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ORIGINAL ARTICLE

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

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Abstract Spatial heterogeneity, especially in mortality risk, is a major factor shaping population dynamics. Here we study the impacts of spatial heterogeneity in hunting pressure on the demography of Eurasian woodcock *Scolopax rusticola*, a relatively long-lived migratory game bird. We develop capture–recapture–recovery models in which both seasonality and spatial variation in hunting pressure are accounted for, and fit them to individual-based data collected across the French wintering range (>44000 banded individuals) as well as recoveries from spring stopovers and breeding grounds in Europe. Our results quantify spatial variation in survival probability in the wintering areas. They highlight the role of source-sink dynamics involving juvenile settlement decisions, as well as the importance of mortality outside the winter quarters. We also discuss the impact of spatial heterogeneity for demographic parameter estimation and data collection at the range scale.

Keywords Capture–recapture · Capture–recovery · Hunting management · *Scolopax rusticola* · Spatially explicit · Survival

Introduction

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

Here we focus on how spatial variation in hunting pressure shapes local population dynamics in Eurasian woodcocks *Scolopax rusticola* that winter in France. In this long-lived species (known to exceed 20-year old in the wild) with relatively low offspring production (Hoodless and Coulson 1998; Ferrand et al. 2008), and known to live

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at low densities (Duriez et al. 2005a, b), the prediction is that hunting pressure, *via* its impact on local survival rates, should shape population dynamics (Pfister 1998; Nilsen et al. 2009). However, the rates at which local populations are able to compensate for hunting mortality (e.g., *via* density-dependent variation in mortality rates from other sources: Burnham and Anderson 1984) can markedly modify the shape of that relationship.

Capture–recovery data and statistical analyses (Williams et al. 2002) can be made spatially explicit to investigate these issues (Royle and Dubovsky 2001; Péron et al. 2011a). Moreover, the benefits of making survival and recovery probability estimates spatially explicit go beyond the biological implications, since in many cases aggregating heterogeneous data over large spatial scales can produce biased estimates of the average value of the parameters at stake (Bauthian 2005; Fletcher et al. 2011). Yet, spatially explicit analyses are computer-intensive, data-hungry, and require the use of elaborate techniques, which reduces their general applicability. Here we use a more easy-to-implement approach, based on a proxy derived from the capture–recovery data, with the caveat that we cannot get rid of sampling covariance between the proxy and survival estimates. This proxy is used to investigate and discuss the role of spatial variation in hunting pressure in woodcock demography, as well as issues associated with data collection and parameter estimation.

Materials and methods

Previous works about the French-wintering woodcock population have highlighted dramatically low survival probability (Hémery et al. 1978; Gossmann et al. 1994; Tavecchia et al. 2002, providing survival estimates up to 1998). These previous estimates are nevertheless incompatible with the observed population trend (Ferrand et al. 2008): there has been no decrease from 1990 onwards and even a probable increase in recent years. We were therefore interested in updating the survival estimates, in order to detect a potential increase in survival probability after 1990, as well as to correct some potential flaws of the previous studies. Firstly, previous banding efforts were mainly concentrated around well-known, high woodcock density areas where hunting pressure could be considered higher than on average. The geographic area that was sampled for the present study was much more exhaustive than previously, and included both highly and lightly hunted areas. Secondly, we refined the analysis by (1) using data from both fall/winter and spring/summer to document seasonal variation more precisely, which is important given the migratory nature of the population and that documented spatial variation occurs in fall/winter, (2) allowing age effects on summer survival probability, (3) using a measure of hunting pressure to account for spatial variation and varying contributions of the different banding locations to the dataset, and (4) relieving a constraint of linear temporal variation that was put on recovery probability in previous modeling efforts.

Data collection

Detail on the field procedures can be found in Gossmann et al. (1994) and Ferrand et al. (2008). Briefly, on the winter grounds most woodcocks commute between night-time feeding grounds (mainly meadows) where banding occurs, and day-time roost sites in forests, where hunting occurs (Duriez et al. 2005b, c). Woodcocks are marked with metal bands from October to February. Age determination (adult or juvenile) is done using plumage features (Ferrand and Gossmann 2009), but males and females are not distinguishable. Recovered bands are reported to the woodcock network group at the Office National de la Chasse et de la Faune Sauvage (ONCFS; French Hunting and Wildlife Service). These recoveries occur on the wintering grounds in France, but also during migration and on the breeding grounds in Eastern Europe. Recaptures of banded birds occur during the banding sessions in winter in France. Here we used data collected between October 1989 and February 2009 (20 years). These data come from 44902 different individuals, 12078 of which were recovered in France and 737 recovered in Eastern Europe, plus 2873 different recapture events in France.

