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Running title: Weather, survival and escape migration

Abstract   During unpredictable adverse conditions, endotherms can engage in emergency behaviours (movement, torpor, hyperphagia) to maintain energy balance and reduce mortality hazards. Bird 'escape migration' is one of the most visible of these behaviours. In this study we focus on a Eurasian Woodcock *Scolopax rusticola* population. Seasonal migrations bring this population from its breeding grounds in Eastern and Northern Europe to its wintering grounds in France. A varying number of these birds are also regularly reported from Spain, supposedly during additional escape movements that occur in winter. Using models that account for the imperfect detection rate of individuals and a large (>44,000 individuals) dataset combining information from the wintering and breeding ranges, we show that severe winters significantly reduced survival probability, but that migration to Spain increased only during the most intense cold spell that occurred over the 20 year study period. This suggests that the decision to resume migration during the winter is submitted to a threshold mechanism, which we discuss in the light of current models of migratory behaviour.

1 Introduction

2 Extreme weather events put the energy allocation trade-offs of individuals into question

3 (Boyle et al. 2010). Documented consequences include massive death tolls (e.g., Cezilly et al.

4 1996), sometimes associated with rapid microevolution (Brown and Brown 1998), and

5 generally with major consequences on population dynamics (Coulson et al. 2001; Saether et

6 al. 2004; Sutherland 2006). Iteroparous species thus endure strong selective pressures to

7 evolve coping strategies. Birds have been especially studied in that respect because of their

8 highly visible migrations. Contrasting the well-known compulsory seasonal migration of

9 many species, which appears as an answer to predictable changes in the environment, escape

10 migration refers to the facultative movement of a varying fraction of the population, in

11 response to unpredictable adverse conditions (Berthold 1995; Newton 2008). Examples of

12 these adverse conditions triggering escape migration include poor seed production in boreal

13 forests regulating the winter invasions of nomadic boreal finches Fringillidae and waxwings

14 *Bombycilla* sp. (Berthold 1995; Newton 2008), and hot temperatures and droughts triggering

15 movements in arid habitats (e.g., Great Bustard *Otis tarda*; Alonso et al. 2009). The

16 associated physiological mechanisms are only starting to be quantified (Lohmus et al. 2003;

17 Landys et al. 2006; Boyle et al. 2010). The fitness consequences of these individual migration

18 decisions have moreover very rarely been measured (but see Rivalan et al. 2007). While the

19 ability to escape adverse conditions should enhance survival probability, non-negligible costs

20 of migration are expected. One thereby expects a trade-off between the risks of migration and

21 the risks of remaining in place and enduring adverse conditions (Alerstam and Lindström

22 1990). Here we study the demographic consequences of such individual trade-off.

23   We consider three hypotheses describing a continuum of potential behavioral

24 responses to exceptional weather events. (1) Escape migration probability could be higher in

25 years with an event than in years without one, indicating that escape migration is less costly

26 than enduring adverse conditions. (2) Escape migration probability could be low and/or

27 constant, or be explained by factors other than weather (population density, e.g.: Fowler

28 2009), indicating that escape migration is more costly than enduring adverse conditions. (3)

29 The answer to extreme weather events could be submitted to a threshold mechanism: below a

30 given intensity, few individuals modify their behavior while above that threshold, individuals

31 start expressing escape behaviors. These three hypotheses are all based on the existence of a

32 cost of remaining in place during adverse conditions, but differ in the way this cost scales to

33 the cost of migration. They can be tested by comparing the variation in the frequency of

34 migratory movements and in the weather conditions.

35   We studied a migratory game species, the Eurasian Woodcock Scolopax rusticola, and

36 in particular the population that winters in France. These birds are usually particularly faithful

37 to their wintering site (Gossmann et al. 1994), but some are recovered in Spain (and to a lesser

38 extent Northern Africa) each year. We tested whether those Spanish recoveries corresponded

39 to individuals that had migrated further in answer to weather, which has never been formally

40 investigated before. Capture-recapture-recovery models make it possible to estimate survival

41 and migration probabilities of the banded individuals, while accounting for the fact that not all

42 dead individuals are reported and not all live individuals are recaptured. First, we analyzed the

43 capture-recovery data to investigate between-year variations in survival probability and their

44 relation to weather, in order to test for the existence of a cost of harsh winter weather. Second,

45 we estimated the temporal variation in the proportion of birds that reached Spain each winter.

