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Age demographics of a non-breeding Eurasian Woodcock *Scolopax rusticola* population in relation to environmental factors

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ABSTRACT

Capsule: Environmental conditions in non-breeding areas cause differential winter distribution patterns between age classes in a Eurasian Woodcock *Scolopax rusticola* population wintering in northern Iberia.

Aims: To determine the factors driving spatial distribution of first-winter and adult birds in the non-breeding period of a population of the Eurasian Woodcock, in order to make decisions for the management of the species.

Methods: Using a data set of 10 consecutive winters (2009/10–2018/19), we tested for the effect of year, geographical and habitat-related variables on age ratio and body condition of Eurasian Woodcocks wintering in two nearby zones with different hunting regimes in northern Iberia.

Results: Our results suggest that the age ratio depended mainly on year, month, and altitude. As winters progressed, we observed a higher proportion of first-winter birds occurring at sites with lower altitude. First-winter birds were in poorer body condition than adults, and body condition was higher in mid-winter and spring. The effect of hunting on body condition was unclear.

Discussion: Variation in the population structure and body condition between age classes are discussed in the context of age-dependent wintering strategies, which to a large extent depend on survival thresholds that take into account foraging efficiency and the risk of predation. The lack of detectable effects of hunting on age structure and body condition precludes us from giving any management recommendations for northern Iberia.

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Migratory species occupy very large geographic areas across the annual cycle, and conditions in both the breeding and non-breeding areas can have a strong influence on reproductive success (Ockendon *et al.* 2013, Meller *et al.* 2018, Tobolka *et al.* 2018) and/or survival (Wilson *et al.* 2018). Moreover, many species show differential migration, with segregation between age or sex classes on the non-breeding grounds (Kettersson & Nolan 1983, Cristol *et al.* 1999). This segregation occurs at various spatial scales, from large (i.e. regional and/or continental – Cristol *et al.* 1999, Catry *et al.* 2005, Bai & Schmidt 2012, Arizaga *et al.* 2014b) to small scales (Figuerola *et al.* 2001, Catry *et al.* 2004, Catry *et al.* 2007). Since environmental conditions on the non-breeding grounds can vary substantially between regions or habitats, the survival or prospects for future reproductive success can also differ between age or sex classes that show segregation outside the breeding season. Generally, there has been less research on age segregation at small spatial scales, such as habitat segregation on the non-breeding grounds, than at larger scales. This segregation, however, could be important from a demographic perspective, especially if it coincides with other variables such as predation or hunting pressure.

The Eurasian Woodcock *Scolopax rusticola* (hereafter, Woodcock) is a migratory wader which breeds mostly in Eurosiberian woodland across the Palearctic region (Cramp & Simmons 1983). Most Eurosiberian populations move to southern Europe in winter (Hoodless & Coulson 1994, Guzmán *et al.* 2011, Arizaga *et al.* 2014a); hence such wintering areas play a key role in the conservation of the western and central-Eurasian breeding population. At an individual level, Woodcocks move through their wintering area in relation to environmental factors such as food availability, density of lush vegetation, and temperature (Duriez *et al.* 2004, 2005b, 2005c, 2005d, Braña *et al.* 2010, Péron *et al.* 2012).

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Little is known, however, about how environmental factors shape the potential segregation between age classes in winter. The distribution of the Woodcock in winter is positively correlated with vegetation cover, which is associated with predator avoidance (Duriez 2003, Duriez *et al.* 2005c), but also with food availability, in particular earthworms (Duriez & Ferrand 2005). Since earthworms show much higher biomass in open habitats, such as meadows, when compared to forests (Duriez & Ferrand 2005), Woodcocks must find a trade-off between foraging efficiency and the risk of predation (Boos *et al.* 2005). This is achieved by changing habitat between the day, when they remain hidden in places with dense vegetation cover, and night, when they move to open habitats to forage. Guzmán *et al.* (2017) observed that, on average, adults perform longer commuting flight distances and related it to a greater efficiency in finding more suitable feeding areas. This could lead to a greater density of adults in open areas at night.

