Behav Ecol Sociobiol (2011) 65:1949–1955
DOI 10.1007/s00265-011-1204-4

ORIGINAL PAPER

Escape migration decisions in Eurasian Woodcocks: insights from survival analyses using large-scale recovery data

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Received: 8 December 2010 / Revised: 5 May 2011 / Accepted: 31 May 2011 / Published online: 11 June 2011

Abstract During unpredictable adverse conditions, endotherms can engage in emergency behaviors (movement, torpor, hyperphagia) to maintain energy balance and reduce mortality hazards. Bird "escape migration" is one of the most visible of these behaviors. 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 behavior.

Keywords Allostasis · Capture–mark–recapture · Capture–recovery · Climate change · Optimal migration · Recoveries

Communicated by W. Wiltschko

Electronic supplementary material The online version of this article (doi:10.1007/s00265-011-1204-4) contains supplementary material, which is available to authorized users.

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Introduction

Extreme weather events put the energy allocation trade-offs of individuals into question (Boyle et al. 2010). Documented consequences include massive death tolls (e.g., Cezilly et al. 1996), sometimes associated with rapid microevolution (Brown and Brown 1998), and generally with major consequences on population dynamics (Coulson et al. 2001; Saether et al. 2004; Sutherland 2006). Iteroparous species thus endure strong selective pressures to evolve coping strategies. Birds have been especially studied in that respect because of their highly visible migrations. Contrasting the well-known compulsory seasonal migration of many species, which appears as an answer to predictable changes in the environment, escape migration refers to the facultative movement of a varying fraction of the population, in response to unpredictable adverse conditions (Berthold 1995; Newton 2008). Examples of these adverse conditions triggering escape migration include poor seed production in boreal forests regulating the winter invasions of nomadic boreal finches Fringillidae and waxwings *Bombycilla* sp. (Berthold 1995; Newton 2008), and hot temperatures and droughts triggering movements in arid habitats (e.g., Great Bustard *Otis tarda*; Alonso et al. 2009). The associated physiological mechanisms are only starting to be quantified (Lohmus et al. 2003; Landys et al. 2006; Boyle et al. 2010). The fitness consequences of these individual migration decisions have moreover very rarely been measured (but see Rivalan et al. 2007). While the ability to escape adverse conditions should enhance survival probability, non-negligible costs of migration are expected. One thereby expects a trade-off between the risks of migration and the risks of remaining in place and enduring adverse conditions (Alerstam and Lindström 1990). Here, we study the demographic consequences of such individual trade-off.

We consider three hypotheses describing a continuum of potential behavioral responses to exceptional weather events. (1) Escape migration probability could be higher in years with an event than in years without one, indicating that escape migration is less costly than enduring adverse conditions. (2) Escape migration probability could be low and/or constant, or be explained by factors other than weather (e.g., population density; Fowler 2009), indicating that escape migration is more costly than enduring adverse conditions. (3) The answer to extreme weather events could be submitted to a threshold mechanism: below a given intensity, few individuals modify their behavior while above that threshold, individuals start expressing escape behaviors.

We studied a migratory game species, the Eurasian Woodcock *Scolopax rusticola*, and in particular the population that winters in France. These birds are usually particularly faithful to their wintering site (Gossmann et al. 1994), but some are recovered in Spain (and to a lesser extent Northern Africa) each year. We tested whether those Spanish recoveries corresponded to individuals that had migrated further in answer to weather, which has never been formally investigated before. Capture–recapture–recovery models make it possible to estimate survival and migration probabilities of the banded individuals, while accounting for the fact that not all dead individuals are reported and not all live individuals are recaptured. First, we analyzed the capture–recovery data to investigate between-year variations in survival probability and their relation to weather, in order to test for the existence of a cost of harsh winter weather. Second, we estimated the temporal variation in the proportion of birds that reached Spain each winter. We used that proportion as a measure of the probability of escape migration, which made it possible to test the above-mentioned three hypotheses regarding migration decisions.

