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RESEARCH

The relative role of local temperature in the winter occurrence of woodcock *Scolopax rusticola* in the northern Iberian Peninsula

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Abstract

The dynamics of migratory populations at wintering quarters can inform on population state and size because these areas act as demographic funnels, assembling birds from different origins. Previous evidence on survival probability of woodcock *Scolopax rusticola* wintering in northern Spain suggested a high harvesting pressure, but whether this pressure is causing a decline of woodcock occurrence at wintering quarters is still to be assessed. We used data from 3411 surveys conducted during the winter at 434 selected grasslands in the Gipuzkoa region, Northern Spain, to investigate the dynamics of woodcock occurrence probability, conditional on detection, over a period of 10 years (2009–2019). A 47% of the variation in woodcock occurrence within and across winters was explained by the monthly average minimum temperature. The remaining variation was due to a marked increase during the winters 2016 and 2017, contrary to the progressively decreasing values detected in previous years. At present, these abrupt yearly fluctuations prevent clear predictions on woodcock presence in the Gipuzkoa region. Future studies should explore woodcock occurrence probability according to scenarios of climate and habitat changes.

Keywords Demography · Population trend · Forest-dwelling shorebirds · Migrant species · Wintering area

Introduction

Many migratory bird populations in the Palearctic region are declining (Kirby et al. 2008; Runge et al. 2015) due to climate warming, habitat changes (Saino et al. 2010; Studds et al. 2017; Howes et al. 2019) and/or over-exploitation (McCulloch et al. 1992; Brochet et al. 2016). As their distribution encompasses large geographic areas, threats can change spatially throughout their annual cycle (Alerstam 1993; Newton 2004, 2008). Because wintering conditions can determine the next spring population (Peach et al. 1991; Brochet et al. 2016; Johnston et al. 2016; Halupka et al. 2017), understanding those factors influencing the presence and wintering strategy of migratory birds is important for a sustainable management of these species. Trends of European migratory bird populations are more closely related to climate impacts at their breeding areas than habitat changes at their wintering areas; however, both effects explain 40% of the variation in breeding populations (Howard et al. 2020), and other factors might be involved, e.g. habitat quality or hunting pressure (Inger et al. 2010; Strandberg et al. 2010; Prieto et al. 2019).

The Eurasian woodcock *Scolopax rusticola* is a game bird living in woodlands across the Palearctic region. Their populations vary from sedentary to migratory (Cramp and Simmons 1983). Worldwide, the species has been listed as 'least concern' with a stable population (BirdLife International 2023). In Europe, the majority of woodcocks winters in the southwestern part of the continent (mainly Iberia and France; Duriez 2003; Arroyo and Guzmán 2010). Its breeding population in Europe is currently declining (BirdLife International 2021), although the trend can vary according to the scale and time series considered (Hoodless 1995; Tucker and Health 2004; Fokin et al. 2012; Hoodless and Heward 2013; Heward et al. 2015). A large proportion of woodcocks

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from Russian populations spend the winter in southwestern Europe (Bauthian et al. 2007; Guzmán et al. 2011; Hobson et al. 2013; Arizaga et al. 2014). Here, despite a high hunting-related mortality (Péron et al. 2011a, 2012), the number of woodcocks presents a poorly defined trend due to important inter-annual fluctuations in France and Spain (Ferrand et al. 2008; González-Quirós 2015). The causes of these fluctuations remain unclear, but environmental factors, such as cold spells (Tavecchia et al. 2002; Boos et al. 2005) and habitat changes (Heward et al. 2018) and harvesting (Péron et al. 2012; Guzmán et al. 2017; Prieto et al. 2019), can influence woodcock wintering numbers. In Cantabrian mountains, northwestern Iberia, wintering abundance during the 23-year period 1992/1993–2014/2015 did not change significantly (González-Quirós 2015). However, a recent study showed that woodcocks in north-eastern Iberia had low apparent survival rates, mainly due to high harvesting pressure (Prieto et al. 2019). As woodcocks show a high degree of philopatry to their wintering sites (Hoodless and Coulson 1994; Duriez et al. 2005), a high harvesting pressure can lead to negative local population trends. To assess a possible negative trend of woodcock winter population in north-eastern Spain, we used data of woodcock surveys collected during 10 winters in Gipuzkoa (northern Iberia), a region with a high harvesting pressure and an important wintering area for the species. In addition to a possible temporal trend, as warm conditions are known to influence overwinter population of migratory birds (Tavecchia et al. 2002; Arroyo and Guzmán 2010; Saino et al. 2010), we assessed the influence of winter temperature in determining the observed dynamics of woodcock presence. We expect to find a negative trend of woodcock presence over the years due to the high apparent mortality (Prieto et al. 2019) and a negative association with winter temperature, as found in other wintering areas (Tavecchia et al. 2002; Boos et al. 2005).