46 We used that proportion as a measure for the probability of escape migration, which made it

47 possible to test the above-mentioned three hypotheses regarding migration decisions.

48 **Material and Methods**

49 *Study individuals*

50 On the winter grounds most woodcocks commute between night-time feeding grounds

51 (mainly meadows) where banding occurs and day-time roost sites in forests where hunting

52 occurs (Duriez et al. 2005a). The study individuals were marked with metal bands, from the

53 beginning of October to the end of February. Recoveries (reports of hunted banded birds)

54 occurred in France (usual wintering grounds), in Spain (unusual wintering ground) and in

55 Eastern and Northern Europe (spring migration stopovers and breeding grounds). We used the

56 data collected between October 1989 and February 2009 (20 years), which corresponded to

57 44,902 different individuals, 12,078 of which were recovered in France, 263 in Spain and 737

58 in Eastern Europe, plus 2,873 different recapture events in France.

59 Hunting pressure is suspected to vary subsequently between banding locations, which

60 might influence the estimation of survival. To account for variation in hunting pressure while

61 estimating survival, we used a proxy that we built as follows. For each locality, the percentage

62 of banded birds that were recovered through hunting less than 10km from their banding place

63 (as opposed to the remaining recoveries that occurred elsewhere during weather-mediated

64 dispersal) were considered to be representative of the local hunting pressure. Localities were

65 then divided between two groups corresponding to above-median (high) and below-median

66 (low) hunting pressure. We refer to this two-level variable as the hunting pressure index (HPI)

67 hereafter. We restricted the dataset to the 714 localities where at least 20 birds have been

68 banded over the study period. Yearly location-specific sample sizes did not allow the

69 computation of a yearly HPI for each location; in the following we thus account for the

70 temporal average of hunting pressure using HPI.

71   *Weather variables*

72   For each winter (October to February) of our 20-year study period, we obtained four weather

73   variables from nine Météo France stations spread across the French wintering range of our

74   study population: the number of freezing days, the average winter temperature, the minimum

75   recorded temperature, and the amount of precipitation (ESM 1). We used principal component

76   analyses (PCA; Jolliffe 2002) as implemented in the R-package ADE 4 (Thioulouse et al.

77   1997) to create one summary index for each weather variable. Detail about these indexes is

78   provided in ESM 1 (Fig. S1: locations of the Météo France stations, Table S1: correlation

79   between summary indexes and absence of temporal trend, Fig. S3: correlation circles). To

80   avoid using highly correlated explanatory variables in our capture-recovery models, we

81   selected the two most biologically relevant indexes (see discussion) out of four that were

82   available: the variation in the total number of freezing days recorded over the winter, denoted

83    $N_{<0}$, and the variation in the total amount of precipitation recorded over the winter, denoted

84   P_{tot}. The relationship between these weather indexes and the station-specific weather data is

85   described in Fig. S3 in ESM1. Further details on the use of such condensed weather indexes in

86   capture-recapture analyses are found in Grosbois et al. (2008).

87   These weather indexes described the average conditions during winter. However it is

88   generally understood that extreme events are of greater influence than average conditions

89   (e.g., Boyle et al. 2010). We thereby also obtained from Météo France a classification of

90   winters according to the occurrence and severity of exceptional events, namely cold spells

91   (http://comprendre.meteofrance.com/content/2009/10/21331-48.pdf; in French). This

92   classification is based on the comparison of daily mean temperatures with the long-term

93   average. The period between December 25 1996 and January 8 1997 was qualified as 'high

94   intensity cold spell' by Météo France. We hereafter use the notation 'c96' when we

95   distinguish winter 1996-1997 from other winters in a model. Less intense cold spells occurred

96   in the winters 1990-91, 2001-02, 2002-03, 2005-06, and 2008-09.