Material and methods

Study individuals

On the winter grounds, most woodcocks commute between nighttime feeding grounds (mainly meadows) where banding occurs and daytime roost sites in forests where hunting occurs (Duriez et al. 2005a). The study individuals were marked with metal bands, from the beginning of October to the end of February. Recoveries (reports of hunted banded birds) occurred in France (usual wintering grounds), in Spain (unusual wintering ground), and in Eastern and Northern Europe (spring migration stopovers and breeding grounds). We used the data collected between October 1989 and February 2009 (20 years), which corresponded to 44,902 different individuals, 12,078 of which were recovered in France, 263 in Spain, and 737 in Eastern Europe, plus 2,873 different recapture events in France.

Hunting pressure is suspected to vary subsequently between banding locations, which might influence the estimation of survival. To account for variation in hunting pressure while estimating survival, we used a proxy that we built as follows. For each locality, the percentage of banded birds that were recovered through hunting less than 10 km from their banding place (as opposed to the remaining recoveries that occurred elsewhere) were considered to be representative of the local hunting pressure. Localities were then divided between two groups corresponding to above-median (high) and below-median (low) hunting pressure. We refer to this two-level variable as the hunting pressure index (HPI) hereafter. We restricted the dataset to the 714 localities where at least 20 birds have been banded over the study period. Yearly location-specific sample sizes did not allow the computation of a yearly HPI for each location; in the following, we thus account for the temporal average of hunting pressure using HPI.

Weather variables

For each winter (October to February) of our 20-year study period, we obtained four weather variables from nine Météo France stations spread across the French wintering range of our study population: the number of freezing days, the average winter temperature, the minimum recorded temperature, and the amount of precipitation (ESM 1). We used principal component analyses (PCA; Jolliffe 2002) as implemented in the R-package ADE4 (Thioulouse et al. 1997) to create one summary index for each weather variable. Details about these indexes are provided in ESM 1 (Fig. S1: locations of the Météo France stations, Table S1: correlation between summary indexes and absence of temporal trend, Fig. S3:

correlation circles). To avoid using highly correlated explanatory variables in our capture–recovery models, we selected the two most biologically relevant indexes (see "Discussion" section) out of four that were available: the variation in the total number of freezing days recorded over the winter, denoted $N_{<0}$, and the variation in the total amount of precipitation recorded over the winter, denoted P_{tot}. The relationship between these weather indexes and the station-specific weather data is described in Fig. S3 in ESM 1. Further details on the use of such condensed weather indexes in capture–recapture analyses can be found in Grosbois et al. (2008).

These weather indexes described the average conditions during winter. However, it is generally understood that extreme events are of greater influence than average conditions (e.g., Boyle et al. 2010). We thereby also obtained from Météo France a classification of winters according to the occurrence and severity of exceptional events, namely cold spells (http://comprendre.meteofrance.com/content/2009/10/21331-48.pdf; in French). This classification is based on the comparison of daily mean temperatures with the long-term average. The period between December 25, 1996 and January 8, 1997 was qualified as "high intensity cold spell" by Météo France. We hereafter use the notation "c96" when we distinguish winter 1996–1997 from other winters in a model. Less intense cold spells occurred in the winters 1990–1991, 2001–2002, 2002–2003, 2005–2006, and 2008–2009.

From the woodcock's natural history, we predicted that $N_{<0}$ and P_{tot} should correlate positively and negatively, respectively, to starvation risk and thus mortality probability (see "Discussion" section). The decision to migrate should also depend on these variables under hypothesis 1, but should be independent of weather in hypothesis 2, and should vary only during the most intense cold spell (c96) under hypothesis 3. We also tried models in which the demographic parameters followed a temporal trend either alone or in addition to the effect of the weather variables.

