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Waterbird demography as indicator of wetland health: the French-wintering common snipe population

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Abstract

The population dynamics of waterbirds constitute an indicator of wetland conservation status. However, waterbird population censuses are difficult to implement because the individuals are very mobile, and some species are elusive or breed in remote areas. Therefore, demographic models based on the estimation of survival and breeding success appear as a reliable alternative to population censuses. Here we present this model-based approach in the case of the French-wintering snipe population (*Gallinago gallinago*), which breeds mainly in Northern and Eastern Europe. Using a multi-state model to accommodate the mobile nature of waterbirds, we estimate snipe survival using a joint analysis of capture-recapture and band-recovery data. Then, we use matrix population models to estimate the minimum recruitment rate required to maintain the population at its current size. Although we call for more data to reduce uncertainty, we conclude that occasional declines are likely after years with poor breeding success, but that the French-wintering snipe population is on average stable. Individual-based monitoring data and population modeling make it possible to use waterbirds as indicator species at the flyway scale.

Key-words: Capture-recapture; Common snipe; Sustainable harvest; Climate change; Leslie matrix; Drainage; Flyway Approach to Conservation; Multistate model

1 **Introduction**

2 Wetland degradation (drainage and pollution) is one of the first consequences of landscape
3 anthropization (Baldock 1984). Yet wetlands provide ecosystem services that are essential to
4 our societies (denitrification, flood water retention, etc.; Gleason et al. 2008); thus wetland
5 preservation represents a major conservation challenge (Ramsar-Convention-Secretariat
6 2010). A distinctive suite of birds are specialized on wetlands and need them to breed, roost
7 and feed. These birds can be used as indicator species for the conservation status of the
8 wetlands that correspond to their species-specific habitat requirements. For example, the
9 assemblage of species that use reedbeds depend on water levels and reed harvesting
10 (Graveland 1999; Barbraud et al. 2002; Polak et al. 2008); see also Davidson and Stroud
11 (2006); DeLuca et al. (2008); Paillisson et al. (2002). Several historically abundant species are
12 currently among the fastest declining species in the world (Amano et al. 2010; Greenberg et
13 al. 2011), suggesting that wetland degradation can jeopardize even common species' survival.
14 Here we focus on a particularly widespread European waterbird, Common snipe *Gallinago*
15 *gallinago* (snipe hereafter). Snipes inhabit all types of freshwater marshes, migrate on a broad
16 front, and are not restricted to coastal areas as are most other waders that winter in Europe. A
17 large part of the northern and eastern European population winters in France, making the
18 French-wintering population an indicator of wetland health along this flyway (Dodman and
19 Boere 2010). Recent trends from some breeding population surveys are currently raising
20 concerns for this species (BirdLife-International 2012). In addition, snipe is a gamebird with a
21 French hunting bag reaching 250,000 to 300,000 birds annually (Tesson and Leray 2000).
22 This hunting bag has decreased recently, further suggesting population decline. A proper
23 quantification of the European snipe population dynamics thereby appears necessary to

24 inform the status of this indicator species. This quantification can also be used to aid decision-
25 making about sustainable hunting.

