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

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.

Material 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 this analysis 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. 2005a, c). Woodcocks are marked with metal rings 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 rings 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 44,902 different individuals, 12,078 of which were recovered in France and 737 recovered in Eastern Europe, plus 2,873 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 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 probabilities (denoted $\tilde{s}_t$) 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; Appendix 1).

Variation in survival probability, model selection and inference

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.

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 1000 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 variance 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 #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: $-0.91 \pm \text{SE } 0.03$) and high recovery probabilities (difference between high and low HPI on the logit-scale: $0.54 \pm \text{SE } 0.17$), 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 ring are reported) did not depend on hunting pressure, the difference in recovery probability between low and high HPI areas suggests that two-fold variation in hunting pressure were commonplace between different 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). 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 vs. 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: $-0.83 \pm \text{SE}$ 0.20 in winter, $-0.58 \pm \text{SE}$ 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 $\pm$ SE over time). The statistical bias on average survival due to unaccounted for heterogeneity was therefore low in this analysis.

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. The difference in local growth rate between high and low HPI areas was significant in most years (95% confidence intervals in Fig. 2).

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, although they were obtained without taking temporal variation in fecundity into account, 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 (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).

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 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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References

- Bauthian I (2005) Dynamiques spatiales des espèces d'intérêt cynégétique. L'apport des modèles de dynamique de populations. PhD Thesis. Université Pierre et Marie Curie - Paris 6.
- Besnard A, Novoa C, Gimenez O (2010) Hunting impact on the population dynamics of Pyrenean grey partridge *Perdix perdix hispaniensis*. *Wildlife Biology* 16: 135-143

- 273 Blokhin YY, Mezhnev AP, Fokin SY (2006) Woodcock hunting bag statistics in Russia since
274 1996. In Ferrand Y (ed) Sixth European Woodcock and Snipe Workshop – Proceedings of
275 an International Symposium of the Wetlands International Woodcock and Snipe Specialist
276 Group, 25-27 November 2003, Nantes, France. Wetlands International Global Series
277 N°18, International Wader Studies 13, Wageningen, The Netherlands. pp. 16-22.
- 278 Boyce MS, Sinclair ARE, White GC (1999) Seasonal compensation of predation and harvesting.
279 *Oikos* 87: 419-426.
- 280 Burnham KP, Anderson DR (1984) Tests of compensatory versus additive mortality in Mallards.
281 *Ecology* 65:105–112.
- 282 Burnham KP, Anderson DR, White, GC, Brownie C, Pollock, KP (1987) Design and analysis
283 methods for fish survival experiments based on release-recapture. Bethesda, MD:
284 American Fisheries Society Monograph 5.
- 285 Carother AD (1973) Effects of unequal catchability on Jolly-Seber estimates. *Biometrics* 29: 79-
286 100.
- 287 Choquet R, Rouan L, Pradel R (2009) Program E-SURGE: a software application for fitting
288 Multievent models. *Modeling Demographic Processes In Marked Populations* (eds
289 Thomson DL, Cooch EG, Conroy MJ), pp. 845-865. Springer, New York.
- 290 Duriez O, Eraud C, Barbraud C, Ferrand Y (2005a) Factors affecting population dynamics of
291 Eurasian woodcocks wintering in France: assessing the efficiency of a hunting-free
292 reserve. *Biological Conservation* 122: 89-97.
- 293 Duriez O, Ferrand Y, Binet F, Corda E, Gossmann F, Fritz H (2005b) Habitat selection of the
294 Eurasian woodcock in winter in relation to earthworms availability. *Biological*
295 *Conservation* 122: 479-490.

