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# **Spatial heterogeneity in mortality and its impact on the population dynamics of Eurasian woodcocks**

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**Running title:** Spatial heterogeneity and seasonal woodcock survival

## 1 **Abstract**

2 Spatial heterogeneity, especially in mortality risk, is a major factor shaping population dynamics.  
3 Here we study the impacts of spatial heterogeneity in hunting pressure on the demography of  
4 Eurasian woodcock *Scolopax rusticola*, a relatively long-lived migratory gamebird. We develop  
5 capture-recapture-recovery models in which both seasonality and spatial variation in hunting  
6 pressure are accounted for, and fit them to individual-based data collected across the French  
7 wintering range (> 44,000 banded individuals) as well as recoveries from spring stopovers and  
8 breeding grounds in Europe. Our results quantify spatial variation in survival probability in the  
9 wintering areas. They highlight the role of source-sink dynamics involving juvenile settlement  
10 decisions, as well as the importance of mortality outside the winter quarters. We also discuss the  
11 impact of spatial heterogeneity for demographic parameter estimation and data collection at the  
12 range scale.

## 13 **Introduction**

14 Spatial variation in environmental factors shapes population dynamics (Hanski 1991; Ozgul et al.  
15 2009). However, most studies focus on variation in habitat features (e.g., Ozgul et al. 2006;  
16 Mueller et al. 2009). Predation pressure is another factor expected to vary spatially, which is  
17 known to shape space use by prey species at the landscape scale (Kauffman et al. 2007), but does  
18 not compulsorily depend on habitat features especially on a broader scale. Predation pressure can  
19 thereby, independently from other factors, determine habitat quality. This is particularly true of  
20 “human predation” (hunting), which is more linked to road access than to other habitat features,  
21 and against which avoidance behaviors (e.g., Salo et al. 2008) are less likely to be effective than  
22 against natural predation.

23 Here we focus on how spatial variation in hunting pressure shapes local population  
24 dynamics in Eurasian woodcocks *Scolopax rusticola* that winter in France. In this long-lived  
25 species (known to exceed 20 year old in the wild) with relatively low offspring production  
26 (Hoodless and Coulson 1998; Ferrand et al. 2008), and known to live at low densities (Duriez et  
27 al. 2005b, c), the prediction is that hunting pressure, *via* its impact on local survival rates, should  
28 shape population dynamics (Pfister 1998; Nilsen et al. 2009). However, the rates at which local  
29 populations are able to compensate for hunting mortality (e.g., *via* density-dependent variation in  
30 mortality rates from other sources: Burnham and Anderson 1984) can markedly modify the shape  
31 of that relationship.

32 Capture-recovery data and statistical analyses (Williams et al. 2002) can be made  
33 spatially-explicit to investigate these issues (Royle and Dubovski 2001; Péron et al. 2011).  
34 Moreover, the benefits of making survival and recovery probability estimates spatially-explicit go

35 beyond the biological implications, since in many cases aggregating heterogeneous data over  
36 large spatial scales can produce biased estimates of the average value of the parameters at stake  
37 (Bauthian 2005; Fletcher et al. 2011). Yet, spatially-explicit analyses are computer-intensive,  
38 data-hungry, and require the use of elaborate techniques, which reduces their general  
39 applicability. Here we use a more easy to implement approach, based on a proxy derived from the  
40 capture-recovery data, with the caveat that we cannot get rid of sampling covariance between the  
41 proxy and survival estimates. This proxy is used to investigate and discuss the role of spatial  
42 variation in hunting pressure in woodcock demography, as well as issues associated with data  
43 collection and parameter estimation.

## 44 **Material and methods**

45 Previous works about the French-wintering woodcock population have highlighted dramatically  
46 low survival probability (Hémery et al. 1978; Gossmann et al. 1994; Tavecchia et al. 2002,  
47 providing survival estimates up to 1998). These previous estimates are nevertheless incompatible  
48 with the observed population trend (Ferrand et al. 2008): there has been no decrease from 1990  
49 onwards and even a probable increase in recent years. We were therefore interested in updating  
50 the survival estimates, in order to detect a potential increase in survival probability after 1990, as  
51 well as to correct some potential flaws of the previous studies. Firstly, previous banding efforts  
52 were mainly concentrated around well-known, high woodcock density areas where hunting  
53 pressure could be considered higher than on average. The geographic area that was sampled for  
54 this analysis was much more exhaustive than previously, and included both highly and lightly  
55 hunted areas. Secondly, we refined the analysis by 1) using data from both fall/winter and  
56 spring/summer to document seasonal variation more precisely, which is important given the  
57 migratory nature of the population and that documented spatial variation occurs in fall/winter, 2)