26 Large-scale population censuses yet remain very challenging in snipes as in other
27 waders (Amano et al. 2010; Davidson and Stroud 2006) because of the large breeding and
28 wintering ranges that encompass remote areas, and because of the long-range migrations and
29 short-term response to fluctuations in water levels. Snipes further challenge field biologists
30 because of their elusive nature. Therefore, process-based population models that separate the
31 demographic processes of survival, fecundity, and movement appear as reliable alternative to
32 pattern-based models based on population censuses (Beissinger and Westphal 1998). To
33 document survival probability and harvest rates, a nation-wide banding program has been set
34 in place in recent years for French-wintering snipes (starting during the 1999/2000 hunting
35 season). Recaptures of live birds and recoveries of dead birds have been recorded, which
36 provide information about the survival of snipes that winter in France. These data are
37 typically analyzed using capture-recapture-recovery models (e.g., Gauthier and Lebreton
38 2008). Snipe behavior, however, challenges typical assumptions of capture-recapture-
39 recovery models. Although snipes do exhibit site-fidelity both within and across winters when
40 the conditions allow (Davies 1977; Spence 1988), when the conditions are unfavorable
41 (droughts, floods, and freezing conditions) they undertake within-winter movements that are
42 similar to nomadism; they track water levels and avoid areas that become unsuitable. This is a
43 behavior typical to most waterbirds, including ducks (Roshier et al. 2002), gulls (McNichols
44 1975), and raptors (Martin et al. 2006). From a modeling standpoint, both recapture and
45 recovery probabilities are influenced by this behavior: snipes that exit the area where they
46 were banded are unlikely to land in another banding area, and will thus not be subject to
47 recapture anymore. Similarly, hunting pressure tends to be concentrated around traditional
48 locations, which coincide with banding locations in many cases, and thus mobile snipes may

49 avoid recapture and hunting altogether. To address that issue, we designed multistate capture
50 recapture models (Lebreton et al. 2009) that allowed marked individuals to transit between a
51 state “In banding area” subject to recapture and a state “Out of banding area” not subject to
52 recapture. By doing so, we estimated survival while accounting for possible movements of
53 individuals between these states. Hereafter we describe this model and its implementation.
54 Then we use matrix population models to discuss the implication of our data and findings for
55 the characterization of snipe population trend.

56 **Material and methods**

57 *Field procedures and data selection*

58 Two methods of capture were used. Most snipes were caught with mist-nets at dawn or dusk
59 in marshes or meadows. The remaining snipes were caught during daytime with traps placed
60 along the water line of ponds or in intensively used feeding sites. Age determination (hatch
61 year bird or adult) was made after examination of wing and tail feathers (CICB-&-OMPO
62 2002; Włodarczyk et al. 2008). A total of 10,721 snipes were banded between 1999 and 2011,
63 of which 563 were recaptured later and 584 were recovered by hunters.

64 From this extensive dataset we selected the records corresponding to birds banded
65 between November and February, i.e., we excluded birds most likely to still be migrating. We
66 also excluded recaptures occurring outside of this period. We discarded records when the age
67 at banding was not recorded (c. 250 records) as well as records from the Mediterranean region
68 (c. 200 records) because many of these birds came from a more southerly flyway (breeding
69 areas in central Europe). This selection yielded a final dataset containing records from 4,029
70 snipes (1,420 banded as adults, 2,609 banded as hatch-year birds). Of these, 113 were
71 recovered by hunters and 150 were recaptured at least once during a hunting season different

72 from the season during which they were banded. The maximum number of encounters per
73 individual was 3. Annual survival probability was estimated from November 1st to October
74 31st the following year. The 12 month period starting on November 1st following the birth of
75 an individual is hereafter termed its “Hatch year”.

76 *Goodness of fit tests*

77 We tested the goodness of fit of the Cormack-Jolly-Seber model (Lebreton et al. 1992) to the
78 recapture data only (not the recovery data). We used the “overall test” in software U-CARE
79 (Choquet et al. 2009a) for that purpose. This test can be divided into components (Pradel et al.
80 2005). Among these components, the test for short-term transience (component 3.SR testing
81 for a difference in encounter probability between previously captured and newly-marked
82 snipes) and the test for short-term trap-dependence (component 2.CT testing for a difference
83 in the probability to be encountered in hunting season $t+1$ between the snipes captured during
84 season t and those not captured that season), when they are both significant, suggest
85 individual or spatial heterogeneity in recapture probability (Péron et al. 2010). Such
86 heterogeneity would for example be expected if banded snipes were a mixture of migrants and
87 resident wintering birds.