Capture–recovery models with escape migration and seasonal variation

We built multistate capture–recovery models (e.g., Gauthier and Lebreton 2008) using program E-SURGE (version 1.6.4; Choquet et al. 2009). These models are parameterized using survival probabilities s_t (the probability for a bird to survive between year t and $t+1$), migration probabilities ψ_t (the probability for a bird to migrate to Spain during the winter of year t), recovery probabilities r_t (the probability for a bird dying during year t to have died from hunting and been reported as such to the ONCFS woodcock network), and recapture probabilities p_t (the probability for a bird alive and already wearing a band to be re-trapped during the banding sessions in winter in France during year t). For methodological reasons, the decision to migrate to Spain or remain in France was modeled to occur at the beginning of each winter, i.e., before winter survival. This is a constraint inherent to the seasonal capture-recapture model that we used and not a biological hypothesis. We also adapted this general framework to the woodcock case as follows: (1) We distinguished "winter" (October to February) and "summer" (March to September) survival probabilities. (2) We distinguished "French," "Spanish," and "summer" (in Eastern Europe) recovery probabilities. (3) Following Tavecchia et al. (2002), winter recovery probability was divided between direct (same winter as the banding) and indirect (subsequent winters) recovery probabilities. (4) Banding and hunting occurred roughly at the same time in winter. Thereby, the months at banding influenced the duration for which an individual was submitted to mortality hazards during its first winter after banding. We accommodated that issue by computing monthly winter survival probabilities (denoted $\tilde{s}_{\mathrm{w,t}}$). We raised that monthly survival to the power corresponding to the number of months the individual was exposed to mortality hazards (see ESM 2 for details on the practical implementation). For example, individuals ringed in December had a first winter survival probability of $s_{\mathrm{w,t_1}} = \tilde{s}^{3}_{\mathrm{w,t_1}}$, instead of $s_{\mathrm{w,t_1}} = \tilde{s}^{5}_{\mathrm{w,t_1}}$ if they had been ringed in October.

Due to the computer burden, and because we observed instabilities in the likelihood optimization procedure, we ran the capture–recovery analysis in two steps. First, we discarded the data from Spain and looked for the best model of winter survival probability in France (step A hereafter). Based on general knowledge about avian and particularly gamebird demography, confirmed by unpublished analyses, the following effects were not tested but included a priori in the models:

- the effect of season (winter vs. summer) on survival and recovery probabilities,
- the effect of age (adults vs. juveniles) on winter and summer survival probability,
- the effect of HPI on winter survival and recovery probabilities,
- between-year variations in winter and summer survival probability,
- between-year variations in recapture and recovery probabilities in France, and
- constant recovery probability in Eastern Europe.

The model selection in step A focused on the effect of weather covariates on winter survival probability (Grosbois et al. 2008).

Next (step B), we added to the data the recoveries from Spain. We now needed to include the migration probabilities in the model. We investigated between-year variations and the effect of weather variables on migration probability.

Table 1 Model selection for the effect of weather variables on winter survival in France (step A)

					ANODEV		
Number	φ	#p	Dev	ΔAIC	*F* value	*P* value	R^2
A1	Age+HPI	64	81,358.9	89.8			
A2	Age+HPI+t	83	81,234.0	2.9			
A3	Age+HPI+T	65	81,288.1	21	45.93	$<10^{-4}$	0.56
A4	Age+HPI+$N_{<0}$+P_{tot}	66	81,333.7	68.6	16.34	$<10^{-4}$	0.21
A5	**Age+HPI+$N_{<0}$+P_{tot}+T**	**67**	**81,263.1**	**0**	**62.13**	**$<10^{-4}$**	**0.77**

Given is the model structure for winter survival (φ), departing from known effects of age (adult vs. juveniles) and hunting pressure (HPI). Formulas for the other model parameters (summer survival, resighting, and recovery probabilities) are omitted for clarity and did not vary among models. 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 details on these tests

t full year effect (20 parameters), *T* temporal trend, $N_{<0}$ effect of the number of freezing day per winter, P_{tot} amount of precipitation per winter, *#p* number of parameters, *Dev* deviance, *ΔAIC* difference in AIC score to the preferred model