58 allowing age effects on summer survival probability, 3) using a measure of hunting pressure to  
59 account for spatial variation and varying contributions of the different banding locations to the  
60 dataset, and 4) relieving a constraint of linear temporal variation that was put on recovery  
61 probability in previous modeling efforts.

## 62 Data collection

63 Detail on the field procedures can be found in Gossmann et al. (1994) and Ferrand et al. (2008).  
64 Briefly, on the winter grounds most woodcocks commute between night-time feeding grounds  
65 (mainly meadows) where banding occurs, and day-time roost sites in forests, where hunting  
66 occurs (Duriez et al. 2005a, c). Woodcocks are marked with metal rings from October to  
67 February. Age determination (adult or juvenile) is done using plumage features (Ferrand and  
68 Gossmann 2009), but males and females are not distinguishable. Recovered rings are reported to  
69 the woodcock network group at the Office National de la Chasse et de la Faune Sauvage  
70 (ONCFS; French Hunting and Wildlife Service). These recoveries occur on the wintering grounds  
71 in France, but also during migration and on the breeding grounds in Eastern Europe. Recaptures  
72 of banded birds occur during the banding sessions in winter in France. Here we used data  
73 collected between October 1989 and February 2009 (20 years). These data come from 44,902  
74 different individuals, 12,078 of which were recovered in France and 737 recovered in Eastern  
75 Europe, plus 2,873 different recapture events in France.

## 76 Seasonal CR models for the French-wintering Woodcock population

77 Based on the result that woodcocks are very faithful to their wintering location both within and  
78 among years (Gossmann et al. 1994), we considered the banding location as representative of the  
79 location where an individual would spend most of its winters. Our multistate CR models adopted

80 the general structure described by Lebreton (2005) and Gauthier and Lebreton (2008). They were  
81 parameterized using season-specific survival probabilities  $s_t$  (the probability for a bird to survive  
82 during time step  $t$  to  $t+1$ ), recovery probabilities  $r_t$  (the probability for a bird dying to have died  
83 from hunting and been reported as such to the ONCFS woodcock network), and recapture  
84 probabilities  $p_t$  (the probability for a bird already wearing a band to be trapped again during the  
85 winter banding sessions at time step  $t$ , given that it is alive).

86 Recoveries in winter occurred in France and in summer in Eastern Europe and an effect of  
87 season on recovery probability was therefore included in all models. Following Tavecchia et al.  
88 (2002), yearly winter recovery probability was also divided between direct (same winter as the  
89 banding) and indirect (subsequent winters) recovery probabilities. This effect accounted for  
90 various phenomena (Williams et al. 2002, pp. 393-399), including the fact that most woodcocks  
91 were submitted to only a part of their first hunting season, and variation in hunters' reporting rate.

92 A further technical issue was raised by the fact that banding and hunting occur roughly at  
93 the same time in winter. In this study, we accounted for that feature by computing monthly winter  
94 survival probabilities (denoted  $\tilde{s}_t$ ) and raising that probability to the adequate power. Thus,  
95 individuals banded in, e.g., December had a first winter survival probability of  $s_{t_1} = \tilde{s}_{t_1}^3$ , instead  
96 of  $s_{t_1} = \tilde{s}_{t_1}^5$  if they had been banded in October. We used program E-SURGE (version 1.6.4;  
97 Choquet et al. 2009; Appendix 1).

98 Variation in survival probability, model selection and inference

99 We considered the following potential factors of variation in survival:

100 1) Season: ‘Winter  $t$ ’ was the period from October of the year  $t$  to February of the year  $t+1$ .

101 ‘Summer  $t$ ’ was the period from March to September of the year  $t+1$ .

102 2) Age: We separated first-year (juveniles) and adults. The age effect could impact both winter  
103 and summer survival

104 3) Year: one estimate per year (full effect), or linear trend.