Food availability, in part determined by climatic conditions, affects the distribution patterns of birds during non-breeding periods (Senar & Borras 2004, Newton 2008, Tellería *et al.* 2008). Woodcocks tend to be more abundant along the coast (Arizaga *et al.* 2015), where the temperature is more stable, thus avoiding frosts which hamper food acquisition. In Europe, wintering Woodcocks tend to concentrate in regions to the west and south of the +2.5°C January isotherm (Duriez 2003). Altitude, and the distance to coast, therefore, should be expected to be negatively correlated with the presence of Woodcocks. *A priori*, we might predict that first-winter birds should occupy less populated areas: suboptimal places at higher altitude or further from the coast. However, if good habitats are not distributed near/along the coast, then the opposite distribution pattern between age categories may be found.

The analysis of body condition can play a key role in understanding potential spatial segregation between age classes, particularly as young Woodcocks tend to be in poorer condition (Sorace *et al.* 1999). Individuals foraging in areas with greater vegetation (forest) cover could be in poorer body condition than those able to forage in open habitats, where there is more food available (Duriez & Ferrand 2005). Overall, therefore, we can hypothesize that (1) independent of their age, birds foraging in more open habitats, with presumably a greater availability of food, will be in a better body condition and (2) adults will be in better body condition than young birds, since their experience would allow them to be more efficient foragers (Guzmán *et al.* 2017).

Non-natural causes might also shape the population structure of the Woodcock during the winter. Human activities can influence habitat selection processes, for example, through hunting and habitat change (Duriez *et al.* 2005a, Fuller *et al.* 2007, Péron *et al.* 2012, Ferrand *et al.* 2013). Hunting pressure can directly impact on survival rates in the non-breeding season (Prieto *et al.* 2019), and could affect the structure of populations. We hypothesize that higher mortality, through hunting and natural factors, should be correlated with populations that have more young birds than average. The mechanism underlying this prediction is that Woodcocks are faithful to their wintering sites (Duriez *et al.* 2005d, Duriez & Ferrand 2005, Fadat 1993, Guzman *et al.* 2017), so if the hunting pressure at a site is very high, the chance of a bird reaching older categories is reduced.

Here, we aim to determine the variables shaping the potential spatial distribution between age classes of a population of Woodcocks wintering in northern Iberia. As the Woodcock is widely shot for sport in Iberia and elsewhere in Europe, this information can provide the fundamental demographic data required to improve the management and conservation of the species. We predict a greater concentration of older birds in open areas, while the first-winter birds remain in the shelter of the forest. We also predict that body condition will be related to age and that adults should be in better condition than first-year birds due to their greater foraging efficiency. Additionally, we explore the impact of hunting on these effects.

Methods

Sampling area and data collection

This study was carried in northern Iberia (Figure 1), a region hosting important wintering Woodcock populations (Lucio & Sáenz de Buruaga 2000). We focused our work in two provinces of the Basque country: Gipuzkoa, with an area of 2000 km^2 and Álava, with 3000 km^2. The zones have different environments. Gipuzkoa is a mountainous zone (altitude from 0 to 1551 m above sea level), bordered by the Bay of Biscay to the north; it has an oceanic climate, with mild winters (Ruiz Urrestarazu & Galdós Urrutia 2008) and mostly comprises a mosaic of mainly pine plantations, other woodland and meadows. Álava is less mountainous, with altitudes ranging from 130 to 1482 m above sea level; it has a sub-Atlantic climate with a Mediterranean influence, so the winters are colder and drier. The landscape in Álava is more diverse than that of Gipuzkoa, and varies from areas