Seasonal CR models for the French-wintering woodcock population

Based on the result that woodcocks are very faithful to their wintering location both within and among years (Gossmann et al. 1994), we considered the banding location as representative of the location where an individual would spend most of its winters. Our multistate CR models then adopted the general structure described by Lebreton (2005) and Gauthier and Lebreton (2008). They were parameterized using season-specific survival probabilities s_t (the probability for a bird to survive during time step t to $t + 1$), recovery probabilities r_t (the probability for a bird dying 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 already wearing a band to be trapped again during the winter banding sessions at time step t, given that it is alive).

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

A further technical issue was raised by the fact that banding and hunting occur roughly at the same time in winter. In this study, we accounted for that feature by computing monthly winter survival probability $\tilde{s}_t$ and raising that probability to the adequate power. Thus, individuals banded in, e.g., December had a first winter survival probability of $s_{t_1} = \tilde{s}_{t_1}^3$ instead 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; Choquet et al. 2009; ESM 1 in Electronic Supplementary Material).

Variation in survival probability, model selection and inference

We considered the following potential factors of variation in survival:

1. Season: 'Winter *t*' was the period from October of the year t to February of the year $t + 1$. 'Summer *t*' was the period from March to September of the year $t + 1$.
2. Age: we separated first-year (juveniles) and adults. The age effect could impact both winter and summer survival
3. Year: one estimate per year (full effect), or linear trend.
4. Location: to characterize on a fine scale the spatial variation in hunting pressure (which would be closer to the actual situation than broader geographical classifications), we separated banding locations into classes based on a hunting pressure index (HPI) built as follows. For each banding locality, we computed the percentage over the 20-year study period of the banded birds that were recovered (shot and reported as such) <10 km from their banding place (as opposed to those recovered further away). Localities were then categorized into two groups corresponding to above-median (high) and below-median (low) percentage of birds recovered within 10 km. We restricted the dataset to the 714 localities where at least 20 birds have been banded over the study period. We computed HPI for the whole period, i.e., we looked at a temporal average of local hunting pressure. Both during seasonal migration and during periods of deepest snow cover, woodcocks transit through large geographic areas. The HPI can thereby be interpreted as a comparison between the local hunting pressure (within the 10 km radius) and the average hunting pressure (as encountered when wandering). More detail on HPI and the limits and advantages of that approach are presented in ESM 2 (Electronic Supplementary Material). In particular, since HPI was computed from the same CR data as survival and recovery, it shared a sampling variance with these parameters, which reduced the power of the tests for the effect of hunting pressure.

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

Growth rate computation

With an offspring production of 1.8 per female per year (Hoodless and Coulson 1998; Ferrand et al. 2008), and using post-breeding, two age class matrix population models, we obtained an estimate of population growth rate λ based on the survival estimates of the preferred CMR model. We computed the growth rate specific to each of the HPI classes, for each year. Confidence intervals around λ estimates were computed using a bootstrap procedure (Givens and Hoeting 2005), in which we sampled 10000 times within the approximate normal distributions of the logit-transformed survival probabilities (as provided by E-SURGE), and obtained the empirical distribution of λ. All estimates of temporal variances were corrected for sampling variance using equation 4.2 p. 263 in Burnham et al. 1987, solved using MAPLE.