105 4) Location: To characterize on a fine scale the spatial variation in hunting pressure (which would  
106 be closer to the actual situation than broader geographical classifications), we separated banding  
107 locations into classes based on a hunting pressure index (HPI) built as follows. For each banding  
108 locality, we computed the percentage over the 20 year study period of the banded birds that were  
109 recovered (shot and reported as such) less than 10km from their banding place (as opposed to  
110 those recovered further away). Localities were then categorized into two groups corresponding to  
111 above-median (high) and below-median (low) percentage of birds recovered within 10km. We  
112 restricted the dataset to the 714 localities where at least 20 birds have been banded over the study  
113 period. We computed HPI for the whole period, i.e., we looked at a temporal average of local  
114 hunting pressure. Both during seasonal migration and during periods of deepest snow cover,  
115 woodcocks transit through large geographic areas. The HPI can thereby be interpreted as a  
116 comparison between the local hunting pressure (within the 10 km radius) and the average hunting  
117 pressure (as encountered when wandering). More detail on HPI and the limits and advantages of  
118 that approach are presented in Appendix 2. In particular, since HPI was computed from the same  
119 CR data as survival and recovery, it shared a sampling variance with these parameters, which  
120 reduced the power of the tests for the effect of hunting pressure.



121 We considered 21 different combinations of the above four factors in our set of candidate  
122 models (Table 1). The model selection followed a step by step procedure, in which we first  
123 selected the structure for encounter probabilities (recovery and recapture) and then selected the  
124 structure for survival probabilities (Table 1). We relied on AIC (Akaike Information Criterion;  
125 Burnham and Anderson 2002) to select the preferred model in the set of 21 models. We found  
126 local minima in the deviance (combinations of parameters values for which the likelihood surface  
127 reached a peak that was not the absolute maximum), which were handled by, for each model,  
128 running the optimization procedure several times starting from different sets of initial values.

#### 129 Growth rate computation

130 With an offspring production of 1.8 per female per year (Hoodless and Coulson 1998; Ferrand et  
131 al. 2008), and using post-breeding, two age class matrix population models, we obtained an  
132 estimate of population growth rate  $\lambda$  based on the survival estimates of the preferred CMR model.  
133 We computed the growth rate specific to each of the HPI classes, for each year. Confidence  
134 intervals around  $\lambda$  estimates were computed using a bootstrap procedure (Givens and Hoeting  
135 2005), in which we sampled 1000 times within the approximate normal distributions of the logit-  
136 transformed survival probabilities (as provided by E-SURGE), and obtained the empirical  
137 distribution of  $\lambda$ . All estimates of temporal variance were corrected for sampling variance using  
138 equation 4.2 p. 263 in Burnham et al. 1987, solved using MAPLE.

## 139 **Results**

### 140 Model selection

141 The model selection procedure (Table 1) favored models in which HPI affected both survival and  
142 recovery probabilities. Other retained structures were the effect of age on survival probabilities in

143 winter and summer, as well as between-year variation in winter and summer survival, winter  
144 recovery and winter recapture probabilities (model #17 in Table 1). Including time-dependence in  
145 summer survival and summer recovery probabilities only moderately improved the fit (models  
146 #17 vs. 18 and #5 vs. 1), probably because of the relatively sparse data from the summer period.

147 Parameter estimates: seasonality, time, hunting pressure, and age-effects

148 Parameter estimates indicated that the high HPI localities were characterized by low survival  
149 (difference between high and low HPI on the logit-scale:  $-0.91 \pm \text{SE } 0.03$ ) and high recovery  
150 probabilities (difference between high and low HPI on the logit-scale:  $0.54 \pm \text{SE } 0.17$ ),  
151 suggesting a spatial cross-correlation between survival and recovery probabilities from different  
152 locations, mediated by HPI. This correlation was not found when tested using temporal instead of  
153 spatial variation (*a posteriori* correlation between time-specific winter survival and winter  
154 recovery probabilities:  $r^2 = 0.07$ ). If reporting rate (the rate at which shot birds with a ring are  
155 reported) did not depend on hunting pressure, the difference in recovery probability between low  
156 and high HPI areas suggests that two-fold variation in hunting pressure were commonplace  
157 between different locations.

