Revisiting the habitat selection of a specialist forest bird, *Scolopax rusticola,* during its wintering in the Mediterranean region

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Abstract

Habitat selection is a key mechanism that enables animals to optimize their fitness in response to varying environmental conditions. Differences in habitat selection between geographical areas may imply behavioral adaptations to local environmental conditions. Understanding the potential of adaptation of species along broad geographical ranges is of primary interest to anticipate potential changes in species behavior or distribution range in the context of climate changes.

In this study, we investigated the habitat selection and the daily movement patterns of the Eurasian Woodcock, *Scolopax rusticola*, a bird species that winters across widely varying climatic zones. We tracked 89 individuals wintering in the Mediterranean regions with GPS-VHF transmitters, where climate and habitats conditions differ significantly from the oceanic regions. To assess how they responded to varying habitat and environmental conditions, we collected data across four geographical regions spanning a gradient of Mediterranean climatic influence — ranging from

northern subareas with denser forest and deeper soil to southern subareas characterized by less productive forests, garrigues, and rocky soil.

In wetter regions, woodcocks generally commuted between diurnal resting in forested areas and nocturnal feeding in open habitats, though less frequently than described in studies from other climatic regions. Under drier conditions, they often remained within forest habitats, displaying higher daytime activity and reduced nocturnal movement. Across all subareas, denser forests were selected during the day. The selection for nocturnal forest microhabitats varied by subarea, e.g., denser low vegetation was more strongly selected in southern subareas, while forest habitats highly covered by forest herbs were mostly avoided in northern subareas.

Our findings underscore the remarkable behavioral flexibility of woodcocks, highlighting their potential to adapt to global change. However, the occurrence of escape movements under the driest conditions suggest that this change in behavior and habitat selection may be an early warning sign of the effects of climate change on the wintering areas. Overall, our study emphasizes the need to study the ecology of species across diverse environmental conditions to better understand their habitat requirements and adaptive capacity.

Introduction

Global change is driving species to respond rapidly to new environmental conditions and altered biotic interactions (IPBES, 2019). While empirical niche models predicting the future species distribution and survival underscore the urgency of planning conservation and management strategies to protect biodiversity, they often fall short in capturing species' vulnerability or their potential for adaptation in response to rapid changes. Yet, understanding these processes is essential for developing effective conservation strategies (Bellard et al., 2012; Dawson et al., 2011).

Habitat selection — the disproportionate use of resources or conditions by an animal (Mayor et al., 2009) — is one of the behavioral mechanisms enabling species to cope with global changes and persist in their environment (e.g., Bailey et al., 2019). The study of habitat selection is crucial for understanding the distribution and abundance of species. It also helps to identify priority habitats that should be preserved or

managed to support the persistence of species in a region, providing practical and effective devices for conservation strategies.

Habitat selection occurs at multiple scales, both temporally and spatially (Mayor et al., 2009), sometimes across large and heterogeneous distribution areas that do not necessarily provide optimal conditions for the species. These areas may also be remote or difficult to access, further complicating data collection. Consequently, habitat selection studies often rely on data from a small part of an animal's range and cover only a limited period of the animal's lifespan. The insights gained from such studies and the management recommendations derived from them are therefore rarely transferable to other contexts within the species' range (Beyer et al., 2010) or to other taxa (Yates et al., 2018). This underlines the need for broader, integrative studies that take into account the spatiotemporal variability of habitat selection (Yates et al., 2018).

Habitat selection is a complex process shaped by the interaction between habitat availability and the behavioral motivations of individuals to meet their biological needs (Beyer et al., 2010; Roever et al., 2014). For example, habitat selection may be influenced by factors such as the physiology of the individual (e.g., age, Skórka et al., 2016), access to specific resources (e.g., landfill availability for *Larus fuscus*, Langley et al., 2021) and predation risk (Wasserlauf et al., 2023). This flexibility in habitat selection is particularly critical for species occupying habitats that are spatially heterogeneous or/and subject to temporal changes (e.g., climate and land use changes), as optimal space occupancy decisions may vary according to these variable conditions (Mabille et al., 2012; Merkle et al., 2022; Pearse et al., 2024; Shahsavarzadeh et al., 2023; Verzuh et al., 2021).

Behavioral flexibility is one of the key mechanisms by which animal species can swiftly adapt to a changing environment. However, it remains underexplored and exhibits considerable taxonomic and geographic disparities (Beever et al., 2017; Thurman et al., 2020). Research on behavioral adaptation has often been restricted to limited areas and short time periods or focused on the responses to chronic stimuli (e.g., interannual fluctuation in average temperature, Mazerolle et al., 2011), limiting insights into species' capacity for flexible responses to more extreme environmental changes, such as those involving climate variability (Beever et al., 2017).