- 296 Duriez O, Fritz H, Said S, Ferrand Y (2005c) Wintering behaviour and spatial ecology of
 297 Eurasian Woodcock *Scolopax rusticola* in western France. *Ibis* 147: 519-532.
- 298 Fadat C (1981) Age-ratio des tableaux de chasse de bécasses (*Scolopax rusticola*). Signification
 299 biologique et utilisation pour la bonne gestion des populations bécassières. Bulletin
 300 mensuel ONC, n° Spécial Scientifique et Technique, novembre 1981: 141-172.
- 301 Ferrand Y, Gossmann F, Bastat C, Guénézan M (2008) Monitoring of the wintering and breeding
 302 Woodcock populations in France. *Revista Catalana d'Ornitologia* 24: 44-52.
- 303 Ferrand Y, Gossmann F (2009) Ageing and sexing series 5: Ageing and sexing the Eurasian
 304 Woodcock *Scolopax rusticola*. *Wader Study Group Bull.* 116: 75-79.
- 305 Fletcher D, Lebreton J-D, Maescot L, Schaub M, Gimenez O, Dawson S, Slooten E (2011) Bias
 306 in estimation of adult survival and asymptotic population growth rate caused by
 307 undetected capture heterogeneity. *Methods in Ecology and Evolution*. In press.
- 308 Gaillard JM, Yoccoz NG (2003) Temporal variation in survival of mammals: A case of
 309 environmental canalization? *Ecology* 84: 3294-3306.
- 310 Gauthier G, Lebreton JD (2008) Analysis of band-recovery data in a multistate capture-recapture
 311 framework. *Canadian Journal of Statistics-Revue Canadienne De Statistique* 36: 59-73.
- 312 Givens GH, Hoeting JA (2005) *Computational Statistics*. Wiley, New York.
- 313 Gossmann F, Ferrand Y, Bastat C (1994) Mortalité hivernale des bécasses des bois en France
 314 d'après les reprises de bagues. *IWRB Publication* 31: 8-14.
- 315 Gossmann F, Boidot JP, Bastat C, Ferrand Y (2011) Effects of summer 2010 drought in European
 316 Russia on the migrating and wintering Woodcock population in France. Comm. 7th
 317 Woodcock and Snipe Specialist Group Workshop. 16-18 May 2011. Saint Petersburg
 318 (Russia).

- 319 Givens GH, Hoeting JA (2005) Computational Statistics. - Wiley Series in Probability and
 320 Statistics, Hoboken, New Jersey, USA. 418 pp.
- 321 Hanski I (1991) Metapopulations dynamics: empirical and theoretical investigations. Biol. J.
 322 Linn. Soc. Academic Press, London.
- 323 Hémery G, Jarry G, Le Toquin A, Nicolau-Guillaumet P (1978) Etudes préliminaires des
 324 populations de Bécasses des bois migratrices et hivernantes en France. Bulletin mensuel
 325 de l'Office National de la Chasse, numéro spécial sciences et techniques 1978: 5-37.
- 326 Hoodless AN, Coulson JC (1998) Breeding biology of the woodcock *Scolopax rusticola* in
 327 Britain. Bird Study 45: 195-204.
- 328 Hoodless AN, Hirons GJM (2007) Habitat selection and foraging behaviour of breeding Eurasian
 329 Woodcock *Scolopax rusticola*: a comparison between contrasting landscapes. Ibis 149
 330 (Suppl.2): 234-249.
- 331 Kauffman MJ, Varley N, Smith DW, Stahler DR, MacNulty DR, Boyce MS (2007) Landscape
 332 heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters
 333 10: 690-700.
- 334 Lebreton JD (2005) Dynamical and statistical models for exploited populations. Australian and
 335 New Zealand Journal of Statistics 47: 49-63.
- 336 Mueller T, Selva N, Pugacewicz E, Prins E (2009) Scale-sensitive landscape complementation
 337 determines habitat suitability for a territorial generalist. Ecography 32: 345-353.
- 338 Nichols JD, Stokes SL, Hines JE, Conroy MJ (1982) Additional comments on the assumption of
 339 homogeneous survival rates in modern bird banding estimation models. Journal of
 340 Wildlife Management 46: 953-962.

- 341 Nilsen EB, Gaillard JM, Andersen R, Odden J, Delorme D, van Laere G, Linnell JDC (2009) A
342 slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer
343 populations. *Journal of Animal Ecology* 78: 585-594.
- 344 Novaro AJ, Redford KH, Bodmer RE (2000) Effect of hunting in source-sink systems in the
345 neotropics. *Conservation Biology* 14: 713-721.
- 346 Ozgul A, Armitage KB, Blumstein DT, Vanvuren DH, Oli MK (2006) Effects of patch quality
347 and network structure on patch occupancy dynamics of a yellow-bellied marmot
348 metapopulation. *Journal of Animal Ecology* 75: 191-202.
- 349 Ozgul A, Oli MK, Armitage KB, Blumstein DT, Van Vuren DH (2009) Influence of Local
350 Demography on Asymptotic and Transient Dynamics of a Yellow-Bellied Marmot
351 Metapopulation. *American Naturalist* 173: 517-530.
- 352 Péron G, Ferrand Y, Gossmann F, Bastat C, Guénézan M, Gimenez O (2011) Nonparametric
353 spatial regression of survival probability: visualization of population sinks in Eurasian
354 Woodcock. *Ecology preprint*: doi:10.1890/10-2224.1.
- 355 Pfister CA (1998) Patterns of variance in stage-structured populations: Evolutionary predictions
356 and ecological implications. *Proceedings Of The National Academy Of Sciences Of The*
357 *United States Of America* 95: 213-218.
- 358 Pradel R (2009) The stakes of capture-recapture models with state uncertainty. – In: Thomson, D.
359 L. et al. (eds), *Modeling demographic processes in marked populations*. Springer, pp.
360 781–795.
- 361 Pulliam HR (1988) Sources, sinks, and population regulation. *American Naturalist* 132: 652-661.
- 362 Rolland V, Hostetler JA, Hines TC, Percival HF, Oli MK (2010) Impact of harvest on survival of
363 a heavily hunted game bird population. *Wildlife Research* 37: 392-400.