Results

Step A: weather impact on winter survival in France

The model selection procedure indicated that the additive effects of $N_{<0}$ and P_{tot}, acting in conjunction with a linear temporal trend, was preferred over the full time-dependent model (Table 1: Model A5 vs. A2; Fig. 1). The amount of variance in survival probability explained by the covariates in this model reached 77%, of which 56% were accounted for by the temporal trend and 21% by the weather variables (Table 1: Models A5, A3 and A4). From Fig. 1, it can be seen that only the winter 2002–2003 was wrongly described in model A5, and that the cold spell of winter 1996–1997 had no marked impact on survival probability.

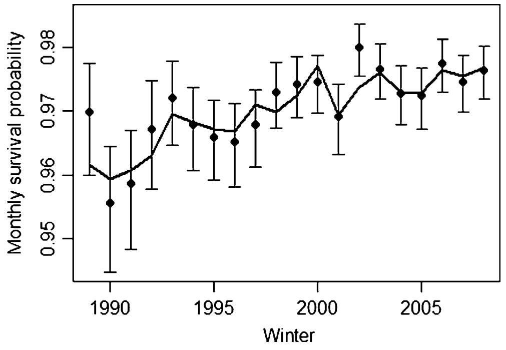

Fig. 1 Monthly survival probabilities in winter of adults banded in a low-hunting area. *Black dots*: estimates from Model A2 (full, unconstrained time dependence). *Vertical lines*: 95% confidence intervals on these estimates. *Bold line*: estimates from preferred Model A5 (temporal variation explained 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 October 1990 to February 1991. Survival probability for juveniles followed the same temporal variation in the model

Our analyses controlled for the effect of hunting pressure, age, and season. Briefly, we found that HPI correlated with survival and recovery probability in opposite directions, that juveniles survived less than adults, and that survival probability over the 7 months of summer was of the same order of magnitude as survival probability over the 5 months of winter.

Step B: weather impact on migration probability

The data supported the existence of between-year variation in the proportion of birds migrating to Spain (Table 2). This variation was successfully retrieved by a temporal trend and the separate modeling of winter 1996–1997 during which a high intensity cold spell occurred (Table 2; Fig. 2). After accounting for the 1996–1997 cold spell, the additive effects of the temporal trend captured 38% of the remaining variance (i.e., 14% of the total variance; Table 2: Model B6 vs. Model B4). Adding the effect of weather variables onto the temporal trend only slightly improved the fit (Table 2: Model B6 vs. B7).

Discussion

The cost of enduring adverse conditions

Our result that survival decreased during winters with numerous freezing days and little precipitation indicates a significant pressure for increased migration during those winters (Sutherland 2006; Rivalan et al. 2007; Boyle et al. 2010). The first explanatory hypothesis for this decrease in survival involves food availability. Indeed, during freezing days, woodcocks cannot reach earthworms (their main food source) because of snow cover and frozen soils (Boos et al. 2005). Rain on the contrary softens soil and attracts earthworms to the surface (Gerard 1967; Duriez et al. 2006). The second explanatory hypothesis involves thermoregulatory cost, which increases with falling temperatures (Duriez et al. 2004).

Woodcocks remaining in place during a cold spell might be those whose fat reserves were insufficient to resume migration (Alerstam and Lindström 1990), or they could in contrast be those whose fat reserves were sufficient to undergo a long period of deprivation without starving (Wingfield et al. 1998). It would be interesting to compare the fat load of woodcocks (Boos et al. 2005) hunted just after and just before a cold spell. In addition, it could be possible to directly document foraging effort and success under varying weather condition using the radio-tracking methodology described by Duriez et al. (2005b).