Results

Model selection

The model selection procedure (Table 1) favored models in which HPI affected both survival and recovery probabilities. Other retained structures were the effect of age on survival probabilities in winter and summer, as well as between-year variation in winter and summer survival, winter recovery and winter recapture probabilities (model

Table 1 Step-by-step model selection for woodcock survival ($s_{a,t}$), recapture (p_t) and recovery (r_t) probabilities

Model number	$s_{a,t}$	p_t	r_t	#p	Dev	ΔAIC	Biological meaning
Selection for the time-dependency of recovery and recapture probabilities							
1	$W(a + \mathrm{HPI}); S(a)$	t	$W(t + \mathrm{HPI}); S(t)$	65	81373.2	103.2	Year-effect on all observation parameters
2	$W(a + \mathrm{HPI}); S(a)$	t	$W(\mathrm{HPI}); S(.)$	29	82548.7	1206.7	Year-effect on recapture probabilities only
3	$W(a + \mathrm{HPI}); S(a)$	–	$W(t + \mathrm{HPI}); S(t)$	47	81453.3	147.3	Year-effect on winter and summer recovery probabilities
4	$W(a + \mathrm{HPI}); S(a)$	–	$W(t + \mathrm{HPI}); S(.)$	28	81468.0	124.0	Year-effect on winter recovery probabilities only
5	**$W(a + \mathrm{HPI}); S(a)$**	**t**	**$W(t + \mathrm{HPI}); S(.)$**	**47**	**81406.7**	**100.7**	Year-effect on winter recovery and recapture probabilities
6	$W(a + \mathrm{HPI}); S(a)$	–	$W(\mathrm{HPI}); S(.)$	11	81701.2	323.2	No year-effect on observation parameters
7	$W(a + \mathrm{HPI}); S(a)$	t	$W(T + \mathrm{HPI}); S(.)$	30	81474.8	134.8	Best model above with linear temporal trend on recovery probabilities
8	$W(a + \mathrm{HPI}); S(a)$	T	$W(t + \mathrm{HPI}); S(.)$	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							
5	**$W(a + \mathrm{HPI}); S(a)$**	**t**	**$W(t + \mathrm{HPI}); S(.)$**	**47**	**81406.7**	**100.7**	HPI-effect on both survival and recovery probabilities
9	$W(a + \mathrm{HPI}); S(a)$	t	$W(t); S(.)$	45	82023.2	713.2	HPI-effect on survival probabilities only
10	$W(a); S(a)$	t	$W(t + \mathrm{HPI}); S(.)$	45	82243.9	933.9	HPI-effect on recovery probabilities only
11	$W(a); S(a)$	t	$W(t); S(.)$	44	82696.4	1384.4	No HPI effect
Selection for the effect of age on survival parameters							
5	**$W(a + \mathrm{HPI}); S(a)$**	**t**	**$W(t + \mathrm{HPI}); S(.)$**	**47**	**81406.7**	**100.7**	Age-effect on both winter and summer survival probabilities
12	$W(a + \mathrm{HPI}); S(.)$	t	$W(t + \mathrm{HPI}); S(.)$	45	81499.4	189.4	Age-effect on winter survival probabilities only
13	$W(\mathrm{HPI}); S(a)$	t	$W(t + \mathrm{HPI}); S(.)$	45	81660.0	350.0	Age-effect on summer survival probabilities only
14	$W(\mathrm{HPI}); S(.) + a$	t	$W(t + \mathrm{HPI}); S(.)$	45	81430.5	120.5	Same age-effect on winter and summer survival probabilities
15	$W(\mathrm{HPI}); S(.)$	t	$W(t + \mathrm{HPI}); S(.)$	44	81749.7	437.7	No age-effect
Selection for the time-dependency of survival parameters							
5	$W(a + \mathrm{HPI}); S(a)$	t	$W(t + \mathrm{HPI}); S(.)$	47	81406.7	100.7	No year-effect on survival probabilities
16	$W(a \times t + \mathrm{HPI}); S(a \times t)$	t	$W(t + \mathrm{HPI}); S(.)$	120	81177.3	17.3	Year-effect on winter and summer survival probabilities, acting differently among age-classes
17	**$W(a + t + \mathrm{HPI}); S(a + t)$**	**t**	**$W(t + \mathrm{HPI}); S(.)$**	**83**	**81234.0**	**0**	Year-effect on winter and summer survival probabilities, additive to age-effect
18	$W(a + t + \mathrm{HPI}); S(a)$	t	$W(t + \mathrm{HPI}); S(.)$	65	81276.9	6.9	Year-effect on winter survival probabilities only
19	$W(a + \mathrm{HPI}); S(a + t)$	t	$W(t + \mathrm{HPI}); S(.)$	64	81358.9	86.9	Year-effect on summer survival probabilities only
20	$W(a + \mathrm{HPI}); S(a) + t$	t	$W(t + \mathrm{HPI}); S(.)$	65	81288.5	18.5	Same year-effect on winter and summer survival probabilities
21	$W(a + T + \mathrm{HPI}); S(a + T)$	t	$W(t + \mathrm{HPI}); S(.)$	48	81331.5	27.5	Best model above with linear temporal trend on winter and summer survival 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). An hyphen '–' 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 '$W(\mathrm{HPI}); S(.) + a$' 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 description of the effects on survival ($s_{a,s,t}$), recapture (p_t) and recovery ($r_{s,t}$) probabilities, number of parameters (#p), deviance, difference in Akaike information criterion to the preferred model (ΔAIC) 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. ΔAIC is computed globally, i.e., represents the distance to the overall preferred model