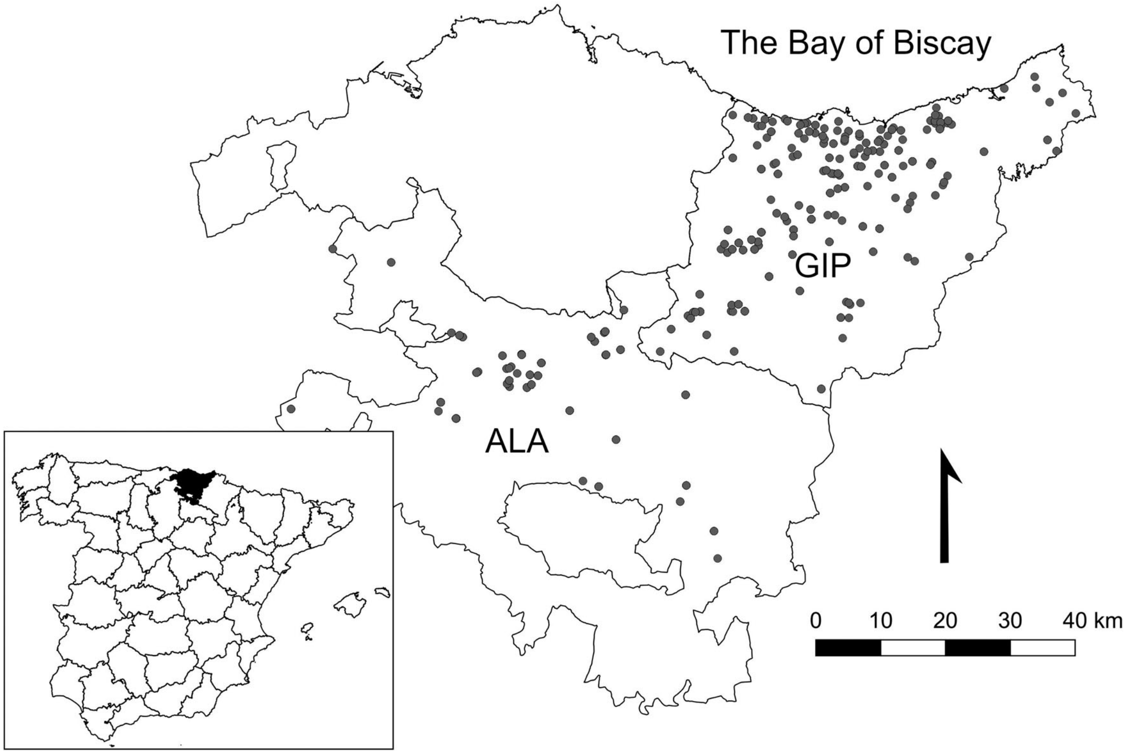

Figure 1. Location of the study area in northern Iberia. Gipuzkoa: Gipuzkoa. ALA: Álava. Dots indicate the sampling sites in which Woodcocks were caught and ringed.

with a high proportion of natural habitat, such as native oak *Quercus* or beech *Fagus* forests with meadows, to areas of cereal crops.

Hunting occurs from mid-October to mid-February but varies between the two zones, with wider access to hunting in Gipuzkoa than Álava. In Gipuzkoa, hunting is allowed by public access across practically all the province, every day of the week. In Álava, hunting is managed mostly through private land, with normally only three hunting days per week allowed. Parts of the private land in Álava are designated as a hunting-free reserve. In previous studies comparing these two zones, we detected a relationship between hunting regime and hunting pressure, since Woodcock mortality increased by approximately 10% per additional day of hunting per week (Prieto *et al.* 2019).