A methodological note is that it was not possible to estimate separately survival in France and Spain. This was not a problem of parameter identifiability which was checked using methods implemented in E-SURGE (Choquet et al. 2009), but rather a problem of optimization. When survival was different in France and Spain, the unobservable state “alive in Spain” became a dummy one (i.e., with an associated survival rate of zero), leading to a model in which the estimated migration probability corresponded indeed to the overall probability to migrate *and* die in Spain. Additional data, such as live encounters in Spain or radio-tracking data, appear necessary to obtain a more biologically useful model in this case.

The cost of escaping adverse conditions

Escape migration to Spain was a rare behavior estimated to occur in less than 1% of individuals during “normal” years (Fig. 2). Escape migration must hence bear non-negligible costs. However, a notable increase in escape migration probability (up to ca. 5%) occurred during, and supposedly as a consequence of, the high intensity cold spell that hit France between December 25, 1996 and January 8, 1997. On the opposite, low-intensity cold spells did not impact migration probability (Fig. 2). There thus seems to be a threshold of cold spell intensity after which woodcocks resume southwards migration. Hypothesis 3 (escape migration is beneficial only during the most intense cold spells) was therefore the most supported. However, we recognize that additional data (more cold spell events) are required in order to rule out the possibility that the result was confounded by some unidentified factors.

The above considerations are in line with the optimal migration theory (Alerstam and Lindström 1990; Hedenstrom 2008). In this framework, the decision to leave the current location depends in part on the expected difference in resource availability between the current and more southern sites. Time between departure from the breeding grounds and arrival to the wintering grounds is the “currency” whose expenditure is optimized (Safriel and Lavee 1988; Hedenstrom 2008). Although this model of migratory behavior was developed to explain stopover strategies during seasonal, compulsory, long-distance migration, it can be extended to the case of a population already settled in its wintering grounds but having the option to perform additional movement. In this situation, time is not a constraint (since the individuals are already settled in the wintering areas and escape migration can be considered to have negligible impact on the timing of spring migration). The decision to leave is indeed expectedly driven by the balance between the

Table 2 Model selection for the probability to migrate from France to Spain during the winter (step B)

						ANODEV		
Number	ψ	r_{SP}	#p	Dev	ΔAIC	*F* value	*P* value	R^2
B1	.	*t*	87	83,515.7	61.0			
B2	*t*	*t*	106	83,430.4	13.7			
B3	*t*	.	87	83,662.0	207.3			
B4	c96	*t*	88	83,463.1	10.4	28.97	$<10^{-4}$	0.62
B5	c96+$N_{<0}$+P_{tot}	*t*	90	83,458.7	10.0	10.73	$<10^{-4}$	0.67
B6	**c96+*T***	***t***	**89**	**83,450.7**	**0.0**	**27.29**	$\mathbf{<10^{-4}}$	**0.76**
B7	**c96+$N_{<0}$+P_{tot}+*T***	***t***	**91**	**83,447.1**	**0.4**	**15.40**	$\mathbf{<10^{-4}}$	**0.80**

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. Formulas for the other model parameters (survival, resighting, and recovery probabilities in France) are omitted for clarity and did not vary among models. 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 details on these tests

t full year effect (20 parameters), $N_{<0}$ effect of the number of freezing day per winter, P_{tot} amount of precipitation per winter, *c96* effect of the intense cold spell that occurred during the winter 1996–1997, *T* temporal trend, *#p* number of parameters, *Dev* deviance, *ΔAIC* difference in AIC score to the preferred model

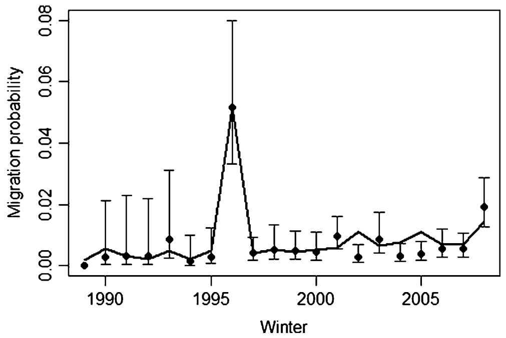

Fig. 2 Probabilities to migrate from France to Spain during the winters. *Black dots*: estimates from Model B1 (full, unconstrained time dependence). *Vertical lines*: 95% confidence intervals on these estimates. *Bold line*: estimates from Model B7 (temporal variation explained by the additive effect 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 October 1990 to February 1991