#17 in Table 1). Including time-dependence in summer survival and summer recovery probabilities only moderately improved the fit (models #17 vs. 18 and #5 vs. 1), probably because of the relatively sparse data from the summer period.

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

Parameter estimates indicated that the high HPI localities were characterized by low survival (difference between high and low HPI on the logit-scale: −0.91 ± SE 0.03) and high recovery probabilities (difference between high and low HPI on the logit-scale: 0.54 ± SE 0.17), suggesting a spatial cross-correlation between survival and recovery probabilities from different locations, mediated by HPI. This correlation was not found when tested using temporal instead of spatial variation (a posteriori correlation between time-specific winter survival and winter recovery probabilities: $R^2 = 0.07$). If reporting rate (the rate at which shot birds with a band are reported) did not depend on hunting pressure, the difference in recovery probability between low and high HPI areas meant that local hunting pressure commonly varied more than two fold between neighboring locations.

Survival probability varied between years in a manner that suggested an increase with time (Table 2; Fig. 1), but the AIC for the model with a temporal trend suggested that significant variation remained around that trend (model #21 vs. 17 in Table 1; Péron et al. 2011b). Summer monthly survival was generally lower than low-HPI winter monthly survival (Fig. 1; average monthly adult *summer* survival 0.95; temporal SD corrected for sampling variance 0.014; average monthly adult *winter* survival in low HPI areas 0.97 ± 0.0049). This meant that summer mortality represented more than two thirds of all adult deaths in birds wintering in low-HPI areas (about half in high HPI areas). Both the comparison of the fit of model #17 versus 20 and Fig. 1 indicated the lack of correlation between winter survival and survival during the following summer.

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

Table 2 Annual survival probability and winter recovery probability of adult woodcock wintering in low HPI areas, with standard deviation (SE)

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

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' starts in October, e.g., 1989 stands for winter 1989–1990 and summer 1990. All estimates are from the preferred model 17 in Table 1

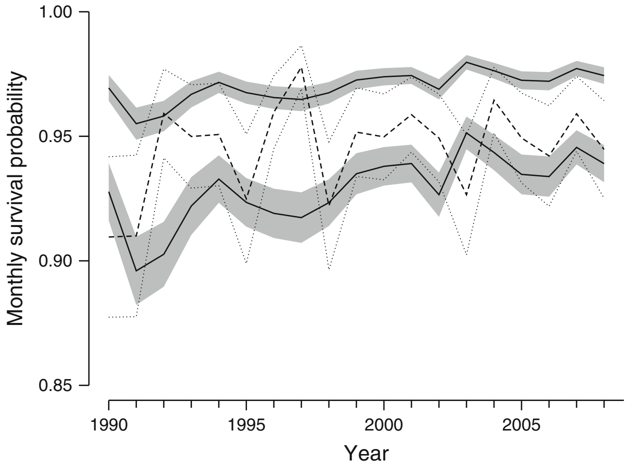

Fig. 1 Monthly survival probabilities of adult woodcocks in summer (*broken line*) and winter (*black lines*; *lower line* for high HPI and *higher line* for low HPI areas). *Dotted lines* for summer and *grey zones* for winter: one standard deviation confidence intervals. All estimates are from the preferred model 17 in Table 1