Over 10 consecutive winters (2009/10–2018/19), Woodcocks were captured from October to March in both zones. Birds were captured at night in open areas, using a 12 V-100 W lamp attached to a helmet and a circular net on a pole of 6 m long (Ferrand & Gossmann 1988). Sampling points were identified using the ETRS89 geo-reference system. Sampling points were selected to cover the areas where the Woodcocks were known to overwinter, but with some logistical limitations, including accessibility, availability of the ringers, and weather. Once captured, each Woodcock was ringed, aged, measured (folded wing length ± 0.5 mm), and weighed (± 0.1 g). Age was categorized as first-winter (EURING code 3 or 5) or adult (EURING code 4 or 6) following examination of wing coverts (Boidot 1999). Body condition index was the residual values of a regression of body mass on wing length (Schulte-Hostedde *et al.* 2005)

Previous studies on Woodcocks wintering in France showed that birds settled in a core area of approximately 120 m radius (Duriez *et al.* 2005d). Guzman *et al.* (2017) observed that Woodcocks wintering in northern Spain moved mean (± SD) distances of 962 ± 1042 m. Accordingly, in order to characterize the potential environmental variables exploited by Woodcocks around each capture site, we generated buffers using the QGIS 3.16.10 program (2020), which comprised areas with radii of 0.5, 1 and 2 km from the centroid of each capture point. Within each buffer, we extracted: (1) the minimum and maximum altitude (digital terrain model with mesh pitch of 200 m), (2) the minimum distance to the seashore, and (3) the land cover calculated as a percentage of each land class over the buffer area. Land cover was obtained from the CORINE Land Cover 2012 classification (European Environment Agency/EEA) using nine land cover categories: artificial surfaces (urban areas, infrastructures), crops, meadows, three types of woodland (broad-leaf, conifer, and mixed forests), shrublands, bare soil, and wetlands.

Data analysis

Before data analysis, we examined the multicollinearity among explanatory or independent variables using the variance inflation factor (VIF; Fox & Weisberg 2011). The VIF avoids adverse effects in regression analysis due to the inclusion of variables that are highly correlated (Akinwande *et al.* 2015); the process consists of eliminating the variable with the highest VIF value and retesting until all the variables present a value below 3. Hence, the independent variables considered for the models differed between buffer sizes (online Table S1).

Analyses were run using R software version 4.0.2 (R Core Team 2020). We used generalized linear mixed models (GLMMs) to test the effect of independent variables on the probability of a captured bird being an adult (coded as a binary response variable; 0 = first-winter, 1 = adult), with our list of environmental, explanatory variables: (1) factors: zone (Gipuzkoa or Álava) and winter (from 2009/10 to 2018/19); (2) linear covariates: month (from October to March), maximum altitude, nine land-cover categories (Table S1) and hunting regime (as a proportion of the days hunted per week: 7 days, 3 days, 2 days, 0 days). The individual (ring number) and the sampling site were included as a random factor, since several birds were captured more than once in the same month, winter, or site. For the analysis, we used the *glmer* function (in the package 'lme4'; Bates *et al.* 2015). Age was fitted using a binomial error distribution and a logit link function.

We used linear mixed models (LMMs) to test the body condition index, using the same explanatory variables resulting from the VIF (Table S1), the month and winter as factors, age, and the ring code and sampling site as random factors. Body condition index was analysed with the *lmer* function of the 'lme4' package, and fitted using Gaussian error distributions with a linear-link function.

Table 1. Beta-parameter estimates, their standard error, and the associated *P*-values of the independent variables affecting the age distribution of Woodcocks wintering in the Basque Country. For details of the results of the best model at 2 km scales, see Table S2. Abbreviations: winter, each of the sampled winter seasons; month, linear covariate of the season, months from October to March; altitude, maximum altitude.