88 *Multistate capture-recapture-recovery model: general structure*

89 Based on our understanding of snipe movement behavior, we considered two “live” states,
90 namely state 1 “alive and in a banding area” and state 2 “alive and out of banding areas”. As
91 typically done when combining recapture and recovery data (Gauthier and Lebreton 2008;
92 Hénaux et al. 2007), these two states were complemented by two “Just dead” states, which
93 represented individuals available for recovery, and a state “Long dead”, which represented
94 individuals dead for more than one year. Each year, birds in state 1 had the probability $1 - f_1$
95 to move to state 2, where f_1 is called state-fidelity; and birds in state 2 had the probability

96 $1 - f_2$ to return to state 1. At first capture, all birds were in state 1. Survival probability was
 97 denoted S . In matrix notation, this model can be represented by the survival-transition matrix
 98 Φ of which the $(i,j)^{\text{th}}$ cell represents the probability to be in state j at time $t+1$ if in state i at
 99 time t :

Eq. 1

$$\Phi = \begin{bmatrix} Sf_1 & S(1-f_1) & 1-S & 0 & 0 \\ S(1-f_2) & Sf_2 & 0 & 1-S & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

100 The model is then fully specified by describing the observation process. The observation
 101 matrix \mathbf{P} is used for this purpose. It has in its $(i,j)^{\text{th}}$ cell the probability to record event j if in
 102 state i . Possible events are $j = 1$ for “individual not recorded”, $j = 2$ for “individual captured
 103 and alive”, and $j = 3$ for “individual shot and reported as such”:

Eq. 2

$$\mathbf{P} = \begin{bmatrix} 1-p & p & 0 \\ 1 & 0 & 0 \\ 1-r_1 & 0 & r_1 \\ 1-r_2 & 0 & r_2 \\ 1 & 0 & 0 \end{bmatrix}$$

104 where p and r denote recapture and (state-dependent) recovery probabilities respectively.

105 An additional complexity had to be accommodated: banding occurred throughout a
 106 protracted period in winter, and was simultaneous with hunting. Thus, an individual banded
 107 early in the season was exposed to mortality risks for a longer period than an individual
 108 banded late in season. To accommodate that feature we used a monthly formulation of
 109 capture-recovery models (Péron et al. 2012a). We denoted \tilde{s}_w the monthly winter survival.
 110 For an individual banded in November, the probability to survive up to the end of winter
 111 (February 29) was then \tilde{s}_w^4 , while an individual banded in February was assigned a first winter
 112 survival probability of \tilde{s}_w . Then we introduced the probability to survive from the end of
 113 February to the beginning of November, denoted s_s and called “summer survival” hereafter
 114 for practicality (although the period spanned from late winter to early autumn). Individuals

115 dying in “summer” were not subject to recovery. In brief, annual survival probability was
116 $S = \tilde{s}_w^4 \cdot s_s$.

117 *Biological hypotheses and model selection*

118 In waders and other gamebirds, survival often varies with age. Hatch year birds exhibit lower
119 survival and higher vulnerability to hunting than adults (Sandercock 2003). Between-year
120 variation is also commonplace, reflecting in particular the effect of weather on survival (Péron
121 et al. 2011; Sandercock 2003). Lastly, we investigated a potential difference between the
122 interior and coastal zones (see map in Fig. S1). The climate is different in those two zones
123 (milder winter on the coast). Hunting pressure is also higher in the coastal zone (as suggested
124 by spatial variation in hunting bags; Tesson and Leray 2000); hunting practices are moreover
125 somewhat different in the two zones (e.g., properties managed specifically for snipe hunting
126 are more frequent on the coast; Tesson and Leray 2000). For each of the six sets of model
127 parameters (survival in winter, survival in summer, state-fidelity, recapture probability,
128 recovery probability), we thereby considered the following effects: full time variation (one
129 parameter per year); age effect (hatch year vs. adults); coarse geographic variation (coastal
130 zone vs. interior zone). Out of the large number of possible combinations of these effects, we
131 selected a set of 17 models representing a sequential selection for the effects of zone, then
132 year, and age (Table 1). Our approach was to start from the most complex model and then
133 simplify it by comparing its Akaike Information Criterion (AIC) with that of simpler models
134 in a stepwise fashion (see the caption of Table 1 for further details). We used the usual
135 difference of two AIC points to choose between models (Burnham and Anderson 2002). Once
136 a preferred model was obtained, we considered variation around this model, namely, we
137 tentatively replaced the full year effects acting on recapture, recovery or survival probabilities
138 by logit-linear trends (representing a gradual increase or decrease in parameter value with
139 time). A linear trend is expected both because of the sampling design (increasingly numerous