158 Survival probability varied between years in a manner that suggested an increase with  
159 time (Table 2, Fig. 1), but the AIC for the model with a temporal trend suggested that significant  
160 variation remained around that trend (model #21 vs. 17 in Table 1). Summer monthly survival  
161 was generally lower than low-HPI winter monthly survival (Fig. 1; average monthly adult  
162 *summer* survival: 0.95; temporal SD corrected for sampling variance: 0.014; average monthly  
163 adult *winter* survival in low HPI areas:  $0.97 \pm 0.0049$ ). This meant that summer mortality  
164 represented more than two thirds of all adult deaths in birds wintering in low-HPI areas (about

165 half in high HPI areas). Both the comparison of the fit of model #17 vs. 20 and Fig. 1 indicated  
166 the lack of correlation between winter survival and survival during the following summer.

167 Juveniles had lower survival rates than adults, during both the winter and the summer  
168 periods (difference between juvenile and adult monthly survival on the logit-scale:  $-0.83 \pm \text{SE}$   
169  $0.20$  in winter,  $-0.58 \pm \text{SE } 0.23$  in summer). Average yearly survival rate of adults was  $0.61$   
170 (temporal SD corrected for sampling variance:  $0.070$ ) in low HPI areas and  $0.49 \pm 0.067$  in high  
171 HPI areas. Average yearly survival rate of juveniles was  $0.47 \pm 0.078$  in low HPI individuals and  
172  $0.33 \pm 0.065$  in high HPI individuals. If conducted without accounting for spatial heterogeneity  
173 (i.e., discarding the HPI effect from the preferred model), the average yearly survival rate was  
174  $0.59 \pm 0.084$  for adults and  $0.43 \pm 0.10$  for juveniles (average  $\pm$  SE over time). The statistical bias  
175 on average survival due to unaccounted for heterogeneity was therefore low in this analysis.

#### 176 Population growth rate

177 Over the 20-year-long study period the average growth rate was  $1.05$  in high HPI areas (temporal  
178 SD corrected for sampling variance:  $0.13$ ), and  $1.27$  in low HPI areas ( $\pm 0.13$ ). The average  
179 growth rate over areas was  $1.16$  ( $\pm 0.13$ ).

180 At the beginning of the study period (1990-1995),  $\lambda$  estimates indicated that the  
181 population was locally not self-sustainable ( $\lambda < 1$  in high HPI areas; Fig. 2). However, the  
182 average  $\lambda$  across areas was  $1.04$  (temporal SD corrected for sampling variance:  $0.12$ ; Fig. 2), thus  
183 compatible with the observed trend in population counts. After 1995, both parts of the population  
184 showed growth rates above one in most years (Fig. 2), thus again compatible with the observed  
185 increase in population counts. The difference in local growth rate between high and low HPI  
186 areas was significant in most years (95% confidence intervals in Fig. 2).

## 187 **Discussion**

### 188 Spatial heterogeneity and population dynamics

189 The population growth rate estimates were on average 12% higher in low than in high HPI areas.  
190 During the earlier years of the study (pre-1990), when survival probabilities were lower, this  
191 probable effect of hunting pressure meant that high HPI areas were sinks while low HPI areas  
192 were sources. The occurrence of local over-harvesting is also in agreement with previous survival  
193 estimates which were mostly based on data collected in highly-hunted areas (Hémery et al. 1978;  
194 Gossmann et al. 1994; Tavecchia et al. 2002). Yet, no local extinction has ever been reported.  
195 Therefore, although they were obtained without taking temporal variation in fecundity into  
196 account, these results suggest an important role for a source-sink dynamic between places of low  
197 and high hunting pressure (Pulliam 1988; Novaro et al. 2000). Given what is known of woodcock  
198 behavior, it is unlikely that sinks were repopulated by direct movements from low- to high-HPI  
199 areas during the winter. Instead, we suggest that juvenile birds, when they first arrive on the  
200 wintering grounds, may distribute themselves more or less independently of hunting pressure, or  
201 *via* density-dependent dispersal, may settle more often in depleted areas. The latter mechanism  
202 was observed experimentally in Brittany where the removal of adult birds allowed juveniles to  
203 occupy free forest sites (Fadat 1981). We thus believe that juveniles regularly replenish high HPI  
204 areas. In agreement with this hypothesis and with Fadat (1981), we found that low HPI areas have  
205 lower age ratios (number of juveniles per adult among recovered individuals) than high HPI areas  
206 (unpublished result).

