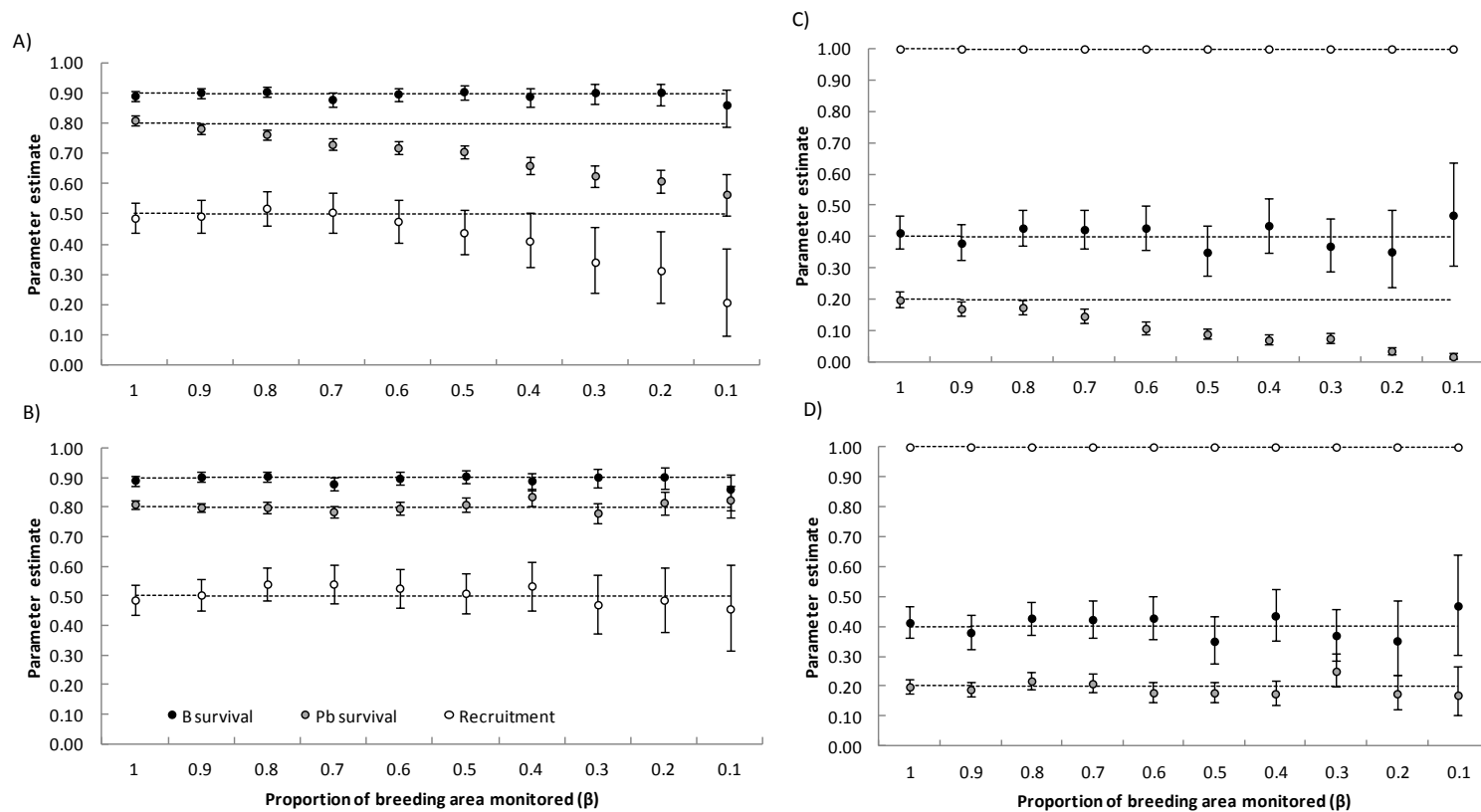
Fig. 3. Estimates (and 95% CI) obtained by multistate (A, C) and multi-event (B, D) capture–recapture models of pre-breeder survival, breeder

survival (noted by Pb and B respectively) and recruitment probabilities for the simulated data sets for long-lived (A, B) and short-lived (C, D)

species under different scenarios of proportions of observable nests in the population (β). Dotted lines indicate the true value of the parameter

used to generate the simulated capture histories.