140 locations were included and the effort was initially focused around a few high-hunting
141 locations) and because of ongoing changes in the wintering habitat of snipes. We also tried
142 removing the state-specificity in recovery probability, representing a homogenous hunting
143 pressure across areas with and without banding effort; as well as adding state-specificity in
144 survival probability, representing a heterogeneous survival probability across areas with and
145 without banding effort. Lastly we investigated whether our multistate approach was indeed
146 supported by the data by merging the two states “in banding area” and “out of banding area”
147 and comparing AIC. Model building and fitting was performed using E-SURGE (Choquet et
148 al. 2009b).

149 *Matrix modeling, recruitment rate and population trend*

150 Most snipes access to reproduction in their first year of life. To describe snipe population
151 dynamics we thus needed two age classes only: “first-year birds” and “adults”. Accordingly
152 we built a two age-class, pre-breeding-census matrix model. In this model, population
153 stability (population growth rate of one) occurs if and only if the number of one-year old
154 recruits perfectly compensates the deaths of breeding adults. This translates into:

$$\text{Eq. 3} \quad R_{MIN} = 1 - S$$

155 where R is the recruitment rate (number of female offspring that reach one year of age, per
156 breeding female) and S is the annual adult survival rate estimated from our data.

157 The best information available about recruitment rate in the French-wintering snipe
158 population is probably the age ratio among captured birds. This metric is however affected by
159 the fact that migration phenology differs between hatch year and later years. We considered
160 the range 30-70% as plausible for the November 1st value of the percentage of hatch-year
161 birds (age-ratio). Our unpublished data indicate 60% as the most plausible value, with lower
162 values believed to correspond to unsuccessful breeding seasons. Furthermore age-ratio in

163 autumn needs to be corrected for uneven sex-ratio (the wintering population is female-
 164 biased). We considered that recruitment occurred on May 1st. Summer survival probability in
 165 Eq. 4 was thus raised to the power corresponding to the number of months of exposure.
 166 Dividing the number of female offspring that recruited (left pair of brackets) by the number of
 167 females that produced those recruits (right pair of brackets), recruitment rate was then
 168 computed as:

$$\text{Eq. 4} \quad R(AR) = \left[AR \cdot (1 - SR_{HY}) \cdot \tilde{s}_W^4 \cdot s_s^{2/8} \right] \left[\frac{(1-AR) \cdot (1-SR_{AD})}{s_s^{6/8}} \right]^{-1}$$

169 where AR is the proportion of hatch year birds in the November population, SR_{HY} is the
 170 proportion of males among hatch year birds (taken to be 45%; unpublished data), SR_{AD} is the
 171 proportion of males among adults birds (taken to be 32%; unpublished data), and s_s and \tilde{s}_W
 172 are as estimated from our data. Sampling uncertainty linked to the relative sparseness of the
 173 data was accounted for in a parametric bootstrap (Davison and Hinkley 1996) producing a
 174 confidence interval for $R(AR)$. The bootstrap was performed within the variation for survival
 175 estimates, but sex-ratios were considered as fixed values.