97   From the woodcock's natural-history, we predicted that $N_{<0}$ and P_{tot} should correlate

98   positively and negatively, respectively, to starvation risk and thus mortality probability (see

99   the discussion section for more detail and references). The decision to migrate should also

100   depend on these variables under hypothesis 1, but should be independent of weather in

101   hypothesis 2, and should vary only during the most intense cold spell (c96) under hypothesis

102   3. We also tried models in which the demographic parameters followed a temporal trend

103   either alone or in addition to the effect of the weather variables.

104   *Capture-recovery models with escape migration and seasonal variation*

105   We built multistate capture-recovery models (e.g., Gauthier and Lebreton 2008) using

106   program E-SURGE (version 1.6.4; Choquet et al. 2009). These models are parameterized

107   using survival probabilities s_t (the probability for a bird to survive between year t and t+1),

108   migration probabilities ψ_t (the probability for a bird to migrate to Spain during the winter of

109   year *t*), recovery probabilities r_t (the probability for a bird dying during year *t* to have died

110   from hunting and been reported as such to the ONCFS woodcock network), and recapture

111   probabilities p_t (the probability for a bird alive and already wearing a band to be re-trapped

112   during the banding sessions in winter in France during year *t*). For methodological reasons

113   (parameter identifiability), the decision to migrate to Spain or remain in France was modeled

114   to occur at the beginning of each winter, i.e., before winter survival. This is a constraint

115   inherent to the seasonal capture recapture model we used and not a biological hypothesis. We

116   also adapted this general framework to the woodcock case as follows. (i) We distinguished

117   'winter' (October to February) and 'summer' (March to September) survival probabilities. (ii)

118   We distinguished 'French', 'Spanish', and 'summer' (in Eastern Europe) recovery

119   probabilities. (iii) Following Tavecchia et al. (2002), winter recovery probability was divided

120   between direct (same winter as the banding) and indirect (subsequent winters) recovery

121   probabilities. (iv) Banding and hunting occurred roughly at the same time in winter. Thereby,

122   the months at banding influenced the duration for which an individual was submitted to

123   mortality hazards during its first winter after banding. We accommodated that issue by

124   computing monthly winter survival probabilities (denoted $\tilde{s}_{w,t}$)We raised that monthly

125   survival to the power corresponding to the number of months the individual was exposed to

126   mortality hazards (see ESM 2 for details on the practical implementation). For example,

127   individuals ringed in December had a first winter survival probability of $s_{w,t_1} = \tilde{s}_{w,t_1}^3$, instead

128   of $s_{w,t_1} = \tilde{s}_{w,t_1}^5$ if they had been ringed in October.

129   Due to the computer burden, and because we observed numerous instabilities in the

130   likelihood optimization procedure, we ran the capture-recovery analysis in two steps. First, we

131   discarded the data from Spain and looked for the best model of winter survival probability in

132   France (step A hereafter). Based on general knowledge about avian and particularly gamebird

133   demography, confirmed by unpublished analyses, the following effects were not tested but

134   included a priori in the models:

135   -   the effect of season (winter vs. summer) on survival and recovery probabilities,

136   -   the effect of age (adults vs. juveniles) on winter and summer survival probability,

137   -   the effect of HPI on winter survival and recovery probabilities,

138   -   between-year variations in winter and summer survival probability,

139   -   between-year variations in recapture and recovery probabilities in France,

140   -   constant recovery probability in Eastern Europe,

141   The model selection in step A focused on the effect of weather covariates on winter

142   survival probability (Grosbois et al. 2008). Next (step B), we added to the data the recoveries

143   from Spain. We now needed to include the migration probabilities in the model. We

144   investigated between-year variations and the effect of weather variables on migration

145   probability.

146   **Results**

147   *Step A: Weather impact on winter survival in France*

148   The model selection procedure indicated that the additive effects of $N_{<0}$ and P_{tot} , acting in

149   conjunction with a linear temporal trend was preferred over the full time-dependent model

150   (Table 1: Model A5 vs. A2; Fig. 1). The amount of variance in survival probability explained

151   by the covariates in this model reached 77%, of which 56% were accounted for by the

152   temporal trend and 21% by the weather variables (Table 1: Models A5, A3 and A4). From

153   Fig. 1 it can be seen that only the winter 2002-2003 was wrongly described in model A5, and

154   that the cold spell of winter 1996-1997 had no marked impact on survival probability.

