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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 1<sup>st</sup> to October  
74 31<sup>st</sup> the following year. The 12 month period starting on November 1<sup>st</sup> 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  $\Phi$  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 1<sup>st</sup> 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 1<sup>st</sup>. 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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## References

- Amano, T., Szekely, T., Koyama, K., Amano, H., Sutherland, W.J., 2010. A framework for monitoring the status of populations: An example from wader populations in the East Asian-Australasian flyway. *Biological Conservation* 143, 2238-2247.
- Baines, D., 1988. The effects of improvement of upland, marginal grasslands on the distribution and density of breeding wading birds (Charadriiformes) in Northern England. *Biological Conservation* 45, 221-236.
- Baldock, D. ed., 1984. Wetland drainage in Europe: the effects of agricultural policy in four EEC countries. Institute for European Environmental Policy; International Institute for Environment and Development, London.
- Barbraud, C., Lepley, M., Mathevet, R., Mauchamp, A., 2002. Reedbed selection and colony size of breeding Purple Herons *Ardea purpurea* in southern France. *Ibis* 144, 227-235.
- Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62, 821-841.
- BirdLife-International, 2012. Species factsheet: *Gallinago gallinago*. Downloaded from <http://www.birdlife.org> on 22/08/2012.
- Burnham, K.P., 1993. A theory for combined analysis of ring recovery and recapture data, In *Marked individuals in the study of bird population*. eds J.D. Lebreton, P.H. North, pp. 199-213. Birkhäuser Verlag, Basel, Switzerland.
- Burnham, K.P., Anderson, D.R., 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edition. Springer-Verlag, New York.

- Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.M., Pradel, R., 2009a. U-CARE: Utilities for performing goodness of fit tests and manipulating CAPture-REcapture data. *Ecography* 32, 1071-1074.
- Choquet, R., Rouan, L., Pradel, R., 2009b. Program E-SURGE: a software application for fitting Multievent models, In *Modeling Demographic Processes In Marked Populations*. eds D.L. Thomson, E.G. Cooch, M.J. Conroy, pp. 845-865. Springer, New York.
- CICB-&-OMPO, 2002. Key to ageing and sexing of the Common Snipe *Gallinago gallinago* by the study of feathers. CIC & OMPO, Paris.
- Davidson, N.C., Stroud, D.A., 2006. African-Western Eurasia flyways: current knowledge, population status and future challenges, In *Waterbirds around the world*. eds G.C. Boere, G. C.A., D.A. Stroud, pp. 63-73, The Stationery Office, Edingburgh, UK.
- Davies, M., 1977. Wintering Snipe in Middlesex. *Ringing and Migration* 1, 173-177.
- Davison, A.C., Hinkley, D.V., 1997. *Bootstrap methods and their applications*. Cambridge University Press, Cambridge.
- DeLuca, W.V., Studds, C.E., King, R.S., Marra, P.P., 2008. Coastal urbanization and the integrity of estuarine waterbird communities: Threshold responses and the importance of scale. *Biological Conservation* 141, 2669-2678.
- Dodman, T., Boere, G.C. eds., 2010. *The Flyway Approach to the Conservation and Wise Use of Waterbirds and Wetlands: A Training Kit*. Wings Over Wetlands Project, Wetlands International and BirdLife International, Ede, The Netherlands.
- Gauthier, G., Lebreton, J.D., 2008. Analysis of band-recovery data in a multistate capture-recapture framework. *Canadian Journal of Statistics-Revue Canadienne De Statistique* 36, 59-73.

- Gleason, R.A., Laubhan, M.K., Euliss Jr, N.H. eds., 2008. Ecosystem services derived from wetland conservation practices in the United States Prairie Pothole Region with an emphasis on the U.S. Department of Agriculture Conservation Reserve and Wetlands Reserve Programs. U.S. Geological Professional Paper 1745.
- Graveland, J., 1999. Effects of reed cutting on density and breeding success of Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *A-schoenobaenus*. *Journal of Avian Biology* 30, 469-482.
- Greenberg, R., Demarest, D.W., Matsuoka, S.M., Mettke-Hofmann, C., Evers, D., Hamel, P.B., Lusnier, J., Powell, L.L., Shaw, D., Avery, M.L., Hobson, K.A., Blancher, P.J., Niven, D.K., 2011. Understanding declines in Rusty Blackbirds, In *Boreal birds of North America: a hemispheric view of their conservation links and significance*. *Studies in Avian Biology* 41. ed. P.V. Wells, pp. 107-126, University of California Press, Berkeley, CA.
- Grishanov, D., 2006. Conservation problems of migratory waterfowl and shorebirds and their habitats in the Kaliningrad region of Russia, In *Waterbirds around the world*. eds G.C. Boere, D.A. Stroud, pp. 63-73, The Stationery Office, Edingburgh, UK.
- Hénaux, V., Bregnballe, T., Lebreton, J.D., 2007. Dispersal and recruitment during population growth in a colonial bird, the great cormorant *Phalacrocorax carbo sinensis*. *Journal Of Avian Biology* 38, 44-57.
- Lebreton, J.D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals - A unified approach with case-studies. *Ecological Monographs* 62, 67-118.
- Lebreton, J.D., Nichols, J.D., Barker, R.J., Pradel, R., Spendelow, J.A., Caswell, H., 2009. Modeling individual animal histories with multistate capture-recapture models, In