	Beta	SE (Beta)	*P*
Intercept	−0.06	0.27	0.82
Altitude	+1.11	0.27	<0.001
Month	−0.11	0.04	0.004
Winter 10/11	−0.72	0.23	0.001
Winter 11/12	−1.05	0.21	<0.001
Winter 12/13	−0.91	0.20	<0.001
Winter 13/14	−1.23	0.21	<0.001
Winter 14/15	−0.01	0.23	0.97
Winter 15/16	−0.38	0.24	0.11
Winter 16/17	−1.25	0.22	<0.001
Winter 17/18	−1.24	0.20	<0.001
Winter 18/19	−1.12	0.24	<0.001

For each dependent variable (i.e. age and body condition) we fitted models including land cover variables at each of the three spatial scales (i.e. the buffers 0.5, 1, and 2 km). We were interested in testing the best spatial scale for fitting the dependent variables, and we thus constructed models which included different sets of independent variables extracted at each spatial scale. For each spatial scale, we applied a selection procedure starting from the saturated model (global) which included an additive effect of all the variables. With the MuMIn package (Barton 2014), we computed a set of candidate models, which accounted for all possible combinations of independent variables, and conducted automatic model selection ranking models according to their small sample size-corrected Akaike (AICc) values (Burnham & Anderson 1998). To avoid over-saturation, we limited the model subsets to those including fewer than four independent variables and then we compared it with the global and null model (Tables S2 and S3). From all the possible models, we retained the model with the lowest AICc as the one that best fitted the data. We used the Pearson correlation coefficients to test for spatial (auto)correlation, using the residual values of the model which best fitted the data and the sampling points.

Results

Age structure

Overall, we analysed 2570 observations of 2328 individuals (1346 in Gipuzkoa, 1224 in Álava) captured at 224 different sampling sites. Of these, 91.0% were captured only once, 7.8% twice, 1.0% three times, 0.2% four times, and 0.04% (1 individual) five times. Age ratios varied between the two zones, with a slightly, though significantly higher proportion of first-winter birds in Gipuzkoa as compared to Álava (Gipuzkoa 65.3%, Álava 59.2%). The proportion of first-winter birds also varied in relation to hunting regime: 7 days, 65.3%; 3 days, 57.1%; 2 days, 64.4%; 0 days, 69.8% ($\chi^2 = 19.23$, df = 3, $P < 0.001$).

Comparing spatial scales, the top-ranked model which showed the lowest AIC considered a buffer area of 2 km, with an effect of winter, month, and altitude on age (Table 1). There was no spatial correlation between the residual values of this top-ranked model and the sampling points ($t = 1.1$, df = 2415, $P = 0.300$). Note that the top-ranked models for a buffer area of 0.5 and 1 km provided similar results to the one for a buffer of 2 km (Table S2). Thus, captured birds were more likely to be first-winter birds in sites at lower altitude. In addition, first-winter birds were more abundant in some winters (Table 1). Thus, the proportion of young birds varied from 48.8% to 71.1% across the study. During the winters of 2009/10, 2014/15, and 2015/16, the age ratio was statistically 1:1, whilst in the other seven winters the proportion of first-winter birds exceeded that of adults (Figure 2). Additionally, models also showed a negative effect of month on the age distribution of captured Woodcocks, with an increasing proportion of first-winter birds towards the end of the winter. Models considering an effect of habitat on age distribution had a much poorer fit to the data and, therefore, should be rejected (Table 2S).

Area and hunting regime variables were discarded by the VIFs (Table S1). These two variables, independent of the buffer used, take on significant values when compared with age individually (*zone*: 0.3 ± 0.1, $P = 0.009$; *hunting regime*: −0.4 ± 0.2, $P = 0.03$).

Body condition

Overall, we analysed 2251 observations of 2136 individuals (1334 of them in Gipuzkoa and 907 in Álava) captured at 224 different sampling sites. Of these, 95.2% were captured only once, 4.3% twice, 0.4% three times, and 0.1% four times. The body masses ranged from 210 to 420 g (mean ± SE: 321.3 ± 0.6 g), and the wing length ranged from 180 to 228 mm (201.0 ± 0.1 mm).