155   Our analyses controlled for the effect of hunting pressure, age, and season. Briefly, we

156   found that HPI correlated with survival and recovery probability in opposite directions, that

157   juveniles survived less than adults, and that survival probability over the seven months of

158   summer was of the same order of magnitude as survival probability over the five months of

159   winter.

160   *Step B: Weather impact on migration probability*

161   The data supported the existence of between-year variation in the proportion of birds

162   migrating to Spain (Table 2). This variation was successfully retrieved by a temporal trend

163   and the separate modelling of winter 1996-1997 during which a high intensity cold spell

164   occurred (Table 2; Fig. 2). After accounting for the 1996-1997 cold spell, the additive effects

165   of the temporal trend captured 38% of the remaining variance (i.e., 14% of the total variance;

166   Table 2: Model B6 vs. Model B4). Adding the effect of weather variables onto the temporal

167   trend only slightly improved the fit (Table 2: Model B6 vs. B7).

168 **Discussion**

169 *The cost of enduring adverse conditions*

170 Our result that survival decreased during winters with numerous freezing days and little

171 precipitation indicates a significant pressure for increased migration during those winters

172 (Sutherland 2006; Rivalan et al. 2007; Boyle et al. 2010). The first explanatory hypothesis

173 involves food availability. Indeed, during freezing days woodcocks cannot reach earthworm

174 resource because of snow cover and frozen soils (Boos et al. 2005). Rain on the contrary

175 softens soil and attracts earthworms to the surface (Gerard 1967; Duriez et al. 2006) making

176 them more available to woodcocks (Duriez et al. 2005a; 2006). The second explanatory

177 hypothesis involves thermoregulatory cost, which increases with falling temperatures (Duriez

178 et al. 2004).

179 Our understanding of woodcock response to adverse weather would clearly benefit from a

180 more focused documentation of these mechanisms. Woodcocks remaining in place during a

181 cold spell might be those whose fat reserves were insufficient to resume migration (Alerstam

182 and Lindström 1990), or they could by contrast be those whose fat reserves were sufficient to

183 undergo a long period of deprivation without starving (Wingfield et al. 1998). It would be

184 interesting to compare the fat load of woodcocks (Boos et al. 2005) hunted just after and just

185 before a cold spell. In addition, it could be possible to directly document foraging effort and

186 success under varying weather condition using the radio-tracking methodology described by

187 Duriez et al. (2005b).

188 A methodological note is that it was not possible to estimate separately survival in France

189 and Spain. This was not a problem of parameter identifiability which was checked using

190 methods implemented in E-SURGE (Choquet et al. 2009), but rather a problem of

191 optimization. When survival was different in France and Spain, the unobservable state 'alive

192 in Spain' became a dummy one (i.e., with an associated survival rate of zero), leading to a

193 model in which the estimated migration probability corresponded indeed to the overall

194 probability to migrate *and* die in Spain. Additional data, such as live encounters in Spain and

195 radio-tracking data, appear necessary to obtain a more biologically useful model in this case.

196 *The cost of escaping adverse conditions*

197 Escape migration to Spain was a rare behavior occurring in less than 1% of individuals during

198 'normal' years (Fig. 2). Escape migration must hence bear non-negligible costs. However, a

199 notable increase in escape migration probability (up to c. 5%) occurred during, and

200 supposedly as a consequence of, the high intensity cold spell that hit France between

201 December 25 1996 and January 8 1997. On the opposite, low-intensity cold spells did not

202 impact migration probability (Fig. 2). There thus seems to be a threshold of cold spell

203 intensity after which woodcocks resume southwards migration. Hypothesis 3 (escape

204 migration is beneficial only during the most intense cold spells) was therefore the most

205 supported. However, we recognize that additional data (more cold spell events) are required in

206 order to rule out the possibility that the result was confounded by some unidentified factor.