Migratory birds often occupy a remarkable diversity of environmental niches throughout their annual cycle, suggesting their behavioral flexibility in optimizing the

use of available resources. Despite this potential adaptability, they often exhibit strong fidelity to their breeding, wintering and stopover sites, likely because such consistency offers advantages such as more efficiency of movement and foraging, as well as better predator avoidance (Piper, 2011). However, when these sites are degraded, migratory birds may prioritize fidelity over relocation to alternative areas, a behavior that can sometimes result in maladaptation (Merkle et al., 2022). This trade-off suggests that species with the highest site fidelity may be particularly vulnerable to the challenges posed by rapid global change (Chan et al., 2023; but see Blackburn & Cresswell, 2016; Wellbrock et al., 2017). To cope with these changes, behavioral compensation within existing habitats could be an important mechanism that enables highly site-faithful species to adapt to local habitat alterations (Merkle et al., 2022). For example, one potential form of behavioral compensation is the adjustment of habitat selection within the occupied site, but few studies have investigated the ability of species to employ these strategies in response to environmental change (Mallet et al., 2023).

The aim of this study is to determine whether a migratory bird occupying a broad geographical wintering range can adjust its habitat selection and behavior along a latitudinal gradient. Specifically, we evaluate the variability in habitat selections of Eurasian Woodcocks wintering in southern France. The ecology of the Eurasian Woodcock has been extensively documented in oceanic and continental regions of Europe (Arizaga et al., 2015; Braña et al., 2010, 2013; Duriez, Ferrand, et al., 2005; Duriez, Fritz, Said, et al., 2005; Guzmán et al., 2017; Hirons & Johnson, 1987; Hoodless & Hirons, 2007; Sládeček et al., 2023). Typically, Eurasian woodcocks commute between open nocturnal foraging sites, where they feed mainly on earthworms, and diurnal forest sectors, where they rest in shelter. This species also winters in the Mediterranean region, which constitutes a significant part of its wintering range (Gonçalves et al., 2019). However, in these regions, observations of woodcocks in open areas at night are less frequent, suggesting a different behavior. To investigate this, we used GPS-VHF devices to track the movements of 89 wintering woodcocks in four subareas with varying degrees of Mediterranean climate influence and winter dryness.

First, we analyzed general movement patterns during wintering to assess woodcock behavior in the different Mediterranean subareas. At the landscape scale (as defined by Mayor et al., 2009), we examined whether woodcocks continued to select forest

habitats during the day and more open habitats at night. At the local scale (as defined by Mayor et al., 2009), we analyzed the habitat structures within the forests selected by woodcocks. Finally, we compared our findings with studies from other climatic regions and discussed their broader implications for the conservation of other taxa in the context of global change.

Material and methods

Study area

Four subareas were selected in distinct sectors of southern France (Figure 1), each of which is characterized by vegetation adapted to dry summers and strong winds (called “le mistral” and “la tramontane”) but is influenced to varying degrees by the Mediterranean climate (Table 1).

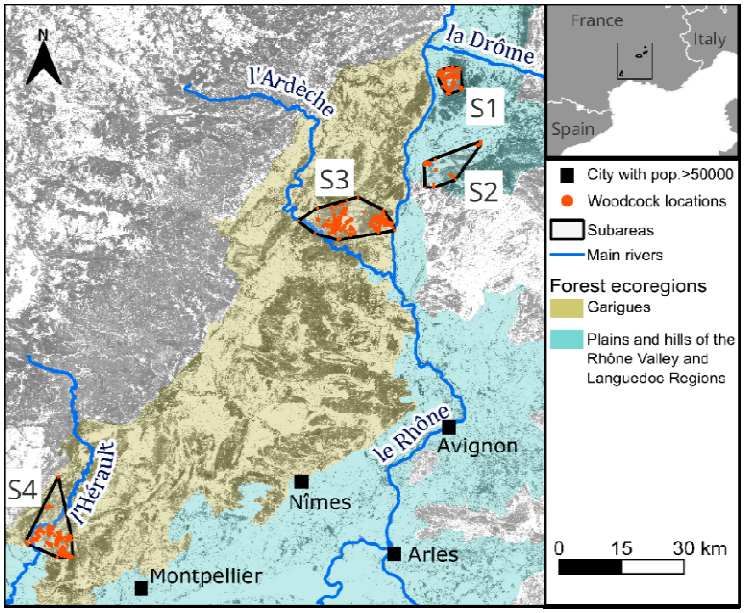

Figure 1: Location of the four subareas and the 14 298 recorded locations of 89 woodcocks in the study area located southern France. Subareas: S1: Central Drôme, S2: Southern Drôme, S3: Ardèche gorges, S4: Hérault gorges. The background of the map is the tree cover density, dark grey corresponding to high level of tree cover density (land.copernicus.eu).

The two Mediterranean subareas of the central Drôme (S1 and S2) belong to the ecoregion of the Plains and Hills of the Rhône Valley and Languedoc Region (see Figure 1). These two subareas are relatively humid due to the influence of the

continental and mountain climate, have moderately deep soils, and the forests are dominated by *Quercus pubescens* (a deciduous tree species). The Ardèche (S3) and Hérault (S4) gorges, located in the southern part of the study area, belong to the same forest ecoregion, the *garrigues* (or shrublands), as defined by the French National Geographic Institute (Figure 1). Their soils are shallower and much rockier than further north, so they drain better. The *garrigues* are characterized by low, slow-growing vegetation. *Quercus ilex* (a sempervirens tree species) is the main tree species. Others are *Pinus halepensis*, *Pinus pinea, Quercus coccifera*, *Erica* spp., *Cistus* spp. and *Arbutus unedo*.