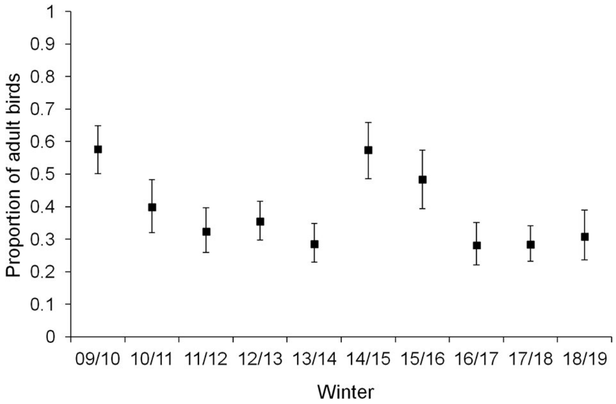

Figure 2. Effect of winter on the probability of a captured bird being an adult in a Woodcock population wintering in northern Iberia. Results obtained from the best model (1) of the 2 km-buffer (AIC < 2) of Table S2. The bars represent the 95% confidence interval.

Independently of the spatial scale, we found that the best model was the saturated one (Table S3), though not all variables had a significant effect (Table 2). In all models, we found that month was one of the factors positively related to body condition. The months in which the birds had a higher body condition were December and March (Figure 3). Moreover, body condition was also higher in some winters; especially in 2015/16 and 2017/18 (Table 2). In general, adults tended to be in better condition than first-winter birds (Table 2). Altitude had a significant positive effect at all scales (0.5 km: 5.1 ± 1.9, $P = 0.01$; 1 km: 5.1 ± 2.2, $P = 0.02$; 2 km: 4.9 ± 2.4, $P = 0.04$). We found that on the 0.5 km scale, coniferous forests was negatively associated with body condition (−6.2 ± 1.9, $P = 0.002$); this type of forest was discarded in the VIFs (Table S1) for the larger 1 and 2 km scales, where no significant habitat effect was seen. Models were unable to demonstrate an effect of zone or hunting regime on body condition, as there were problems of multicollinearity (Table S1). However, when testing variables individually, both variables had a significant effect on body condition (zone: 1.9 ± 0.8, $P = 0.02$; hunting regime: −2.7 ± 1.3, $P = 0.04$).

Table 2. Beta-parameter estimates, their standard error, and the associated *P*-values of the independent variables affecting the body condition of Woodcocks wintering in the Basque Country. For details of the results of the best model at 0.5 km scales, see Table S3. Abbreviations: *winter*, each of the sampled winter seasons; *altitude*, maximum altitude; *age*, first-winter or adult; habitat categories are the proportion of cover at 0.5 km scales.

	Beta	SE (Beta)	*P*
(Intercept)	−23.05	5.48	<0.001
Winter 2010/11	+0.23	1.40	0.87
Winter 2011/12	+0.83	1.29	0.52
Winter 2012/13	+0.79	1.21	0.51
Winter 2013/14	+2.24	1.28	0.08
Winter 2014/15	+2.40	1.48	0.10
Winter 2015/16	+5.21	1.54	<0.001
Winter 2016/17	+0.74	1.36	0.59
Winter 2017/18	+4.24	1.26	<0.001
Winter 2018/19	+1.69	1.58	0.28
November	+14.73	5.23	0.005
December	+20.80	5.23	<0.001
January	+19.03	5.25	<0.001
February	+17.69	5.27	<0.001
March	+28.31	5.31	<0.001
Altitude	+5.05	1.94	0.01
Age	+2.43	0.61	<0.001
Arid	−9.03	36.53	0.80
Artificial	+4.94	5.58	0.38
Coniferous forest	−6.23	1.92	0.002
Broad-leafed forest	−2.70	1.90	0.16
Mixed forest	−0.27	3.59	0.94
Wetland	−16.96	24.85	0.50
Shrubland	−0.42	3.34	0.90
Cropland	−2.11	2.02	0.30