Methods

Sampling area and data collection

From November of 2009 to February of 2019, we conducted 3411 surveys on 434 grasslands, ‘plots’ hereafter, with optimal woodcock foraging habitat, i.e. open grassland near a wooden area (Fig. 1). The number and location of plots to be surveyed were selected semi-randomly according to the availability of observers, looking for a good representativeness in terms of geographical coverage and type of grasslands within the region, resulting, on average, in 135.5 plots visited per winter and 4.8 plot/night (Table 1). The 60.8% of the plots were visited more than once along the study period. We assigned a unique ID code to each plot to control for repeated measures during months and between winters. Each survey was conducted by a single observer who inspected the plot with a 12-V-100 W lamp. We assigned a ‘1’ when at least one woodcock was detected and a ‘0’ otherwise. To assess a possible relationship between the presence probability of woodcock and temperature, we considered four temperature measures. The first measure was the air temperature (ºC) taken during each survey (*temp*) using a portable thermometer. We then considered mean regional values of monthly minimum (*tmin*), average (*tmed*) and maximum

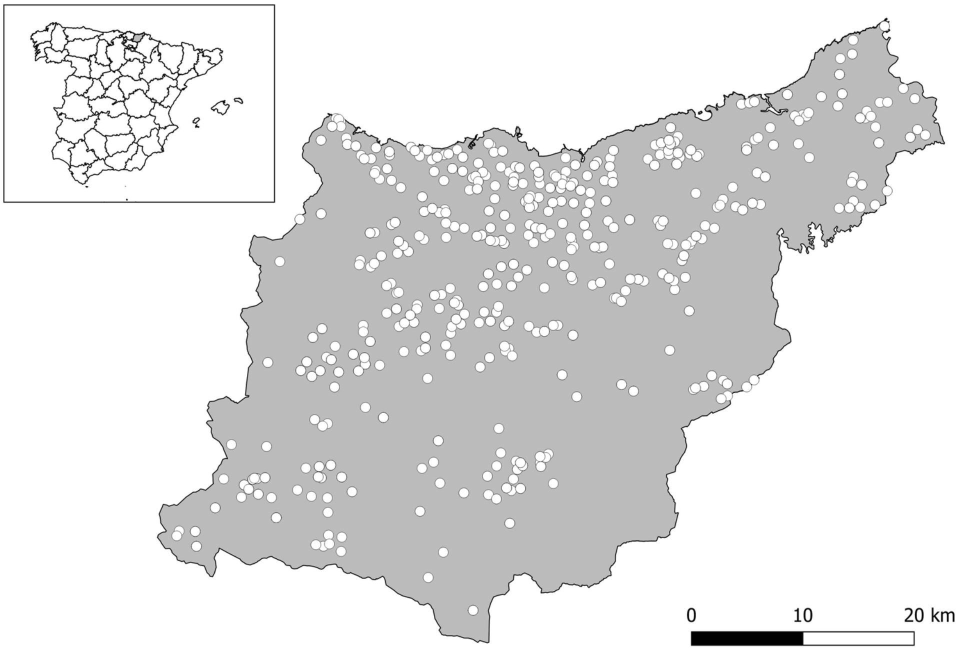

Fig. 1 Location of surveyed grasslands (dots) in Gipuzkoa, Northern Spain (small box)

Table 1 General statistics of woodcock counts in Gipuzkoa, northern Iberia. *SV* number of surveys, *NP* number of survey plots, NP_0 percentage of plots in which no woodcocks were seen, *TSA* total area surveyed (ha). *N* number of individual bird counts