The differences in soil characteristics and climates among subareas lead to different agricultural activities, with orchards and crops predominating in the Drôme subareas, while vineyards predominate in the southern subareas.

Capture and tracking

The study was conducted from winters 2019-20 to 2022-23. For each subarea, Woodcocks were caught over two or three consecutive winters, from late December to early January (Table 1), i.e., a period where the individuals showed high site fidelity (Ferrand et al., 2008). The captures took place mostly at night in fields, vineyards or orchards, where the birds were detected and immobilized using a spotlight (glared) and then caught with a landing net (Gossmann et al., 1988). In the Hérault gorges, half of the birds were caught at night near ponds using vertical nets (misnets) set up before dusk, as woodcocks are sometimes observed visiting these ponds at the beginning of the night to groom themselves. The woodcocks were ringed and aged by plumage characteristics (Clausager, 1973). To determine sex, a feather was collected and analyzed by the CIBIO/CTM laboratory in Portugal (DAN analyses, Griffiths et al., 1998). If the individual weighed more than 300 g and was in good physical and health condition, it was equipped with a VHF-GPS tag (PinPoint VHF 240, Lotek Ltd, ~8 g) using a leg-loop harness made with an elastic rubber cord (1.5 mm EPDM) lined within a silicone sheaths (IN 2.0; OUT 2.6 mm) to limit friction and weighting in total ~ 2 g. Tag plus harness thus weight less than 3% of bird's body mass. The elastic rubber cord sometimes broke too early, few weeks after bird's release, so we use only the silicone tube in 2022-23 in S4 (harness being event

lighter, ~1g). Many of these birds kept the tag for more than one year (half of them being detected with VHF next winter).

Each bird was first located by triangulation and the data (GPS positions) were downloaded every two weeks, from approximately 50 meters to avoid any disturbance (depending on vegetation and topography). The tags were programmed to record four locations every 6 hours, comprising two nocturnal locations (9 pm and 3 am) and two diurnal locations (9 am and 3 pm). In addition to the GPS data, temperature, elevation, and GPS quality metrics (HDPO, eRes, number of satellites used for the location) were recorded. Some tags also recorded activity using accelerometer values (ODBA, Wilson et al., 2006) but this data is not available for all individuals and are thus not considered in this paper. The activity levels and daily distances calculated below (see section Statistical analysis of movement patterns) are however highly correlated.

During the study period, we tagged 97 woodcocks. However, one bird was killed by a hunter a few days after being equipped, another was predated, and for six of them we could not successfully download the GPS data (the birds may have flown out of the study area or been predated, or the tags were defective). Therefore, in this study we analyzed the movements of 89 woodcocks (Table 1).

Table 1: Descriptive data on the four subareas and sample size of woodcocks. N: number of woodcocks fitted with GPS, n: number of GPS locations per woodcock. Temperature and soil wetness were computed based on the daily Safran model (Météo-France) data during the tracking period (Begin date within the subarea to end February). The area of subareas was calculated using the 100% minimum convex hull of woodcock locations.

Subarea	Area (km²)	Year	N	Begin date	**N** Mean [min-max]	Temperature Mean [min-max]	Soil wetness Mean % [min-max]
(S1)	29	2019-2020	8	21st Dec.	187 [61; 261]	7 [-2; 19]	80 [67; 97]
		2020-2021	6	9th Jan.	126 [59; 170]	7 [-5; 18]	80 [72; 83]
		2021-2022	5	25th Dec.	162 [115; 234]	6 [-5; 18]	76 [66; 85]
(S2)	75	2020-2021	4	8th Jan.	172 [161; 187]	6 [-4; 17]	87 [78; 93]
		2021-2022	1	29th Dec.	175	5 [-3; 17]	75 [65; 84]

(S3)	150	2019-2020	7	21st Dec.	168 [62; 273]	7 [-3; 21]	92 [76; 116]
		2020-2021	10	7th Jan.	176 [144; 183]	6 [-5; 17]	91 [84; 97]
		2021-2022	10	29th Dec.	143 [40; 224]	6 [-5; 18]	75 [63; 90]
(S4)	118	2021-2022	20	16th Dec.	141 [42; 207]	8 [-3; 18]	59 [50; 67]
		2022-2023	18	21st Dec.	182 [62; 257]	8 [-4; 20]	45 [40; 51]

Subareas: S1: Central Drôme, S2: Southern Drôme, S3: Ardèche gorges, S4: Hérault gorges

GPS data filtering

Following the manufacturer's instructions, we excluded locations recorded with fewer than four satellites, an HDPO≥10 or an eRes≤0 or ≥0. For isolated locations (i.e., distance >120 meters from other locations, which corresponds to the 75% quartile of nocturnal distance covered by woodcocks with a unique nocturnal feeding place in Duriez, Fritz, Said, et al., (2005), we increased the threshold for satellite to six because woodcock is unexpected to move significant distances during daytime or nighttime without being disturbed. This removed 28 isolated points with doubts about their accuracy, which represented less than 0.2% of the data). Additionally, locations with a significant difference between the recorded elevation and the ground elevation were removed because this may indicate a poor GPS reading (Sládeček et al., 2023). The ground elevation data were estimated using the *elevatr* R package with a resolution of 54 meters (Hollister et al., 2023). We set the threshold at 250 m to account for the large elevation differences in our study area.