176 **Results**

177 *Goodness of fit tests*

178 The global goodness-of-fit test was non-significant ($\chi_{29}^2=28.79$, $P = 0.48$, $\hat{c}=0.99$), suggesting
 179 that the recapture process was unlikely to be subject to major individual or spatial
 180 heterogeneity. However, the test for short-term trap dependence was very significant and in
 181 the direction of trap shyness. Since our multistate model was aimed at accommodating
 182 movements in and out of the banding areas (which possibly explained the trap shyness), and
 183 since the overall test was not significant, we did not correct for over-dispersion in the model
 184 selection procedure.

185 *Model selection*

186 Results of the model selection are presented in Table 1. The effect of geographic zone was
187 retained in winter survival and state-fidelity but not in recapture probability (first section in
188 Table 1). The effect of year was discarded in survival and state-fidelity probabilities but
189 retained in recapture and recovery probability (second section in Table 1). Age-effects were
190 discarded in all parameters except state-fidelity, for which the AIC difference was still less
191 than two points (third section in Table 1). Removing state-specificity in recovery probability
192 decreased the support from the data (Model 18 vs. Model 17), and adding state-specificity in
193 survival slightly increased it (Model 19 vs. Model 17: difference in AIC less than two points,
194 indicating uncertainty about the presence of state-specificity in survival). Replacing year-
195 effects by linear trends decreased the support (Model 20 vs. 17). The preferred model at the
196 end of the model selection procedure had the effect of geographic zone on winter survival and
197 site-fidelity, the effect of age on site-fidelity, the effect of year on recovery and recapture, and
198 the effect of state (within/outside banding sites) on survival and recovery probabilities.

199 *Parameter estimates from the preferred model*

200 Annual survival estimates were 0.52 in the coastal zone and 0.44 in the interior. This
201 probability could be decomposed into the “summer” survival probability of 0.63 (95%
202 confidence interval: [0.45, 0.78]) for an eight month period, and the winter survival
203 probability. In state 2 monthly winter survival probability was a very low 0.20 with 95% CI
204 [0.005, 0.91] and 0.12 with 95% CI [0.003, 0.86] for the coastal and interior zones
205 respectively. In state 1 monthly winter survival probability was 0.95 with 95% CI [0.87, 0.98]
206 and 0.92 with 95% CI [0.79, 0.97] for the coastal and interior zones respectively. As per our
207 model selection, hatch year birds survived as well as adults birds.

208 Recapture probability was, on average over years, 0.03 (estimated range [0, 0.05]).
209 Recovery probability was 0.060 on average over years in state 1 (“in banding locations”)
210 (estimated range [0,002, 0.11]). Recovery probability was higher in state 2 although large
211 uncertainty remained (“out of banding locations”): average estimate over years 0.69,
212 estimated range [0.18, 0.96]. State-fidelity was very high in both states. In state 1 the point
213 estimate for fidelity was lower in hatch year birds, especially on the coast, although large
214 uncertainty remained (estimate for hatch year: 0.84 with 95% CI [0.29, 0.98]; estimate for
215 adults 0.92 with 95% CI [0.44, 0.99]). Fidelity to state 2 was estimated at 100% for all zones
216 and age-classes (boundary estimate indicating that snipes that transitioned to state 2 never
217 returned to state 1). Overall, the model was thus akin to a mixture of a state with high hunting
218 pressure (state 2) and a state with low hunting pressure (state 1).

219 *Non-preferred model without the multistate structure*

220 The model without distinction between a state “in banding location” and a state “out of
221 banding location” (which is not in Table 1) had 9.5 AIC points more than the preferred model.
222 The multistate structure was thereby supported by the data. In this particular analysis, the
223 survival estimates were however relatively robust to the choice of model. Point estimates for
224 annual survival probabilities from the non-preferred model without the multistate structure
225 were 0.49 and 0.45 in the coastal and interior zones respectively (vs. 0.52 and 0.44 in the
226 preferred model).