Winter	SV	NP	NP_0	TSA	*N*	Birds/plots
2009	239	102	12.1	968.1	640	6.3
2010	323	176	24.1	1162.2	385	2.2
2011	518	192	15.3	2149.5	884	4.6
2012	519	201	21.0	2401.4	436	2.2
2013	423	153	17.0	2032.1	413	2.7
2014	286	99	16.1	1410.4	240	2.4
2015	190	82	24.2	994.7	104	1.3
2016	269	116	14.9	1231.3	284	2.4
2017	421	135	8.3	1920.7	553	4.1
2018	223	99	20.2	1102.1	222	2.2
Mean	341.1	135.5	17.3	1537.3	416.1	3.0
Total	3411	434		15,372.5	4161	

(*tmax*) temperatures, recorded in ºC at the Alegia meteorological station (Latitude 43.10ºN, Longitude 2.10ºW; source: Euskalmet). We assessed the collinearity among these four temperature measures using the variance inflation factor (VIF) and retained those with VIF < 3 (Fox and Weisberg 2011) (Appendix Table 4).

Data analysis

Following the collinearity analysis, the variable *tmed* was discarded while *temp*, *tmin* and *tmax* were retained (VIF: $tmin = 2.45$, $temp = 1.25$, $tmax = 2.59$) as possible predictors of the probability of presence of woodcock together with the month (noted 'month') and the year (noted 'year'). None of the retained temperature measures showed a statistically significant trend over time (*tmin*: $t_8 = 0.926$, $P = 0.382$; *temp:* $t_8 = 2.161$, $P = 0.063$, *tmax:* $t_8 = 1.169$, $P = 0.276$). Presence-absence (hereafter, occurrence) data were modelled using generalized mixed models (GLMM) with the *glmer* function and a binomial distribution of errors (package 'lme4'; Bates et al. 2015) in software R v.4.0.4. Note that we modelled occurrence probability (ψ), conditional on detection probability. We were not able to conduct models accounting for detection probability, e.g. site-occupancy models (MacKenzie et al. 2003), since most plots were visited only once. Although we did not account for detection probability, by collapsing counts to presence-absence data and by considering many surveys each month, we think the conditional occupancy is likely to be a good approximation of the 'real' presence. Plot identity was used as a random term whilst the winter and the month were considered as fixed factors to account for the temporal variation within and across winters. When assessing a temporal trend in woodcock occurrence, however, we considered the winter as a random effect. By doing so, we assumed that the yearly variability around a possible trend was distributed as a normal random variable. We used the Bayesian Information Criterion (BIC, Table 2) in order to select the best compromise between model complexity and model residual deviance (Burnham and Anderson 1998; see also Mingozzi et al. 2021). Models differing in less than 2 BIC units would be considered to fit to the data equally well. We calculated the proportion, *G*, of the variance explained by a given covariate, θ, as the proportion of the variance explained by θ to the total variance available, as in Tavecchia et al. (2007). Note that for the sake of simplicity, we shall refer to winter i, $i + 1$ as the i-winter, so that, for example, the winter 2010–2011 will be referred to as winter 2010, though it ends in February of 2011.

Results

Woodcocks were present in 1791 of the surveys (52.5%), corresponding to 248 different plots (57.1%). The average annual occurrence probability ranged from 0.44 to 0.60, and it was negatively associated with *temp* ($t_2 = -7.88$, $P = 0.016$, Fig. 2). The retained model (Table 2) included an effect of the year (i.e. winter as a factor) and an additive effect of the average minimum temperature, *tmin* (Table 3). The second best-ranked model, with difference of ~ 9 points in BIC, included a linear tendency as additional effect. Note that the trend was negative and statistically significant; however, due to the large difference in BIC value, the model was not retained. According to the retained model (model 1), the occurrence probability reached its maximum value (0.68) during the first winter of the study (Fig. 2) and declined during the next six winters (2010–2015). It recovered abruptly during the period 2016–2017 and decreased again in winter 2018. These fluctuations are likely to be responsible for the fact that a linear trend was not retained, although statistically significant. When tested alone, all three measures of temperature had a