Some tags fall off the bird due to harness breakage (those with elastic EPDM 1.5 mm), and some birds have been predated (23, but it is not always possible to tell whether it is predation or harness breakage). To account for cases of detachment or predation, the temperature recorded by the tag dropped suddenly, allowing us to remove all non-informative data. Similarly, we excluded the locations for the birds having been killed by hunters (one bird). Due to these exclusions, two individuals had less than 10 days of tracking data, so we decided to exclude them.

To minimize the influence of capture stress and transmitter attachment on the results, we systematically removed locations recorded within 48 hours of capture from all individuals. However, data collected during the first days of monitoring showed that individuals appeared to recover their normal behavior at varying rates. As a compromise between using a maximum number of data and excluding data that were influenced by capture, we examined the behavior of each bird during the first week

after capture. We removed locations until each bird had stabilized its wintering behavior, i.e., found its first diurnal sector and established a routine commuting flight pattern or not (Duriez, Fritz, Said, et al., 2005). Thus, the final dataset included data from two days after capture for 59 woodcocks, three days for 16 birds, and four to eight days for 14 individuals for which it was more difficult to detect a routine in behavior. All filtering steps and the corresponding sample size are provided in Appendix 1, Figure A1.

In addition, eight woodcocks in the Hérault gorges escaped during the driest period of the study and later returned to their primary wintering area. Data from these escape locations (18 to 74 km away) and points between the primary wintering area and the escape area were excluded from the analysis, resulting in the removal of 413 locations (24% of the total from these eight individuals).

Our study focused on the wintering habitat, so we excluded locations recorded in March and April because woodcocks may change their habits to prepare for migration (Duriez, Fritz, Said, et al., 2005; Tedeschi et al., 2020).

Statistical analysis of movement patterns

To analyze the global movement of woodcock, we computed diurnal and nocturnal distances as well as the distances between diurnal and nocturnal sites (commuting flights). All distances were calculated between pairs of consecutive locations using the “st_distance” function of the *sf* package (Pebesma et al., 2024). Commuting distances were estimated by measuring the distances between consecutive nocturnal and diurnal locations (see Duriez, Fritz, Said, et al., 2005). These include the distances of evening commute flights (occurring between 3 pm and 9 pm) and morning commute flights (occurring between 3 am and 9 am). Nocturnal and diurnal movements were estimated by measuring the distances between consecutive nocturnal locations (9 pm and 3 am) and between consecutive diurnal locations (9 am and 3 pm), respectively. We tested whether distances differed between woodcocks of different age and sex, and whether they varied by subareas and dryness of winter. Winter dryness was assessed using the mean soil wetness index (from the daily Safran-Isba model, Météo-France) as an indicator of food availability, as soil that is too dry may prevent woodcocks from probing the soil to feed on earthworms (Duriez, Ferrand, et al., 2005; Péron et al., 2011). We computed the

mean soil wetness during the tracking period in each subarea for each year and assigned the same value to all woodcocks in the same winter and subarea (Table 1). To identify the main drivers of each pairwise distance, the distances were log-transformed, and since they were normally distributed, we fitted a linear mixed model with the four explanatory variables and the interaction between the subareas and the soil wetness using the *lmerTest* package (Kuznetsova et al., 2017). Confidence intervals were calculated using the *profile* method of the *confint* function of the *lme4* package (Bates et al., 2015). The p-values were produced by the Satterthwaite approximation. The soil wetness variable was scaled. We included individuals as a random intercept to account for repeated measures. The three models were fitted using the following formula, with subarea being a factor with four levels (S1, S2, S3, S4) and *SWI* being the mean soil witness index.

$$\log(distance) \sim age + sex + subarea + SWI + subarea{:}\,SWI + 1|individual$$

Statistical analysis of habitat selection at landscape scale

To analyze the habitat selection of woodcock at the landscape scale, we determined whether woodcock locations were situated in forested or open habitats, using a high-resolution tree cover density (TCD) layer (10m raster from copernicus.eu). The TCD for each location was calculated as the mean value of raster cells within a 30 m radius buffer to account for the accuracy of GPS locations (estimated from data collected by transmitters left in the forest).