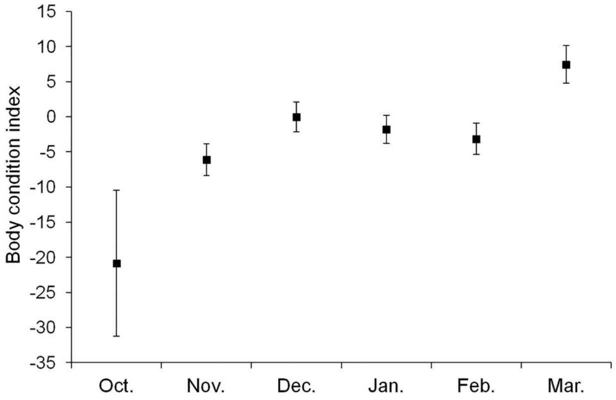

Figure 3. Effect of month ($P < 0.01$) on the body condition of Woodcocks wintering in northern Iberia. Results obtained from the global model (1) of the 0.5 km-buffer (AIC < 2) of Table S3. The bars represent the 95% confidence interval.

Discussion

Our data suggest that age-based variation in the distribution of Woodcocks wintering in a zone of northern Iberia was best explained by models showing an effect of winter, month, and altitude. Furthermore, differences in body condition were best explained by age, month, altitude, and the percentage of area covered by coniferous forests.

The variation in the age ratios between consecutive winters may be partly due to the reproductive output during the breeding season (Guzman *et al.* 2011), as well as complementary factors working on the non-breeding grounds, such as weather, hunting and habitat change. Harsh meteorological conditions, such as cold spells, force birds to move to warmer regions. Adult Woodcocks move longer distances than young birds, possibly due to being more efficient foragers, and so reach more southern latitudes, including northern Iberia, which would give rise to an increasing proportion of adult birds at a local scale. In parallel, cold winters have a negative impact on survival (Tavecchia *et al.* 2002), and this may be age-dependent, with first-winter birds being more vulnerable. Hunting, of course, can also impact survival and this may also be age- or zone-dependent (Prieto *et al.* 2019), and variable hunting pressure between winters could impact the age structure of the population. The climate and climate-related warming processes in particular, such as the North Atlantic Oscillation (NAO), could also play a role affecting the abundance of Woodcocks from one year to the next (Robinson *et al.* 2008). In addition, the joint action of climate change and human disturbance could, over time (Plieninger *et al.* 2016, Seidl *et al.* 2017), cause alterations in the landscape and this may have a strong impact on breeding performance through carryover effects (Saino *et al.* 2004), thus, affecting population structure.

Our models also predicted that a higher proportion of first-winter birds occurred at sites with lower altitudes. However, we cannot confirm whether this pattern was due to a temperature-associated effect, a side effect associated with additional collinear factors that could also influence age distribution, or a combination of these factors. For example, first-winter birds were in lower body condition and this could force them to settle in warmer places where they would have a higher survival prospect against potential freezing events (Duriez *et al.* 2004). However, altitude is associated with higher rainfall, and Woodcocks benefit from this to hide from predators (Braña *et al.* 2013). Overall, adult Woodcocks might gain a net advantage from wintering at higher altitudes, where they could experience better foraging rates due to lower predation risk or by exploiting open habitats rich in food, such as mountain pastures (Granval & Bouché 1993, Duriez & Ferrand 2005).

This altitudinal effect is difficult to separate from two other variables which were also considered in this work: the zone and the hunting regime. For this reason, they were statistically removed from the models. However, their individual effects when compared with both age and body condition support the initial hypothesis that the proportion of young Woodcocks would be higher in those places subjected to a higher hunting pressure. Álava is located further to the south, at higher altitude, and has a lower hunting pressure than Gipuzkoa. Individual results show there is a higher proportion of adults at Álava and that individuals there have a better body condition. Conversely, in Gipuzkoa there was a higher proportion of first-winter birds and individuals had lower body index with greater hunting pressure. If we take into account the lower survival rate in Gipuzkoa (Prieto *et al.* 2019), as well as the fidelity of Woodcocks to their wintering areas (Duriez *et al.* 2005d, Duriez & Ferrand 2005, Fadat 1993), it is possible that this zone was acting as a sink. Other studies with Woodcocks in France (Péron *et al.* 2011, 2012) support the hypothesis that areas with a high hunting pressure act as sinks but that these subpopulations remain stable because juvenile birds produced in eastern and northern Europe are distributed in wintering areas of high and low survival. In other words, it would not be a source–sink in which the individuals of one patch move to another during the winter, but rather, after migration, juveniles would be distributed in areas which were populated at a lower density due to the hunting pressure. In this way, the probability of a captured bird being an adult would be driven by the differential survival rate. Further studies are needed to clarify this issue; however, scale is likely to be important because winter survival and site fidelity could differ between lower and higher spatial scales.