34
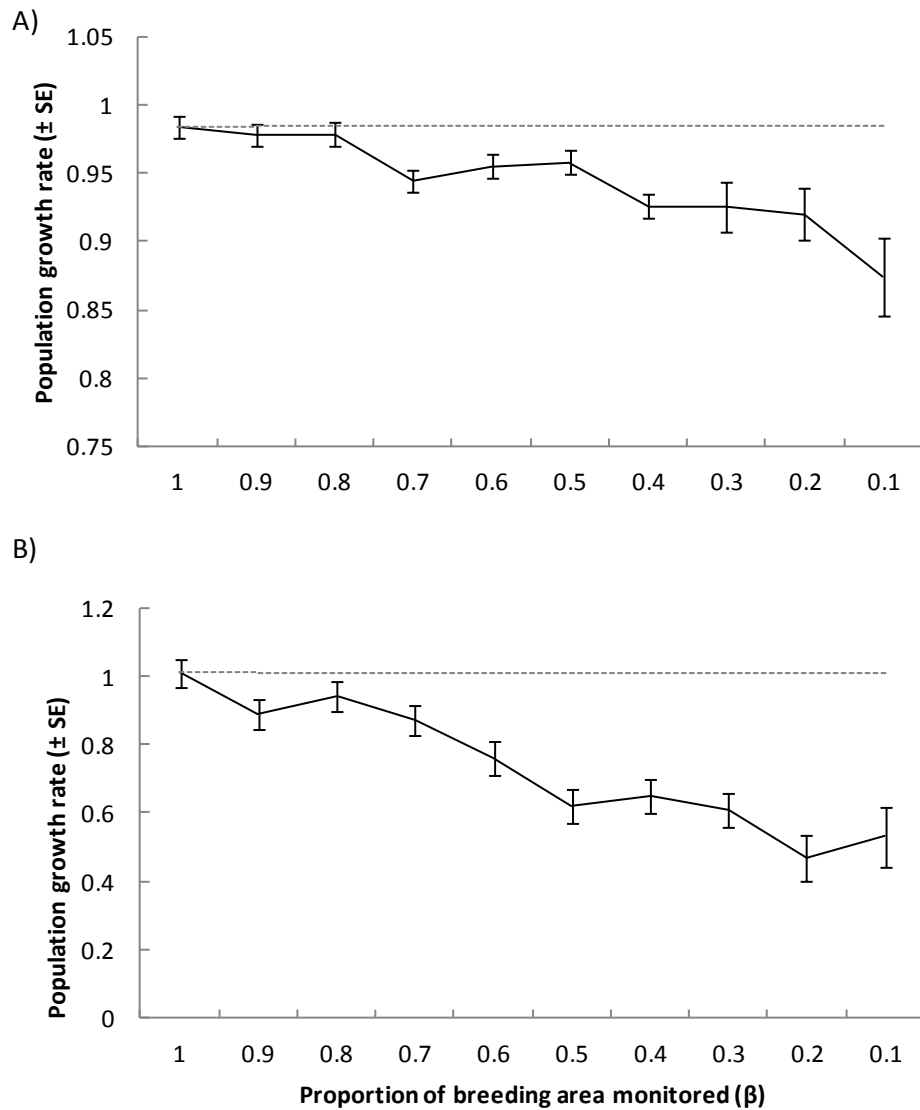
Fig. 4. Estimates (and SE) of population growth rate (λ) for long-lived (A) and short-

lived species (B) using the demographic parameters estimated by multistate models

when the proportion of the breeding area monitored (β) is not included in the model.

The lambda that will result for the true demographic parameters considered when

simulating the data sets is indicated with a dotted line.