To measure the degree of TCD selection by woodcock, we fitted a resource selection function using logistic regression to model use-availability data (Boyce et al., 2002; Fieberg et al., 2021; Northrup et al., 2022). Habitats used by woodcock that were confirmed by GPS locations, were classified as 1, while randomly sampled available habitats were classified as 0 (hereafter named pseudo-absence). Due to the large variation in the number of locations available per woodcock (min= 40; max=273), there was a risk that the model would be more influenced by woodcocks with a higher number of locations. To limit this bias, we added individuals as random intercepts (Gillies et al., 2006). In our study, several woodcocks frequently commuted between areas more than 1 km apart, a behavior that was also observed in other wintering areas (e.g., in Brittany: Duriez, Fritz, Said, et al., 2005; in Spain: Guzmán et al.,

2017) and some reach 5 km. Therefore, for each woodcock, the available habitat was defined as the area within a buffer of 1 km, 3 km or 5 km around all locations and we compared the results according to the size of the buffer considered. For each true location, 100 pseudo-absences were sampled, excluding areas never used by woodcocks, i.e., water bodies or artificial surfaces determined by the Corine Land Cover layer (100m raster from copernicus.eu). Predictor variables included the scaled TCD, a DayNight factor, the four subareas, the scaled soil wetness (Table 1), the sex and the age. The day/night factor for the pseudo-absence data was defined from the nearest available GPS location from each woodcock. The model was fitted using the following formula:

$$used \sim TCD{:}\,DayNight + TCD{:}\,DayNight{:}\,(age + sex + subarea + SWI) + TCD{:}\,DayNight{:}\,subarea{:}\,SWI + 1|individual$$

The response variable *used* take on a value of 0 or 1, DayNight factor have two levels, subarea is a factor of four levels (S1, S2, S3, S4) and *SWI* is the mean soil witness index. We repeated the sampling of the 100 random pseudo-absence locations 10 times for each buffered area (1, 3 and 5 km) to assess the sensitivity of the results to the sampling of these random locations which represented the available habitat. The 10 models were averaged using the default *model.avg* function of the *MuMIn* R package (Bartoń, 2024).

Statistical analysis of forest habitat selection at local scale

To determine the environmental characteristics of habitat selected by woodcock at the local scale, we randomly visited six plots of 25 m x 25 m per woodcock fitted with GPS. Of the six plots, three contained nocturnal locations and three contained diurnal locations. To capture a gradient of selection, for both nocturnal and diurnal plots, we selected one plot containing, before data filtering, less than 3% of raw data locations (low use), one plot containing between 3% and 6% of raw locations (moderate use), and one plot with the maximum number of raw data locations (high use). To avoid disturbing the tracked woodcocks, plots were visited in the winter of the following year, assuming that vegetation would not change significantly within a year, given the slow growth of Mediterranean vegetation. The plot having undergone an obvious

change in vegetation (e.g., local fire or human clearing) were not monitored. In total, we assessed the environmental characteristics of 403 plots in forest habitats.

In the forests, we described the main tree species, the dominant tree height, the proportion of vegetation cover >0.5 meters, the accessibility of the soil (which could be completely covered by rocks), the proportion and distribution of grass and rocks, and the vegetation density at 10 cm, 50 cm, 100 cm and 150 cm (Appendix 1, Figure A2). Vegetation density was determined as the probability of not seeing a mark (a 5 cm long piece of orange tape) at the corresponding height on a 5 cm diameter stick placed approximately in the center of the plot. Observations were made from a distance of 10 meters in eight cardinal directions, with the observer's eyes positioned at the same height as the mark (Appendix 1, Figure A3).

To analyze forest habitat selection, we used a model selection approach to test the selection of environmental variables (Table 2) and their interaction with age, sex, soil wetness, day/night, and the subareas. To limit the number of parameters, we transformed the subarea factor variable into a continuous variable coded 1 (S1), 2 (S2), 3 (S3) and 4 (S4), reflecting the degree of Mediterranean climate influence. We quantified the intensity of plot selection (where environmental variables were described) by summing the number of nocturnal and diurnal locations, respectively, of each woodcock in the corresponding sampled plots and during the studied period (Table 1). An offset in the model controlled the different number of locations per individual (see below). After controlling environmental variables and correlations, we retained six environmental variables (Table 2) as explanatory variables for the model. Due to the strong structuring of the proportion and distribution of forest herbs among the four subareas (Appendix 1, Figure A2), we choose to group these two variables into three classes: forest herbs with scattered distribution, connected patches of forest herbs covering ≥50% or <50% of the plot. Concerning rocks, we choose to retain only the proportion of rocks to describe this environmental variable because there was a redundance of information between the proportion and distribution of rocks, but no evident pattern (Appendix 1, Figure A2). Due to high correlation ($r>0.7$, Spearman's test) between vegetation density of different height and soil wetness, we kept only the vegetation density of 50 cm and 150 cm height (Table 2). After this initial variable selection, only soil wetness and the degree of Mediterranean climate influence were highly correlated ($r=-0.8$, Spearman's test, other variables correlations were below 0.47), so these variables were not used in the same models.

Table 2: Description of the six retained environmental variables measured in plots located in forest.