risks of starving if remaining in place versus resuming migration, i.e., energy is the variable that matters. Our results seem to indicate that the expected energy benefits of resuming migration exceeded costs only during the 1996–1997 cold spell. Interestingly, no particular drop in survival was observed during that winter (Fig. 1), suggesting that escape migration enabled many individuals to survive that particular cold spell. Lastly, migration to Spain might be a two-step phenomenon. During cold spells, woodcocks are known to move away from continental climate and migrate toward the French coastlines. Migration to Spain might occur as a secondary escape behavior, when conditions on the coast become unsustainable too.

Possible physiological mechanisms of escape migration

Allostasis models (Wingfield et al. 1998; McEwen and Wingfield 2003; Landys et al. 2006) are based on the balance between the energy needed to merely survive (homeostatic level), the energy spent in facultative activities, and the energy which is available in the environment. The outcome is the allostatic load. As demand for energy increases when temperature drops (Duriez et al. 2004), the allostatic load may rise above some critical threshold, triggering a physiological response ("emergency life history stage"). One such response is an increase in glucocorticoid hormones secretion (Landys et al. 2006). This increase is considered to trigger behaviors aimed at offsetting the cost of adverse conditions (e.g., escape migration, increased food consumption, and reduced energy expenditure; Boyle et al. 2010; Landys et al. 2006; and references therein). Plasticity of behavioral response may be explained by interactions with the two cytoplasmic binding receptors for glucocorticoids each with distinct binding affinities. Each could affect distinct behavioral responses depending upon the concentration of plasma hormone. This would explain that, although increased during the 1996–1997 cold spell, escape migration probability remained low at ca. 5%. We indeed suspect that only individuals with initially sufficient fat reserve can undertake escape migration, the remaining individuals being compelled to stay in their current location (Alerstam and Lindström 1990) or flying shorter distances (remaining in France). Cold spells being by nature unpredictable, and individuals being available for capture only if they do not migrate, further tests of these hypotheses in the woodcock system are challenging.

Predictions in the face of climate change

A temporal trend was apparent in both the winter survival and escape migration probabilities. Both parameters increased with time, and the trend was more marked in survival. In the absence of a clear trend in the local weather variables (ESM 1), it is unlikely that the temporal trends in demographic parameters reflected an impact of the ongoing climate change. We suggest variation in sampling procedures (change in banding locations) through time as a potential explanation, but this requires further investigation. If a true biological result, these increasing trends might stem from an increase in breeding habitat availability and quality (farmland abandonment in Eastern and Northern Europe). Our results nevertheless have implications for the management of woodcock as a game species in the face of climate change. Milder winters (less freezing days, more rain) are predicted in the woodcock French wintering range (IPCC 2007). Conditions are therefore expected to get better for woodcocks. However, climate models also predict a rise in the frequency of exceptional weather events (IPCC 2007), which might imply more cold spells, and also more drought and fire events in the breeding range. An improvement upon our models would then be their use in a prospective framework including variation in both average conditions and in the regime of stochasticity (e.g., Gotelli and Ellison 2006). Such a study would answer questions related to selection pressure for more or less migratoriness, and the demographic consequences including future population size and winter range.

Acknowledgments Nothing would have been possible without the important field work and dynamism of the banders of the ONCFS/FNC/FDC Woodcock Network. Parts of this manuscript were written while G.P. was supported by a Quinney post-doctoral fellowship at Utah State University. O.G. was supported by a grant from Agence Nationale de la Recherche (ANR-08-JCJC-0088-01). We thank B. Doligez and two anonymous reviewers for very useful insights on previous drafts of this article.

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