Foraging strategies in Woodcocks have been reported to vary individually. For instance, if an individual has successfully foraged in forest habitats during the day, it will be less likely to commute to open meadow foraging sites at night, allowing it to minimize the risk of predation (Braña *et al.* 2010, Duriez & Ferrand 2005). According to our top-ranked model, habitat cover did not have a significant effect on the probability of a captured bird being an adult, but it did have an effect on body condition: Woodcocks wintering in places with higher coniferous forest cover were in poorer body condition. We suggest that coniferous forest could be suboptimal due to the reduced availability of earthworms (Duriez & Ferrand 2005). There could, however, be other trade-offs involved with using forest; for example, by occupying forest habitats, distances between feeding and resting areas would be minimal. However, adult Woodcocks are known to perform longer flight distances when commuting between day and night habitats (Guzman *et al.* 2017). Additionally, ground in forested areas tends to be protected from the effects of frost compared to open habitats (De Frenne *et al.* 2019), so could be available for foraging when open habitats are not. Further work is needed but, overall, our results are compatible with the hypotheses that conifer woodland patches constitute suboptimal habitats.

Compared to adults, first-winter birds had relatively lower body masses for their size. The underlying causes explaining this difference are not easy to disentangle. It is usual in birds that first-winter individuals have less fat or muscle than adults, and the Woodcock is not an exception to this rule (Sorace *et al.* 1999). A possible explanation is that first-winter birds are either less efficient at foraging (Duriez *et al.* 2005c) or if, as Perón *et al.* (2012) hypothesized, they tend to occupy areas of lower density, they could be relegated to feeding in poorer habitats. Note also, however, that relatively light-weight birds might be more efficient at rapid take-off, so might be at an advantage when faced with the risk of predation (Kullberg *et al.* 1996), and that first-winter birds tend to be more vulnerable to predation. Adults and first-winter birds may have different optimal fuel loads if they face different probabilities of predation (Boos *et al.* 2005, Braña *et al.* 2010, Duriez *et al.* 2003, 2005c) or differ in their need to cope with periods of food scarcity during spells of cold weather.

Body condition varied substantially with months, with a peak in late winter, presumably in preparation for the spring migration (Figure 3). Studies of satellite-tracked birds showed that Woodcocks wintering in Spain probably make their first important stopovers after leaving their wintering sites in central to northern France (Arizaga *et al.* 2014a). This suggests that, overall, the amount of fuel load gained in the wintering sites was small but still higher than the mean body condition during the rest of winter. The proportion of first-winter birds was higher in late winter, and this may be partly due to adult Woodcocks departing earlier to their breeding areas (Hoodless *et al.* 2020).

In conclusion, we found that the age ratios of Woodcocks wintering in northern Iberia varied between years but tended to include more adults than first-winter birds at higher altitudes but the proportion of adults decreased across the winter. In parallel, adults also showed a higher mean body condition, which might indicate that they are better able to exploit optimal habitat patches and/or cope more successfully with the risk of predation. Habitat cover did not affect age distribution, but body condition was lower in landscapes with high cover of coniferous woodland. The effect of hunting regime on the population structure was not clear, due to the impact of confounding factors, hence further studies would be required to disentangle those effects.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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