227 *Matrix modeling and computation of recruitment rate*

228 The minimum number of offspring per female was $R_{MIN} = 0.48$ female recruits per female on
229 the coast and $R_{MIN} = 0.56$ female recruits per female in the interior. The actual recruitment
230 rate computed from Eq. 4 varied from a pessimistic 0.18 if November age-ratio was 30% to
231 an optimistic 0.97 if November age-ratio was 70% (Fig 1a). Values of November age ratio

232 below 54% on the coast and 61% in the interior were associated with population decline,
233 although large uncertainties remained (Fig. 1b).

234 **Discussion**

235 In an elusive and mobile species of wader, we used ring recoveries and recapture data to build
236 a population model and make inference about population trend. We argue that in other species
237 with similar characteristics (most migratory gamebirds) this approach is more effective than
238 census data, because the latter are rendered unreliable when birds unpredictably move out of
239 survey areas or escape detection. Here, for the French wintering snipe population, we provide
240 an updated estimate of yearly survival and use age-ratio data to infer that the population is
241 stable, although we call for more data to reduce uncertainty.

242 *Survival estimation and data collection*

243 The spatial scale of our study is much larger than the scope of earlier works on snipe
244 demography (national band-recovery scheme vs. localized capture-recapture program, e.g.,
245 Spence 1988). This constitutes an improvement compared to previous estimations of snipe
246 and other wader survival. Nevertheless, with increasing spatial scope also came new issues. In
247 particular the existence of a huge matrix surrounding banding locations, where snipe could
248 still be reported by hunters but had no chance to be recaptured, called for a multistate capture-
249 recapture analyses. But even then, snipes may some time after their first capture choose to
250 winter in locations with altogether no hunting and no ringing or with no reporting of rings.
251 French-ringed snipes are for example very rarely reported from south of the Pyrenees. This
252 can induce a downward bias in survival as permanent emigration to unmonitored areas is
253 confounded with death (the issue of “apparent survival” which is described in full by
254 Burnham 1993). Second, banding effort was concentrated around a few areas. In particular the
255 locality of Braud-et-Saint-Louis contributed >17% of banding records while the other 347

256 localities contributed an average 0.25% each. In other words, the individuals included in this
257 analysis might not be representative of the whole French-wintering population. To confirm or
258 infirm this, 1) efforts should be made towards documenting the probability that French-
259 banded snipes shot in the Iberian peninsula are reported; and 2) banding and recapture effort
260 in France should be extended to areas known *not* to host a significant number of hunters (e.g.,
261 large protected areas).

262 The solution towards which our multistate model converged was a situation with one
263 state with low recovery probability (state 1), and one state with low survival and high
264 recovery probability (state 2). The existence of locations with strong hunting pressure might
265 explain this result; under this explanatory hypothesis, state-fidelity parameters would capture
266 heterogeneity in hunting pressure rather than movement probabilities.

267 *Population trend*

268 Our point estimates indicate that population declines may occasionally occur after a year of
269 poor breeding success, but that on average the population is stable (Fig. 1: for a November
270 age-ratio of 60% as commonly observed, the point estimate of the growth rate is above 1). We
271 note however 1) that much more data will be necessary to confirm these conclusions with
272 tighter confidence intervals, and 2) our matrix population models did not include age-
273 specificity in breeding success. First-year breeders were assumed to experience the same
274 breeding success as adults, although in many species they are less successful. Thus, Eq. 3
275 gives an optimistic estimation of R_{MIN} . In any case, threats such as wetland drainage, scrub
276 encroachment, urbanization, and other habitat modification may not be as strong in the
277 breeding range of the French-wintering population as they are in other parts of the range
278 (Baines 1988; Grishanov 2006). Population resilience may also come from compensatory

279 density-dependence and the natural response of breeding females to temporal variability in
280 wetland habitat quality (Péron et al. 2012b).