Table 2 Modelling the proportion of plots seen occupied by at least one woodcock using generalized mixed models. In all models, the plot identity is considered as a random effect (noted 'ID') to correct for plot characteristics. np = number of model parameters, BIC = Bayesian Information Criterion, ΔBIC = difference with the lowest BIC value. Model notation: *winter* = factor (winter, 10 levels and month 4 levels); *trend* = linear trend; *temp* = temperature measure in situ at the time of the survey; *tmin* = average minimum monthly temperature at regional scale; *tmax* = average maximum monthly temperature at regional scale

Model	Fixed effect	Random effect	np	BIC	ΔBIC
1	**winter + tmin**	**ID**	**12**	**4375.90**	**0.00**
2	trend + tmin	ID	4	4385.45	9.54
3	tmin	ID	3	4392.70	16.80
4	winter + month + tmin	ID	15	4394.06	18.16
5	winter + tmax	ID	12	4398.23	22.33
6	trend + month + tmin	ID	7	4402.62	26.72
7	trend + tmax	ID	4	4411.98	36.08
8	month + tmin	ID	6	4412.24	36.34
9	winter + month + tmax	ID	15	4418.59	42.69
10	tmax	ID	3	4419.52	43.61
11	winter + month + temp	ID	15	4419.89	43.99
12	winter + temp	ID	12	4421.38	45.48
13	winter + month	ID	14	4432.96	57.06
14	trend + month + tmax	ID	7	4433.48	57.58
15	month + tmax	ID	6	4439.33	63.43
16	winter	ID	11	4451.31	75.41
17	trend + month + temp	ID	7	4455.77	79.87
18	month + temp	ID	6	4458.83	82.93
19	trend + temp	ID	4	4461.10	85.20
20	temp	ID	3	4467.48	91.58
21	trend + month	ID	6	4482.41	106.51
22	month	ID	5	4489.21	113.31
23	trend	ID	3	4513.39	137.49
24	null	ID	2	4527.97	152.07
25	winter*month	ID		4539.10	163.20

*Main terms and their statistical interaction, + Additive relationship (no interaction) between terms. The model retained is in bold

negative and statistically significant effect on occurrence (models 3, 10, 20, Table 3; $\beta_{tmin} = -0.208 \pm 0.018$, $P < 0.001$, $\beta_{\mathrm{tmax}} = -0.162 \pm 0.015$, $P < 0.001$, $\beta_{\mathrm{temp}} = -0.082 \pm 0.010$, $P < 0.001$). However, the variable *tmin* had the strongest effect on occurrence probability and explained the 47% of the within and across winter variation. A negative trend explained the 15% of the yearly variation. A model assuming an

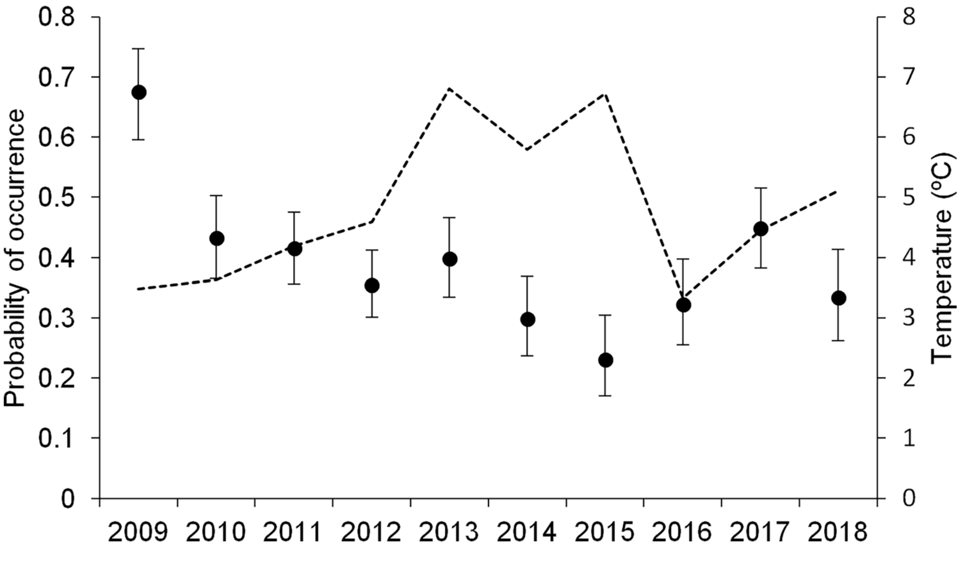

Fig. 2 Probability of occurrence (black dots) and ± 95% confidence interval (vertical lines) as predicted by the retained model (model 1, Table 2). The line indicates the average minimum monthly temperatures. Note that winter *i* refers to a winter starting in November of year *i* up to February of year *i* + 1 (Table 3)