- Advances in Ecological Research 41. ed. H. Caswell, pp. 87-173. Academic Press, London.
- Lebreton, J.D., Pradel, R., 2002. Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics* 29, 353-369.
- Martin, J., Nichols, J.D., Kitchens, W.M., Hines, J.E., 2006. Multiscale patterns of movement in fragmented landscapes and consequences on demography of the snail kite in Florida. *Journal of Animal Ecology* 75, 527-539.
- McNichols, M.K., 1975. Larid site tenacity and group adherence in relation to habitat. *Auk* 92, 98-104.
- Paillisson, J.M., Reeber, S., Marion, L., 2002. Bird assemblages as bio-indicators of water regime management and hunting disturbance in natural wet grasslands. *Biological Conservation* 106, 115-127.
- Péron, G., Crochet, P.-A., Choquet, R., Pradel, R., Lebreton, J.-D., Gimenez, O., 2010. Capture-recapture models with heterogeneity to study survival senescence in the wild. *Oikos* 119, 524-532.
- Péron, G., Ferrand, Y., Choquet, R., Pradel, R., Gossmann, F., Bastat, C., Guénézan, M., Bauthian, I., Julliard, R., Gimenez, O., 2012a. Spatial heterogeneity in mortality and its impact on the population dynamics of Eurasian woodcocks. *Population Ecology* 54, 305-312.
- Péron, G., Ferrand, Y., Gossmann, F., Bastat, C., Guénézan, M., Gimenez, O., 2011. Escape migration decisions in Eurasian Woodcocks: insights from survival analyses using large-scale recovery data. *Behavioral Ecology and Sociobiology* 65, 1949-1955.
- Péron, G., Nicolai, C.A., Koons, D.N., 2012b. Demographic response to perturbations: the role of compensatory density dependence in a North American duck under variable harvest regulations and changing habitat. *Journal of Animal Ecology* 81, 960-969.

- Polak, M., Kasprzykowski, Z., Kucharczyk, M., 2008. Micro-habitat nest preferences of the great bittern, *Botaurus stellaris*, on fishponds in central-eastern Poland. *Annales Zoologici Fennici* 45, 102-108.
- Pradel, R., Gimenez, O., Lebreton, J.D., 2005. Principles and interests of GOF tests for multistate capture-recapture models. *Animal Biodiversity and Conservation* 28, 189-204.
- Ramsar-Convention-Secretariat, 2010. Ramsar handbooks for the wise use of wetlands, 4th edition, Gland, Switzerland.
- Roshier, D.A., Robertson, A.I., Kingsford, R.T., 2002. Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. *Biological Conservation* 106, 399-411.
- Sandercock, B.K., 2003. Estimation of survival rates for wader populations: a review of mark-recapture methods. *Wader Study Group Bulletin* 100, 163-174.
- Spence, I.M., 1988. Mortality of Snipe estimated from a mark and recapture study. *Ringing and Migration* 9, 27-31.
- Tesson, J.-L., Leray, G., 2000. Enquête nationale sur les tableaux de chasse à tir saison 1998-1999. La bécassine des marais et la bécassine sourde. *Faune Sauvage, Cahiers techniques* 251: 160-167. In French.
- Włodarczyk, R., Kaczmarek, K., Minias, P., Janiszewsky, T., 2008. Ageing and sexing of the Common Snipe *Gallinago gallinago gallinago*. *Wader Study Group Bulletin* 115, 45-49.

## 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  $\Delta\text{AIC}^{(s)}$  for step #s. We also computed the overall difference in AIC compared to the overall preferred model (Model 19). This difference is denoted  $\Delta\text{AIC}$  without superscript. Structures that were selected at each step are underlined.

	Summer									
Model#	Winter survival	survival	Fidelity	Recapture	Recovery	np	Deviance	AIC	$\Delta\text{AIC}^{(1)}$	$\Delta\text{AIC}$
1.	Selection for the effect of zone (comparison point: Model 1)									
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	$\Delta AIC^{(2)}$	$\Delta AIC$
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	$\Delta AIC^{(3)}$	$\Delta AIC$
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	$\Delta AIC^{(4)}$	$\Delta AIC$
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	$\Delta AIC^{(5)}$	$\Delta AIC$
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.