281 *Recommendations*

282 Based on our data and analysis, banding data (recoveries and recaptures) constitute a relevant
283 alternative to census data, which can prove unreliable in waterbirds. The obvious drawbacks
284 of the approach are the field effort which increases dramatically compared to a census-based
285 study, and the relative complexity of the statistical analysis. In terms of monitoring, the
286 examination of our own data leads us to recommend some form of stratified sampling in
287 which areas with different land use and land ownership are all represented. The current
288 approach of mostly working near hunting locations can lead to datasets biased towards low
289 survival probabilities. Using a hunting pressure index as a predictor of survival probability is
290 an option which has been attempted in woodcocks (Péron et al. 2012a) but there are multiple
291 challenges: hunting bags are not valid proxies because the population sizes from which they
292 are harvested are generally unknown; and indexes based on banding data are by construction
293 correlated to the recovery and survival estimates (Péron et al. 2012a). Lastly, complexifying
294 the model (adding the multistate structure) was warranted because of the expected spatial
295 heterogeneity in recapture probability: there was a large matrix surrounding banding areas
296 where snipes could escape recapture effort while still being subjected to hunting. Even if we
297 later found that neglecting this aspect had no impact on survival estimates in the present
298 analysis, we note that this was largely due to the sparseness of the dataset which led to
299 imprecise point estimates. It has been shown elsewhere that neglecting the multistate structure
300 of a dataset can lead to biased survival estimates (Lebreton & Pradel 2002). In conclusion, we
301 recommend mark-recapture-recovery data, multistate analyses, and matrix population models
302 for the study of the conservation status of waders and other animal species that can serve as
303 indicator species, but for which reliable census are difficult to implement.

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Tables

Table 1: Model selection for the effects of geographic zone (coastal vs. interior), year, and age (first year vs. adult) on model parameters. Model #1 is the most complex “umbrella” model. Phrases indicated in bold indicate selected model simplifications (e.g., Age+Year when in bold indicates that the Zone effect is dropped from the preferred model). np is the number of parameters in the model, AIC is the Akaike information criterion. Because the data was deemed too sparse to support a model selection including all the typically included combinations of effects (Lebreton et al. 1992), we devised a step-wise approach. For each step, there was a starting model that depended on the previous steps. We computed the difference in AIC between this starting model and other models in the subset considered at this step. This difference is denoted $\Delta AIC^{(s)}$ for step #s. We also computed the overall difference in AIC compared to the overall preferred model (Model 19). This difference is denoted ΔAIC without superscript. Structures that were selected at each step are underlined.

		Summer								
Model#	Winter survival	survival	Fidelity	Recapture	Recovery	np	Deviance	AIC	$\Delta AIC^{(1)}$	ΔAIC
1.	Selection for the effect of zone (comparison point: Model 1)					np	Deviance	AIC	$\Delta AIC^{(1)}$	ΔAIC
1	<u>Age+Zone+Year</u>	<u>Age+Year</u>	<u>Age+Zone+Year</u>	<u>Age+Zone+Year</u>	<u>Fidelity+Age+Zone+Year</u>	81	2777.00	2939.00	0	24.08
2	<u>Age+Year</u>	<u>Age+Year</u>	<u>Age+Zone+Year</u>	<u>Age+Zone+Year</u>	<u>Fidelity+Age+Zone+Year</u>	80	2799.92	2959.92	20.92	45.00
3	<u>Age+Zone+Year</u>	<u>Age+Year</u>	<u>Age+Year</u>	<u>Age+Zone+Year</u>	<u>Fidelity+Age+Zone+Year</u>	79	2779.83	2937.83	-1.16	22.92