- 364 Royle JA, Dubovsky JA (2001) Modeling spatial variation in waterfowl band-recovery data.
365 Journal of Wildlife Management 65: 726-737.
- 366 Royle JA (2008) Modeling individual effects in the Cormack-Jolly-Seber model: a state-space
367 formulation. Biometrics 64: 364–370.
- 368 Salo P, Nordstrom M, Thomson RL, Korpimaki E (2008) Risk induced by a native top predator
369 reduces alien mink movements. Journal of Animal Ecology 77: 1092-1098.
- 370 Sandercock BK, Nilsen EB, Broseth H, Pedersen HC (2011) Is hunting mortality additive or
371 compensatory to natural mortality? Effects of experimental harvest on the survival and
372 cause-specific mortality of willow ptarmigan. Journal of Animal Ecology 80: 244-258.
- 373 Sepik GF, Owen RB, Dwyer TJ (1983) The effect of drought on a local Woodcock population.
374 Trans. of the Northeast Section, The Wildlife Society, 40th Northeast Fish & Wildlife
375 Conference, 15-18 May 1983, West Dover, Vermont, USA. 1-8
- 376 Stearns SC, Kawecki TJ (1994) Fitness sensitivity and the canalization of life-history traits.
377 Evolution 48:1438-1450.
- 378 Tavecchia G, Pradel R, Gossmann F, Bastat C, Ferrand Y, Lebreton JD (2002) Temporal
379 variation in annual survival probability of the Eurasian woodcock *Scolopax rusticola*
380 wintering in France. Wildlife Biology 8: 21-30.
- 381 Widén P (1987) Goshawk predation during winter, spring and summer in a boreal forest area of
382 central Sweden. Holarctic Ecology 10:104-109.
- 383 Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations.
384 Academic Press, San Diego, California.

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 (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.

#	$s_{a,s,t}$	p_t	$r_{s,t}$	#p	Dev	ΔAIC	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
5	$W(a+\text{HPI}); S(a)$	t	$W(t+\text{HPI});$	47	81406.7	100.7	year-effect on winter recovery

			$S(.)$				and recapture probabilities
6	$W(a+HPI); S(a)$	.	$W(HPI); S(.)$	11	81701.2	323.2	No year-effect on observation parameters
7	$W(a+HPI); S(a)$	t	$W(T+HPI); S(.)$	30	81474.8	134.8	Best model above with linear temporal trend on recovery probabilities
8	$W(a+HPI); S(a)$	T	$W(t+HPI); S(.)$	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	$W(a+HPI); S(a)$	t	$W(t+HPI); S(.)$	47	81406.7	100.7	HPI-effect on both survival and recovery probabilities
9	$W(a+HPI); S(a)$	t	$W(t); S(.)$	45	82023.2	713.2	HPI-effect on survival probabilities only
10	$W(a); S(a)$	t	$W(t+HPI); S(.)$	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	$W(a+HPI); S(a)$	t	$W(t+HPI); S(.)$	47	81406.7	100.7	Age-effect on both winter and summer survival probabilities
12	$W(a+HPI); S(.)$	t	$W(t+HPI); S(.)$	45	81499.4	189.4	Age-effect on winter survival probabilities only
13	$W(HPI); S(a)$	t	$W(t+HPI); S(.)$	45	81660.0	350.0	Age-effect on summer survival probabilities only
14	$W(HPI); S(.) + a$	t	$W(t+HPI); S(.)$	45	81430.5	120.5	Same age-effect on winter and summer survival probabilities
15	$W(HPI); S(.)$	t	$W(t+HPI); S(.)$	44	81749.7	437.7	No age-effect
Selection for the time-dependency of survival parameters							
5	$W(a+HPI); S(a)$	t	$W(t+HPI); S(.)$	47	81406.7	100.7	No year-effect on survival probabilities

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

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

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.