Variables	Description
Dominant height of tree	Height <4 meters or >4 meters
Cover	Proportion of the ground covered by vegetation of >0.5 meters
Vegetation density 150 cm	Probability of not seeing the mark at 150cm
Vegetation density 50 cm	Probability of not seeing the mark at 50cm
Forest herb distribution	Scattered, connected covering <50% of the ground, connected covering ≥50% of the ground
Proportion of rocks	Proportion of the ground covered by rocks outcrops and loose rocks

Given the number of variables and sample size, we limited the number of competing models to seven in the model selection procedure to avoid overfitting. These included the null model, the model with environmental variables only, the model with environmental variables interacted with the DayNight factor, and four models in which the environmental variables also interacted with the DayNight factor, age, sex, soil wetness or the influence of the Mediterranean gradient. To account for overdispersion in the count data, we used a negative binomial family. Due to the varying numbers of locations among woodcocks, we included an offset in the models corresponding to the total number of forest locations for each woodcock (log-transformed). During the day, woodcocks were always in forest; therefore, the offset for diurnal locations corresponded to the total number of diurnal locations. At night, woodcocks could use either forest or open areas. Nocturnal locations where the mean TCD exceeded 5% within a 12.5 m radius buffer (to match the 25 m x 25 m plot resolution) were considered forest habitat, which includes clear forests typical of Mediterranean landscapes. Models were ranked based on their AICc values, and we selected the model with the lowest AICc value. Models with ΔAICc <2 were considered equivalent. In this case, we selected the most parsimonious model, i.e., the model with the fewest degrees of freedom (Burnham & Anderson, 2004).

We used R 4.4.1 (R Core Team, 2024) for data processing and statistics, and QGIS 3.28.1 (QGIS.org, 2024) and Inscape 1.3.2 (Inkscape Project, 2023) for data visualization.

Results

In this study we analyzed the movements of 89 woodcocks, including 23 1st winter male, 24 1st winter female, 25 adult males and 17 adult females. From the start of the tracking record (Table 1) to the end of February, there were a total of 14 344 locations with an average of 161 locations per woodcock (min= 40; max=273).

Movement patterns

The movement patterns of woodcocks varied greatly depending on the individual and subarea (Table 3, Appendix 1, Figure A4). The sex and age of individuals were not significant factors in explaining the distances between locations (Table 4).

Table 3: Summary of commute, diurnal and nocturnal distances (meters) in each subarea. The mean, the standard deviation (sd) and the maximum (max) of each type of distance were reported. N: number of individuals. n: number of location pairs to calculate the distances

	S1 (N=19)			S2 (N=5)			S3 (N=27)			S4 (N=38)		
	mean	sd	max	**mean**	sd	max	**mean**	Sd	max	**Mean**	sd	max
Commute (n=6223)	**1087**	1329	5345	**909**	1553	6264	**919**	1148	12230	**358**	578	13796
Diurnal (n=2695)	**32**	43	645	**32**	34	258	**40**	33	327	**74**	57	418
Nocturnal (n=3709)	**182**	592	5284	**251**	832	5879	**178**	633	12237	**76**	206	3511

Subareas: S1: Central Drôme, S2: Southern Drôme, S3: Ardèche gorges, S4: Hérault gorges

woodcocks in S4 commuted less frequently between distinct diurnal and nocturnal sectors than woodcocks in other subareas, and commuting distances tended to be shorter (Table 3, Table 4). For instance, the 75% quartile of commuting distances in S4 was <450m, whereas commuting distances in the other subareas almost always exceeded this value (75% quartile of commuting distances in S1 = 1 608 m, S2 = 763 m, S3 = 1383 m). They were also more active during the day, as shown by the diurnal

distances, which were twice as high as those of woodcocks in the other three subareas (Table 3, Table 4).

Woodcocks in S4 were less active at night than woodcocks in S1 (Table 3, Table 4). In S3, woodcocks were also significantly less active than woodcocks in S1 (Table 4), albeit to a much lesser extent (Table 3) and especially during the dry winter (Appendix 1, Figure A4). This pattern was indeed slightly more pronounced with decreasing soil wetness, although it was not significant as *p-values* were below 0.1 but exceeded the 0.05 threshold (Table 4). For example, woodcocks in S3 covered 137 m [94, 180]$_{CI95\%}$ between consecutive locations at night in the drier winter (2021-2022, Table 1), whereas they covered 169 m [118; 219]$_{CI95\%}$ and 215 m [141; 290]$_{CI95\%}$ in the wetter winters of 2019-2020 and 2020-2021 respectively.

Table 4: Estimates and 95% confidence intervals of the linear mixt models explaining commute, diurnal and nocturnal distances. Females and adults were the references levels for the sex and age factors. The subarea S1 was the reference factor level. SWI: soil wetness index.