Table 3 Linear predictors (β), standard errors (se) and statistic (z and p-vale) of the effects in the retained model (model 1, Table 3). The intercept is equivalent to the linear predictor for winter 2009

	β	se	*Z*	*p*
Intercept	1.61	0.19	8.41	< 0.001
Tmin	− 0.18	0.02	− 8.97	< 0.001
Winter 2010	− 1.00	0.21	− 4.76	< 0.001
Winter 2011	− 1.08	0.20	− 5.37	< 0.001
Winter 2012	− 1.33	0.20	− 6.65	< 0.001
Winter 2013	− 1.15	0.22	− 5.31	< 0.001
Winter 2014	− 1.58	0.23	− 7.01	< 0.001
Winter 2015	− 1.94	0.25	− 7.67	< 0.001
Winter 2016	− 1.48	0.23	− 6.56	< 0.001
Winter 2017	− 0.94	0.21	− 4.51	< 0.001
Winter 2018	− 1.43	0.24	− 6.06	< 0.001

interaction between the effect of the winter and the one of the average minimum temperature had a large BIC value (Table 2) indicating that *tmin* had a negative effect on occurrence regardless the winter considered. The model considering an additive effect of winter, month and the average minimum temperature suggested that the occurrence probability decreases significantly in February ($\beta_{feb} - 0.42 \pm 0.19$, $P = 0.03$; Fig. 3; Model 4, Table 2). When the *tmin* is not controlled for, the occurrence in February is similar to the one registered in the previous 2 months (Model 11, 8 and 18, Table 2). Finally, the annual counts correlate with the occurrence probability predicted by the retained model (Table 2; $R^2 = 0.45$, $t_8 = 2.58$, $P = 0.033$).

Discussion

This is the first study where occurrence (conditional on detection) of woodcocks wintering in northern Spain is estimated over a temporal series of ten consecutive winters (2009–2018). Although occurrence is a 0–1 variable, it can be indirectly used as a proxy of abundance, since higher values of occurrence mean that more plots have been seen occupied by the species. Due to high wintering site fidelity (Hoodless and Coulson 1994; Duriez et al. 2005), a high occurrence is likely to reflect a larger population size (Arizaga et al. 2015). Furthermore, the series of annual woodcock count correlates with the annual estimates of occurrence, supporting the hypothesis that the conditional occurrence probability is a reliable proxy of population abundance. Woodcock occurrence probability varied during the study period, and this variation was negatively related to the minimum temperature measured at regional scale. Hidalgo and Rocha (2001) found a significant negative correlation between the mean monthly temperature and the woodcock occurrence, with a mean temperature threshold of 19 ºC that would determine the start of the prenuptial migration. According to the retained model, the occurrence probability reached a peak in November, when most migratory birds arrived to the Iberian peninsula (Lucio and Sáenz de Buruaga 2000; Mendiburu and Arizaga 2010), followed by a decrease in mid-winter, and a minimum in February, when animals begin to leave to their breeding quarters (Fig. 3).

The temperature-related pattern found within the winter is also evident across winters, as yearly occurrence probability peaked during cold winters. It is interesting to notice that this negative relationship holds even when a temporal trend