207   The above considerations are in line with the Optimal Migration theory (Alerstam and

208 Lindström 1990; Hedenstrom 2008). In this framework, the decision to leave the current

209 location depends in part on the expected difference in resource availability between the

210 current and more Southern sites. Time between departure from the breeding grounds and

211 arrival to the wintering grounds is the preponderant 'currency' whose expenditure is

212 optimized (Saffriel and Lavee, 1988; Hedenstrom 2008). Although this model of migratory

213 behavior was developed to explain stopover strategies during seasonal, compulsory, long-

214 distance migration, it can be extended to the case of a population already settled in its

215 wintering grounds but having the option to perform additional movement. In this situation,

216 time is not a constraint (since the individuals are already settled in the wintering areas and

217 escape migration can be considered to have negligible impact on the timing of spring

218   migration). The decision to leave is indeed expectedly driven by the balance between the risks

219   of starving if remaining in place versus resuming migration, i.e., energy is the currency to be

220   optimized. Our results seem to indicate that the expected benefits of resuming migration

221   exceeded costs only during the 1996-1997 cold spell. Interestingly, no particular drop in

222   survival was observed during that winter (Fig. 1), suggesting that escape migration enabled

223   many individuals to survive that particular cold spell. Lastly, migration to Spain might be a

224   two-step phenomenon. During cold spells, woodcocks are known move away from

225   continental climate and migrate towards the French coastlines. Migration to Spain might

226   occur as a secondary escape behavior, when conditions on the coast become unsustainable

227   too.

228   *Proposed physiological mechanisms of escape migration*

229   Allostasis models (Wingfield et al. 1998; McEwen and Wingfield 2003; Landys et al. 2006)

230   are based on the balance between the energy needed to merely survive (homeostatic level), the

231   energy spent in facultative activities, and the energy which is available in the environment.

232   The outcome is the allostatic load. As demand for energy increases (Duriez et al. 2004), the

233   allostatic load may rise above some critical threshold, triggering a physiological response

234   ('emergency life history stage'). One such response is an increase in glucocorticoid hormones

235   secretion (Landys et al. 2006). This increase has been hypothesized to trigger behaviors aimed

236   at offsetting the cost of adverse conditions (e.g., escape migration, increased food

237   consumption, reduced energy expenditure: Boyle et al. 2010; Landys et al. 2006; and

238   references therein). Plasticity of behavioural response may be explained by interactions with

239   the two cytoplasmic binding receptors for glucocorticoids each with distinct binding affinities.

240   Each could affect distinct behavioural responses depending upon the concentration of plasma

241   hormone. This would explain that, although increased during the 1996-1997 cold spell, escape

242   migration probability remained low at c. 5%. We indeed suspect that only individuals with

243   initially sufficient fat reserve can undertake escape migration, the remaining individuals being

244   compelled to stay in their current location (Alerstam and Lindström 1990) or flying shorter

245   distances (remaining in France). Cold spells being by nature unpredictable, and individuals

246   being available for capture only if they do not migrate, further tests of these hypotheses in the

247   woodcock system are challenging.

248   *Predictions in the face of climate change*

249   A temporal trend was apparent in both the winter survival and escape migration probabilities.

250   Both parameters increased with time, and the trend was more marked in survival. In the

251   absence of a clear trend in the local weather variables (ESM 1), it is unlikely that the time

252   effects on demographic parameters reflected an impact of the ongoing climate change. We

253   suggest variation in sampling procedures (change in banding locations) through time as a

254   potential explanation, but this requires further investigation. If a true biological result, these

255   increasing trends might stem from an increase in breeding habitat availability (farmland

256   abandonment in Eastern and Northern Europe). Our results nevertheless have implications for

257   the management of woodcock as a game species in the face of climate change. Milder winters

258   (less freezing days, more rain) are predicted in the woodcock French wintering range (IPCC

259   2007). Conditions are therefore expected to get better for woodcocks. However, climate

260   models also predict a rise in the frequency of exceptional weather events (IPCC 2007), which

261   might imply more cold spells, and also more drought and fire events in the breeding range. An

262   improvement upon our models would then be their use in a prospective framework including

263   variation in both average conditions and in the regime of stochasticity (e.g., Gotelli and

264   Ellison 2001). Such a study would answer questions related to selection pressure for more or

265   less migratoriness, and the demographic consequences including future population size and

266   winter range.