	Commute			Diurnal			Nocturnal		
	Estimate	CI95%	P	Estimate	CI95%	p	Estimate	CI95%	p
Sex (Male)	0.15	[-0.20; 0.50]	0.420	0.03	[-0.10; 0.16]	0.675	0.00	[-0.18; 0.19]	0.980
Age (1st winter)	-0.17	[-0.54; 0.19]	0.382	0.05	[-0.08; 0.18]	0.498	-0.11	[-0.30; 0.08]	0.280
Intercept (S1)	6.67	[-4.69; 8.66]	<0.001	3.04	[2.26; 3.81]	<0.001	4.11	[3.19; 5.03]	<0.001
Subarea S2	-1.12	[-4.21; 1.96]	0.499	-0.48	[-1.64; 0.68]	0.448	-0.27	[-1.72; 1.18]	0.732
Subarea S3	-1.23	[-3.31; 0.86]	0.275	0.55	[-0.26; 1.37]	0.209	-1.19	[-2.16; -0.21]	0.025
Subarea S4	-1.87	[-3.95; 0.21]	0.097	1.07	[0.26; 1.87]	0.016	-1.16	[-2.16; -0.18]	0.030
SWI (S1)	-1.48	[-5.05; 2.10]	0.443	0.09	[-1.21; 1.37]	0.906	-1.62	[-3.46; 0.23]	0.106
Subarea S2:SWI	1.74	[-2.63; 6.10]	0.461	0.39	[-1.17; 1.95]	0.648	1.27	[-0.98; 3.51]	0.295
Subarea S3:SWI	1.89	[-1.74; 5.52]	0.333	-0.34	[-1.65; 0.97]	0.628	1.73	[-0.16; 3.60]	0.090
Subarea S4:SWI	1.11	[-2.52; 4.74]	0.570	0.05	[-1.26; 1.36]	0.942	1.80	[-0.08; 3.68]	0.077

Subareas: S1: Central Drôme, S2: Southern Drôme, S3: Ardèche gorges, S4: Hérault gorges

Habitat selection at the landscape scale

During the day, woodcocks almost always stayed in tree-covered area (Figure 2). Only 1% of diurnal locations were recorded in open areas (TCD<5%), which included *garrigues* with sparse vegetation, hedgerows, and orchards. The selection of nocturnal habitat at the landscape scale varied between individuals. There were 20 individuals that frequently used open habitats at night, with more than 50% of their nocturnal locations in non-tree-covered areas. In contrast, 69 individuals used less than 50% open areas, including 27 woodcocks that had less than 5% of their locations in non-tree-covered areas. Nevertheless, woodcocks that remained in the

forest at night generally stayed in areas with lower TCD at night than during the day (Appendix 1, Figure A5).

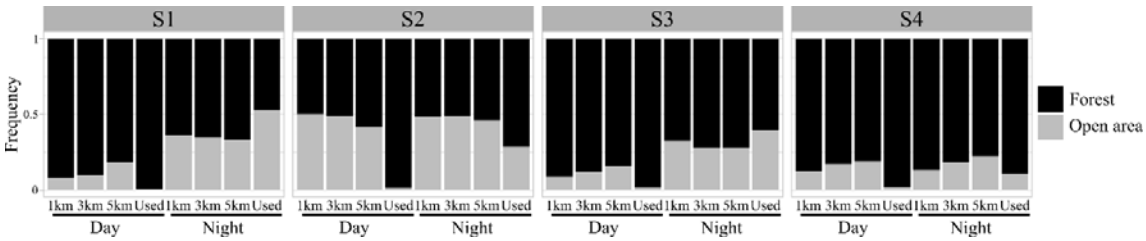

Figure 2: Frequency of open areas and forest in used habitats in comparison with the available habitats, computed with a buffer size of 1 km,3 km and 5 km around used bird's locations. The area was considered as forest if the tree cover density (TCD) was ≥ 5%. Each bar displays the mean habitat composition observed for all individuals pooled within the same subarea during nighttime and daytime. Subareas: S1: Central Drôme, S2: Southern Drôme, S3: Ardèche gorges, S4: Hérault gorges.

Parameter estimates were generally consistent regardless of the size of the buffer used to sample the pseudo-absence around the bird's location (Figure 3, Appendix 2 Table A1).

During the day, woodcocks significantly selected habitats with a higher tree cover density (TCD) than available in the surrounding area. This selection was slightly more pronounced in males and in wetter conditions in S1 and S2. In contrast, in S3 and S4, woodcocks showed a stronger preference for higher TCD under drier conditions than under wetter conditions (Figure 3). During the drier winter in S3 (2021-2022), the mean TCD of pseudo-absence during daytime within the 1-km, 3-km and 5-km buffers was 57%, 55% and 50%, respectively, while the mean TCD of woodcock locations during daytime was 66% (i.e., 16 to 32% higher). In contrast, during the wetter winter in S3 (2019-2020), the mean TCD of pseudo-absence during the day within 1-km, 3-km and 5-km buffers was 58%, 55% and 49%, respectively, and woodcocks selected diurnal habitats with a mean TCD of 57% (i.e., variation of -2% to +16%).