4	Age+Zone+Year	Age+Year	Age+Zone+Year	<u>Age+Year</u>	Fidelity+Age+Zone+Year	80	2777.01	2937.01	-1.99	22.09
5	Age+Zone+Year	Age+Year	Age+Zone+Year	Age+Zone+Year	Fidelity+Age+Year	80	2787.65	2947.65	8.66	32.74
2. Selection for the effect of year (comparison point: Model 4)						np	Deviance	AIC	$\Delta AIC^{(2)}$	ΔAIC
4	Age+Zone+Year	Age+Year	Age+Zone+Year	Age+Year	Fidelity+Age+Zone+Year	80	2777.01	2937.01	0	22.09
6	<u>Age+Zone</u>	Age+Year	Age+Zone+Year	Age+Year	Fidelity+Age+Zone+Year	67	2796.17	2930.17	-6.84	15.25
7	Age+Zone+Year	<u>Age</u>	Age+Zone+Year	Age+Year	Fidelity+Age+Zone+Year	68	2796.80	2932.80	-4.21	17.88
8	Age+Zone+Year	Age+Year	<u>Age+Zone</u>	Age+Year	Fidelity+Age+Zone+Year	67	2800.57	2934.57	-2.44	19.66
9	Age+Zone+Year	Age+Year	Age+Zone+Year	Age	Fidelity+Age+Zone+Year	67	2806.02	2940.02	3.01	25.10
10	Age+Zone+Year	Age+Year	Age+Zone+Year	Age+Year	Fidelity+Age+Zone	67	2812.35	2946.35	9.34	31.43
11	<u>Age+Zone</u>	<u>Age</u>	<u>Age+Zone</u>	Age+Year	Fidelity+Age+Zone+Year	42	2839.20	2923.20	-13.81	8.28
3. Selection for the effect of age (comparison point: Model 11)						np	Deviance	AIC	$\Delta AIC^{(3)}$	ΔAIC
11	Age+Zone	Age	Age+Zone	Age+Year	Fidelity+Age+Zone+Year	42	2839.20	2923.20	0	8.28
12	<u>Zone</u>	Age	Age+Zone	Age+Year	Fidelity+Age+Zone+Year	41	2839.28	2921.28	-1.91	6.37
13	Age+Zone	.	Age+Zone	Age+Year	Fidelity+Age+Zone+Year	41	2839.52	2921.52	-1.68	6.60
14	Age+Zone	Age	Zone	Age+Year	Fidelity+Age+Zone+Year	41	2842.19	2924.19	0.99	9.27
15	Age+Zone	Age	Age+Zone	<u>Year</u>	Fidelity+Age+Zone+Year	41	2840.04	2922.04	-1.16	7.12

16	Age+Zone	Age	Age+Zone	Age+Year	<u>Fidelity+Zone+Year</u>	41	2839.29	2921.29	-1.91	6.37
17	<u>Zone</u>	.	Age+Zone	<u>Year</u>	<u>Fidelity+Zone+Year</u>	38	2839.90	2915.90	-7.29	0.99
4. Selection for the effect of fidelity (comparison point: Model 17)						np	Deviance	AIC	$\Delta AIC^{(4)}$	ΔAIC
17	Zone	.	Age+Zone	Year	Fidelity+Zone+Year	38	2839.90	2915.90	0	0.99
18	Zone	.	Age+Zone	Year	Zone+Year	37	2847.19	2921.19	5.29	6.28
19	<u>Fidelity+Zone</u>	.	Age+Zone	Year	Fidelity+Zone+Year	39	2836.92	2914.92	-0.99	0
5. Selection for linear trend in time effect (comparison point: Model 17)						np	Deviance	AIC	$\Delta AIC^{(5)}$	ΔAIC
17	Zone	.	Age+Zone	Year	Fidelity+Zone+Year	38	2839.90	2915.90	0	0.99
20	Zone	.	Age+Zone	LYear	Fidelity+Zone+LYear	14	2934.96	2962.96	47.06	48.05

Figure legends

Fig. 1: (a) Recruitment rate (female offspring that reach one year of age per breeding female) and (b) Population growth rate, estimated for varying values of November age ratio (proportion of hatch year birds in the November population). Plain lines: coastal zone; Dashed lines: interior zone. Grey areas: 95% confidence from a parametric bootstrap within the estimated sampling (co)variation in survival probabilities; the darkest area represents overlaps in the confidence intervals.