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Tables

Table1 Model selection for the effect of weather variables on winter survival in France (step A). Given is the model structure for winter survival (φ), departing from known effects of Age (adult vs. juveniles) and hunting pressure (HPI). t denotes the full year effect (20 parameters). T denotes a temporal trend. $N_{<0}$ represents the effect of the number of freezing day per winter. P_{tot} represents the amount of precipitation per winter. Formulas for the other model parameters (summer survival, resighting, and recovery probabilities) are omitted for clarity and did not vary among models. #p, Dev, and ΔAIC stand for number of parameters, deviance, and difference in AIC score to the preferred model. Model with lowest AIC is in bold; it has more than two points difference with the nearest model. F-values refer to the test of the effect of the considered time-dependent variable against Model A2 (full time dependence), while accounting for the overdispersion in Model A1 (time-independence). See Grosbois et al. (2008) for detail on these tests.

#	φ	#p	Dev	ΔAIC	ANODEV F-value	P-value	r^2
A1	Age+HPI	64	81358.9	89.8			
A2	Age+HPI+t	83	81234.0	2.9			
A3	Age+HPI+T	65	81288.1	21	45.93	$< 10^{-4}$	0.56
A4	Age+HPI+$N_{<0}$+P_{tot}	66	81333.7	68.6	16.34	$< 10^{-4}$	0.21
A5	**Age+HPI+$N_{<0}$+P_{tot}+T**	**67**	**81263.1**	**0**	**62.13**	**$< 10^{-4}$**	**0.77**

Table 2 Model selection for the probability to migrate from France to Spain during the winter (step B). Given is the model structure for migration probability (ψ) and for recovery probability in Spain (r_{SP}). A dot denotes that the corresponding parameter is constant. t denotes the full year effect (20 parameters). $N_{<0}$ represents the effect of the number of freezing day per winter. P_{tot} represents the amount of precipitation per winter. c96 denotes the effect of the intense cold spell that occurred during the winter 1996-1997. T denotes a temporal trend. Formulas for the other model parameters (survival, resighting, and recovery probabilities in France) are omitted for clarity and did not vary among models. #p, Dev, and ΔAIC stand for number of parameters, deviance, and difference in AIC score to the preferred model. Model with lowest AIC are in bold; they have more than two points difference with the nearest model. F-values refer to the test of the effect of the considered time-dependent variable against Model B2 (full time dependence), while accounting for the overdispersion in Model B1 (time-independence). See Grosbois et al. (2008) for detail on these tests.

#	ψ	r_{SP}	#p	Dev	ΔAIC	ANODEV F-value	P-value	r^2
B1	.	t	87	83515.7	61.0			
B2	t	t	106	83430.4	13.7			
B3	t	.	87	83662.0	207.3			
B4	c96	t	88	83463.1	10.4	28.97	$<10^{-4}$	0.62
B5	c96+$N_{<0}$+P_{tot}	t	90	83458.7	10.0	10.73	$<10^{-4}$	0.67
B6	**c96+T**	**t**	**89**	**83450.7**	**0.0**	**27.29**	**$<10^{-4}$**	**0.76**
B7	**c96+$N_{<0}$+P_{tot}+T**	**t**	**91**	**83447.1**	**0.4**	**15.40**	**$<10^{-4}$**	**0.80**

Figure legends

Fig. 1 Monthly survival probabilities in winter of adults banded in a low-hunting area. Black dots: estimates from Model A2 (full, unconstrained time-dependence). Vertical lines: 95% confidence intervals on these estimates. Bold line: estimates from preferred Model A5 (temporal variation explained by the additive effect of two weather variables and a temporal trend). On the x-axis the year corresponds to the beginning of the winter, e.g., 1990 stands for the period from Oct 1990 to Feb 1991. Survival probability for juveniles followed the same temporal variation in the model.

Fig. 2 Probabilities to migrate from France to Spain during the winters. Black dots: estimates from Model B1 (full, unconstrained time-dependence). Vertical lines: 95% confidence intervals on these estimates. Bold line: estimates from Model B7 (temporal variation explained by the additive effect of the 1996-1997 cold spell, of weather indexes and of a temporal trend). On the x-axis the year corresponds to the beginning of the winter, e.g., 1990 stands for the period from Oct 1990 to Feb 1991.

Figures