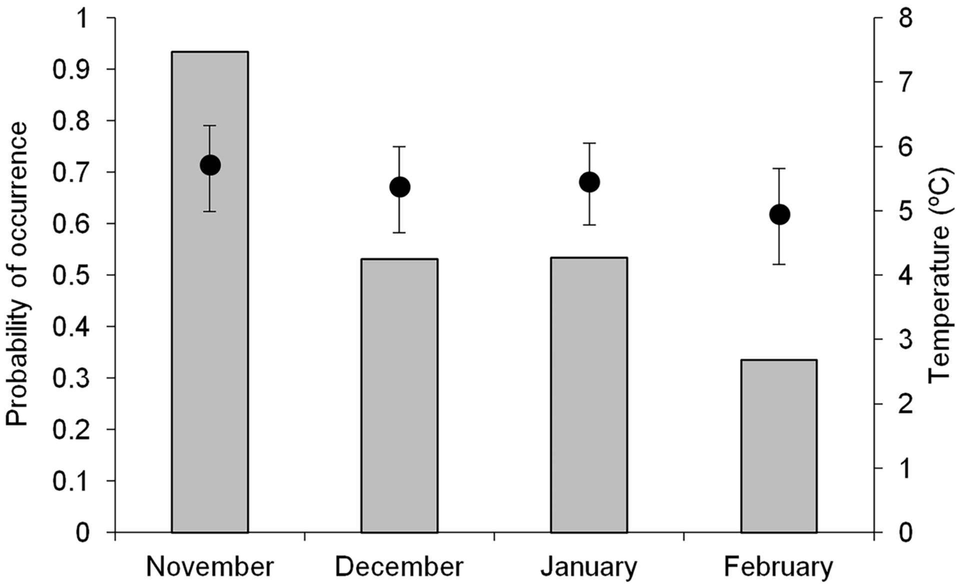

Fig. 3 Probability of woodcock occurrence (black dots) and ± 95% confidence interval (vertical lines) within the winter estimates from Model 4 (Table 2). Vertical bars indicate the average minimum monthly temperatures measured at regional level (see text)

was controlled for. Previous studies on woodcocks wintering in France showed a positive effect of temperatures on apparent survival (Tavecchia et al. 2002; Péron et al. 2012). This may suggest movements toward warmer regions during cold spells as woodcocks avoid frozen areas where foraging opportunities are scarce (Péron et al. 2011b; Guzmán et al. 2017). During cold spells, the higher occurrence probability in Gipuzkoa can be due to the presence of birds that used to spend the winter at northern latitudes. Note in this context that the average monthly minimum temperatures in Gipuzkoa always reach values above zero, highlighting the role of this region (and of the Cantabrian coast in general) as a refuge for the species under harsh wintering conditions.

Although this effect of temperature on occurrence is somehow in contrast with the high wintering site fidelity, it is likely that dispersal can be triggered by some threshold values of temperature. Arroyo and Guzmán (2010) suggested that the mobility of this species depends on local winter weather conditions even in the absence of cold spells. The presence of snow or a dry winter could also affect the availability of earthworms. A second, non-exclusive hypothesis is that birds venture more into open field at lower temperatures (hence increasing their 'apparent' occurrence) since they need to prioritize food ingestion in detriment of predator avoidance (Braña et al. 2010). Finally, a third hypothesis is that harvesting pressure increased during mild winters. This is however unlikely because average monthly minimum temperatures never went below zero °C.

In conclusion, our top-ranked model showed that woodcock occurrence in Gipuzkoa varied annually through the winters 2009–2018, but in a non-linear way (so we reject a linear trend). These oscillations are partly due to the change in the average minimum temperature in the same way that this measure influences the monthly probability of occurrence within the winter. Causes underlying the trend found from 2009 to 2015 remain unknown, since they might respond to several factors. Further studies and longer time series are needed to clarify this point and the future trajectory of woodcock population in light of the scenarios of climate and habitat change in the region.

Appendix

Table 4 Variance inflation factors (VIF) of temperature measures. *temp* temperature at the time of sampling, *tmin* the mean monthly minimum temperature, *tmed* the mean monthly average temperature, *tmax* the mean monthly maximum temperature

	VIF
temp	1.25
tmin	2.45
tmed	–
tmax	2.59

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Author contributions All authors contributed to the study conception. NP conducted the analyses and compiled the first draught of the manuscript. NP, JA and GT wrote the main manuscript text; JA prepared Fig. 1; NP prepared Figs. 2 and 3 and the tables. Members of the Gipuzkoa Administration, EI, FA, AG and AU provided part of the data analysed in this study. All the authors reviewed the manuscript.

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Declarations

Conflicts of interest The authors declare no competing interests.

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