## 207 Life history strategy

208 Woodcocks have a slower life history than most gamebird species, especially those facing the  
209 same hunting pressure. As such, woodcocks' population dynamics should be more sensitive than  
210 other gamebirds' to changes in adult survival probability (Pfister 1998). Furthermore, woodcock  
211 natural mortality rate (i.e., from causes other than hunting) should be more "canalised" (Stearns  
212 and Kawecki 1994; Gaillard and Yoccoz 2003), conferring woodcock populations lower ability to  
213 compensate for hunting mortality by changes in natural mortality. The latter prediction is  
214 reinforced by the fact that woodcocks also live in a lower density than other gamebirds, and thus  
215 density regulation is less likely to induce compensatory mortality (Williams et al. 2002). In  
216 agreement, our study showed a change in survival probability between locations with high and  
217 low hunting pressures that was larger than observed in galliformes (Rolland et al. 2010; Besnard  
218 et al. 2010; Sandercock et al. 2011, studying respectively Northern bobwhites, Pyrenean grey  
219 partridges, and Willow ptarmigan). Although it is difficult to draw definitive conclusions from  
220 four data points, we suggest nevertheless that woodcock survival shows a more direct response to  
221 hunting pressure than galliformes, which a direct estimation of compensation rates could confirm.

## 222 Seasonality

223 For woodcocks that wintered in low-HPI areas, mortality on the spring staging and breeding  
224 grounds ('summer') was clearly not negligible. The determinants of this relatively high mortality  
225 outside of the wintering grounds remain unknown, and could include weather (cold springs,  
226 droughts and fires in summer: Gossmann et al. 2011; Sepik et al. 1983), predation (on nesting  
227 females as well as displaying males; Hoodless and Hirons 2007; Widén 1987) and spring hunting  
228 (on displaying males; Blokhin et al. 2006).

229 Winter and summer survival did not show any correlation over time, either positive or  
230 negative. We did not find that summer survival was higher after a winter of high mortality, which  
231 would have been predicted under the hypothesis of summer compensation for hunting mortality  
232 (Boyce et al. 1999). Similarly, the absence of a positive relationship between winter and summer  
233 survival contradicted the hypothesis of a carry-over effect (effect of winter harshness on survival  
234 during the next breeding season). Eventually, since there was no synchrony between the  
235 variation in winter and summer survival, the potential weather-related drivers of survival  
236 probability in the different phases of the yearly cycle are likely local, i.e. not related to a global  
237 scale climate variable.

#### 238 Implications for parameter estimation and data collection

239 The existence of spatial variation in hunting pressure, which was mirrored in the survival rate,  
240 raises two issues. 1) The spatial distribution of sampling effort (capture of un-banded woodcocks)  
241 may not compulsorily match the spatial distribution of hunting pressure, especially at a large  
242 (country) scale. Thereby, some part of the survival distribution may be over-represented in the  
243 data, flawing the overall survival estimate if it is not made spatially explicit. In our case, we  
244 suspect a bias towards highly-hunted areas, because these are also areas of high woodcock  
245 density and because knowledge about woodcock presence in non-hunted locations may be  
246 limited. 2) If not accounted for in the survival model, spatial variation in hunting pressure may  
247 lead to a statistical bias, i.e., the inability of the model fitting method to retrieve the actual  
248 average of survival probability within sampled individuals. Unpublished simulation-based  
249 estimation of this bias suggests it can often be large (Bauthian 2005), though in our case we  
250 estimated a small effect only. Both issues are related to the recurrent problem of individual

251 heterogeneity in capture-recapture models (Carothers 1973; Nichols 1982; Royle 2008; Pradel  
252 2009) and require further investigation.

253         In conclusion, by adding a spatial component to a seasonal CR model, we obtained  
254 insights into the extent to which spatial heterogeneity in winter mortality patterns could  
255 potentially shape population dynamics of a migratory species. The proportion of individuals that  
256 winters in high HPI areas likely determines to a large extent the country-level woodcock  
257 population growth rate. This suggests a way for managers to act upon that growth rate by  
258 spatially regulating hunting access or intensity, where possible. Our results also highlight the  
259 importance of fluxes of individuals into high-HPI areas (most probably juveniles). Lastly, they  
260 illustrate that potential biases linked to data collection and model fitting can be avoided by  
261 making survival estimates spatially explicit.