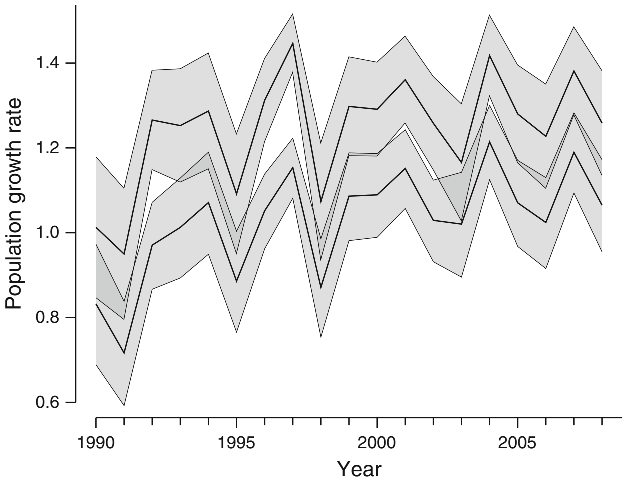

Fig. 2 Annual population growth rate in low HPI (*upper line*) and high HPI (*lower line*) areas. *Grey zones* one standard deviation confidence intervals

Population growth rate

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

At the beginning of the study period (1990–1995), λ estimates indicated that the population was locally not self-sustainable ($\lambda < 1$ in high HPI areas; Fig. 2). However, the average λ across areas was 1.04 (temporal SD corrected for sampling variance 0.12; Fig. 2), thus compatible with the observed trend in population counts. After 1995, both parts of the population showed growth rates above one in most years (Fig. 2), thus again compatible with the observed increase in population counts.

Discussion

Spatial heterogeneity and population dynamics

The population growth rate estimates were on average 12% higher in low than in high HPI areas. During the earlier years of the study (pre-1990), when survival probabilities were lower, this probable effect of hunting pressure meant that high HPI areas were sinks while low HPI areas were sources. The occurrence of local over-harvesting is also in agreement with previous survival estimates which were mostly based on data collected in highly hunted areas (Hémery et al. 1978; Gossmann et al. 1994; Tavecchia et al. 2002). Yet, no local extinction has ever been reported. Therefore, these results suggest an important role for a source-sink dynamic between places of low and high hunting pressure (Pulliam 1988; Novaro et al. 2000). Given what is known of woodcock behavior, it is unlikely that sinks were repopulated by direct movements from low- to high-HPI areas during the winter. Instead, we suggest that juvenile birds, when they first arrive on the wintering grounds, may distribute themselves more or less independently of hunting pressure, or *via* density-dependent dispersal, may settle more often in depleted areas. The latter mechanism was observed experimentally in Brittany where the removal of adult birds allowed juveniles to occupy free forest sites (Fadat 1981). We thus believe that juveniles regularly replenish high HPI areas. In agreement with this hypothesis and with Fadat (1981), we found that low HPI areas have lower age ratios (number of juveniles per adult among recovered individuals) than high HPI areas (Y. Ferrand et al., unpublished data). Further tests of the source-sink hypothesis would require data on fecundity: here we assumed fecundity was constant over time and space, but this assumption was mostly due to lack of data.

Life history strategy

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

Seasonality

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

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

Implications for parameter estimation and data collection

The existence of spatial variation in hunting pressure, which was mirrored in the survival rate, raises two issues. (1) The spatial distribution of sampling effort (capture of un-banded woodcocks) may not compulsorily match the spatial distribution of hunting pressure, especially at a large (country) scale. Thereby, some part of the survival distribution may be over-represented in the data, flawing the overall survival estimate if it is not made spatially explicit. In our case, we suspect a bias towards highly hunted areas, because these are also areas of high woodcock density and because knowledge about woodcock presence in non-hunted locations may be limited. (2) If not accounted for in the survival model, spatial variation in hunting pressure may lead to a statistical bias, i.e., the inability of the model fitting method to retrieve the actual average of survival probability within sampled individuals. Unpublished simulation-based estimation of this bias suggests it can often be large (Bauthian 2005), though in our case we estimated a small effect only. Both issues are related to the recurrent problem of individual heterogeneity in capture–recapture models (Carothers 1973; Nichols et al. 1982; Royle 2008; Pradel 2009) and require further investigation.

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

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