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## Tables

Table 1. Step-by-step model selection for woodcock survival ( $s_{a,s,t}$ ), recapture ( $p_t$ ) and recovery ( $r_{s,t}$ ) probabilities. In the description of the effects,  $W$  and  $S$  stand for winter and summer,  $a$  stands for age (juveniles vs. adults),  $t$  stands for complete year-effect (20 parameters),  $T$  for linear year effect (2 parameters) and HPI stands for hunting pressure index (2 levels). A dot indicates a constant parameter. + and \* are the usual operators for additive and interacting effects. A semicolon separates models for winter and summer probabilities. For example ‘ $W(\text{HPI}); S(.) + a$ ’ indicates that the effect of  $a$  is additive to the effect of season, that there is no year effect and that HPI affects the winter probability. Given are model numbers (#), description of the effects on survival ( $s_{a,s,t}$ ), recapture ( $p_t$ ) and recovery ( $r_{s,t}$ ) probabilities, number of parameters (np), Deviance, difference in Akaike Information Criterion to the preferred model ( $\Delta\text{AIC}$ ) and a short description of the model biological meaning and difference from neighbouring models. For each step of the model selection, the preferred model is indicated in bold.  $\Delta\text{AIC}$  is computed globally, i.e., represents the distance to the overall preferred model.

#	$s_{a,s,t}$	$p_t$	$r_{s,t}$	#p	Dev	$\Delta\text{AIC}$	Biological meaning
Selection for the time-dependency of recovery and recapture probabilities							
1	$W(a+\text{HPI}); S(a)$	$t$	$W(t+\text{HPI}); S(t)$	65	81373.2	103.2	year-effect on all observation parameters
2	$W(a+\text{HPI}); S(a)$	$t$	$W(\text{HPI}); S(.)$	29	82548.7	1206.7	year-effect on recapture probabilities only
3	$W(a+\text{HPI}); S(a)$	.	$W(t+\text{HPI}); S(t)$	47	81453.3	147.3	year-effect on winter and summer recovery probabilities
4	$W(a+\text{HPI}); S(a)$	.	$W(t+\text{HPI}); S(.)$	28	81468.0	124.0	year-effect on winter recovery probabilities only
<b>5</b>	<b><math>W(a+\text{HPI}); S(a)</math></b>	<b><math>t</math></b>	<b><math>W(t+\text{HPI}); S(t)</math></b>	<b>47</b>	<b>81406.7</b>	<b>100.7</b>	year-effect on winter recovery probabilities only

			$S(\cdot)$				and recapture probabilities
6	$W(a+\text{HPI}); S(a)$	.	$W(\text{HPI}); S(\cdot)$	11	81701.2	323.2	No year-effect on observation parameters
7	$W(a+\text{HPI}); S(a)$	$t$	$W(T+\text{HPI}); S(\cdot)$	30	81474.8	134.8	Best model above with linear temporal trend on recovery probabilities
8	$W(a+\text{HPI}); S(a)$	$T$	$W(t+\text{HPI}); S(\cdot)$	29	81471.9	129.9	Best model above with linear temporal trend on recapture probabilities
Selection for the presence of HPI effect on survival and recovery parameters							
<b>5</b>	<b><math>W(a+\text{HPI}); S(a)</math></b>	<b><math>t</math></b>	<b><math>W(t+\text{HPI}); S(\cdot)</math></b>	<b>47</b>	<b>81406.7</b>	<b>100.7</b>	HPI-effect on both survival and recovery probabilities
9	$W(a+\text{HPI}); S(a)$	$t$	$W(t); S(\cdot)$	45	82023.2	713.2	HPI-effect on survival probabilities only
10	$W(a); S(a)$	$t$	$W(t+\text{HPI}); S(\cdot)$	45	82243.9	933.9	HPI-effect on recovery probabilities only
11	$W(a); S(a)$	$t$	$W(t); S(\cdot)$	44	82696.4	1384.4	no HPI effect
Selection for the effect of age on survival parameters							
<b>5</b>	<b><math>W(a+\text{HPI}); S(a)</math></b>	<b><math>t</math></b>	<b><math>W(t+\text{HPI}); S(\cdot)</math></b>	<b>47</b>	<b>81406.7</b>	<b>100.7</b>	Age-effect on both winter and summer survival probabilities
12	$W(a+\text{HPI}); S(\cdot)$	$t$	$W(t+\text{HPI}); S(\cdot)$	45	81499.4	189.4	Age-effect on winter survival probabilities only
13	$W(\text{HPI}); S(a)$	$t$	$W(t+\text{HPI}); S(\cdot)$	45	81660.0	350.0	Age-effect on summer survival probabilities only
14	$W(\text{HPI}); S(\cdot) + a$	$t$	$W(t+\text{HPI}); S(\cdot)$	45	81430.5	120.5	Same age-effect on winter and summer survival probabilities
15	$W(\text{HPI}); S(\cdot)$	$t$	$W(t+\text{HPI}); S(\cdot)$	44	81749.7	437.7	No age-effect
Selection for the time-dependency of survival parameters							
5	$W(a+\text{HPI}); S(a)$	$t$	$W(t+\text{HPI}); S(\cdot)$	47	81406.7	100.7	No year-effect on survival probabilities

16	$W(a^*t+HPI);$ $S(a^*t)$	$t$	$W(t+HPI);$ $S(.)$	120	81177.3	17.3	Year-effect on winter and summer survival probabilities, acting differently among age-classes
<b>17</b>	<b><math>W(a+t+HPI);</math></b> <b><math>S(a+t)</math></b>	$t$	<b><math>W(t+HPI);</math></b> <b><math>S(.)</math></b>	<b>83</b>	<b>81234.0</b>	<b>0</b>	Year-effect on winter and summer survival probabilities, additive to age-effect
18	$W(a+t+HPI); S(a)$	$t$	$W(t+HPI);$ $S(.)$	65	81276.9	6.9	Year-effect on winter survival probabilities only
19	$W(a+HPI); S(a+t)$	$t$	$W(t+HPI);$ $S(.)$	64	81358.9	86.9	Year-effect on summer survival probabilities only
20	$W(a+HPI); S(a)$ $+t$	$t$	$W(t+HPI);$ $S(.)$	65	81288.5	18.5	Same year-effect on winter and summer survival probabilities
21	$W(a+T+HPI);$ $S(a+T)$	$t$	$W(t+HPI);$ $S(.)$	48	81331.5	27.5	Best model above with linear temporal trend on winter and summer survival probabilities

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Table 2: Annual survival probability and winter recovery probability of adult woodcock wintering in low HPI areas, with standard deviation (SE). Age effect (adult/juvenile) and hunting pressure effect (low/high HPI) were additive to that temporal variation and are presented in the main text. ‘Year’ start in October, e.g. 1989 stands for winter 1989-1990 and summer 1990. All estimates are from the preferred model 17 in Table 1.

Year	Survival	SE	Recovery	SE
1990	0.426	0.039	0.107	0.024
1991	0.619	0.027	0.275	0.082
1992	0.606	0.030	0.151	0.041
1993	0.626	0.035	0.177	0.059
1994	0.505	0.025	0.090	0.016
1995	0.640	0.018	0.224	0.044
1996	0.723	0.016	0.392	0.113
1997	0.493	0.020	0.090	0.012
1998	0.629	0.021	0.167	0.032
1999	0.623	0.019	0.112	0.019
2000	0.666	0.018	0.137	0.025
2001	0.605	0.017	0.171	0.024
2002	0.543	0.018	0.090	0.011
2003	0.699	0.019	0.190	0.043
2004	0.617	0.017	0.141	0.021
2005	0.585	0.018	0.122	0.016
2006	0.678	0.019	0.146	0.028



2007	0.604	0.025	0.138	0.025
2008	0.753	0.015	0.245	0.056

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## Figures legends

Figure 1. Monthly survival probabilities of adult woodcocks in summer (grey lines) and winter (black lines; lower line for high HPI and higher line for low HPI areas). Dotted lines: 95% confidence intervals. All estimates are from the preferred model 17 in Table 1.

Figure 2. Annual population growth rate in low HPI (black lines) and high HPI (grey lines) areas. Dotted lines: 95% confidence intervals.