At night, woodcocks selected habitats with a lower TCD (considering available habitats within the 1-km, 3-km and 5-km buffers), except in S2 and in drier winters. Under drier soil conditions, selection for higher TCD was significant in S3 and S4 (Figure 3). 1st winter birds showed slightly stronger selection for lower TCD than

adults (Figure 3), although 1st winter birds were not more likely to commute in open areas at night than adults, i.e., the proportion of nocturnal location in open areas was similar for 1st winter birds and adults (1st winter birds = 28%, adults = 26%). Indeed, adult and 1st winter birds used similar TCD, but TCD in available habitats was lower for adults than for 1st winter birds. For example, in S1, 1st winters birds and adults used habitats at night with a mean TCD of 29% and 26%, respectively, while the mean TCD of pseudo-absence within the 1-km, 3-km and 5-km buffers was 41%, 43% and 43%, and 30%, 36% and 39%, respectively.

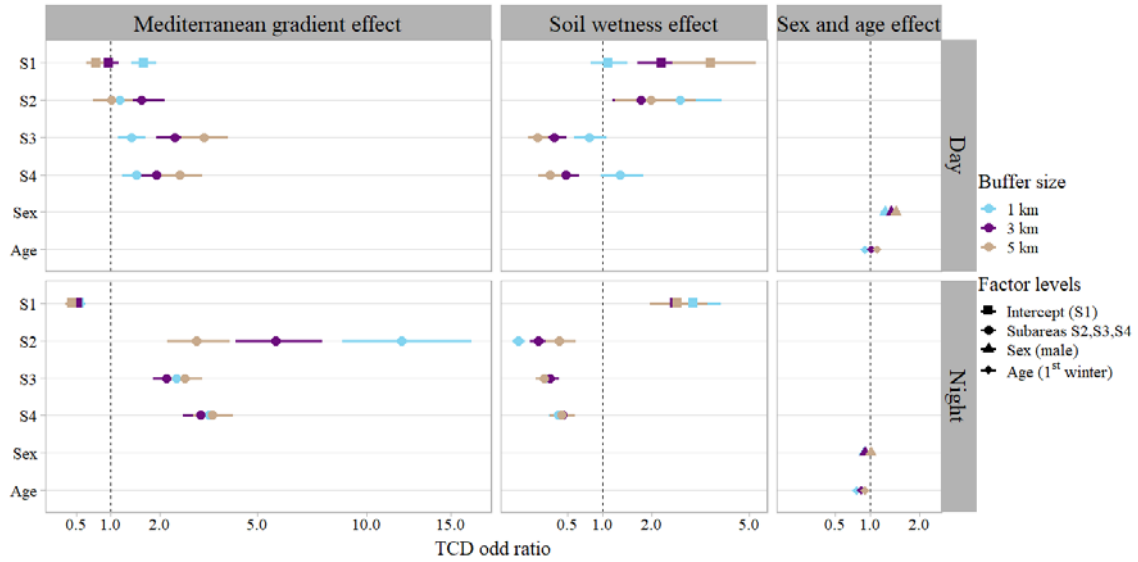

Figure 3: Odd ratios of the tree cover density (TCD) at the landscape scale obtained from the model averaging. The available habitat was computed with a buffer size of 1 km, 3 km and 5 km. The abscise axis was set as square root scale. Females and adults were the references levels for the sex and age factors. TCD: tree cover density, Subareas: S1 (reference factor): Central Drôme, S2: Southern Drôme, S3: Ardèche gorges, S4: Hérault gorges.

Forest habitat selection at the local scale

Selection for specific environmental characteristics within the forest habitat was low, but significant in the selected model (Appendix 2, Table A2) for several environmental characteristics, especially during the night (Figure 4, Figure 5, Appendix 2, Table A3). Within the forest, woodcocks preferred more covered plots during the day, while at night they selected less covered areas and a higher proportion of rocks (Figure 4,

Figure 5). Visited plots were mainly covered with dispersed forest herbs in all subareas, and plots with ≥ 50% forest herb cover were avoided at night, especially in subareas with low degree of Mediterranean climate influence (Figure 4, Figure 5).

The dominant height of trees differed significantly between S1/S2 and S3/S4, as trees in the south are rarely >4m, while they are well above 4 m in the north (Figure 5). The selection for a dominant height of trees >4m increased with the degree of Mediterranean climate influence (Figure 4). This pattern could be explained by specific forest structures or an atypical behavior of a few individuals. Indeed, forests <4m are represented on <10% of the plots in the northern subarea (S1), but the two plots frequently used during the night with a dominant height of trees <4m are highly used, i.e., >20% of the nocturnal locations in the forest, by these two different woodcocks. In the southern subarea (S4), the forests rarely reached a height of 4 m (80% of the plots were <4m), yet three woodcocks very frequently used plots with a dominant height of trees >4m, i.e., >20% of the nocturnal locations in the forest.

Woodcocks mainly visited plots that were moderately occupied by shrubs and low branches (mean vegetation density at 50 cm: 0.41 [0.12; 0.62]$_{75\%IQR}$, mean vegetation density at 150 cm: 0.37 [0.12; 0.50]$_{75\%IQR}$, Figure 3). With increasing degree of Mediterranean climate influence, woodcocks preferred significantly higher vegetation densities at 50 cm and 150 cm (Figure 4).

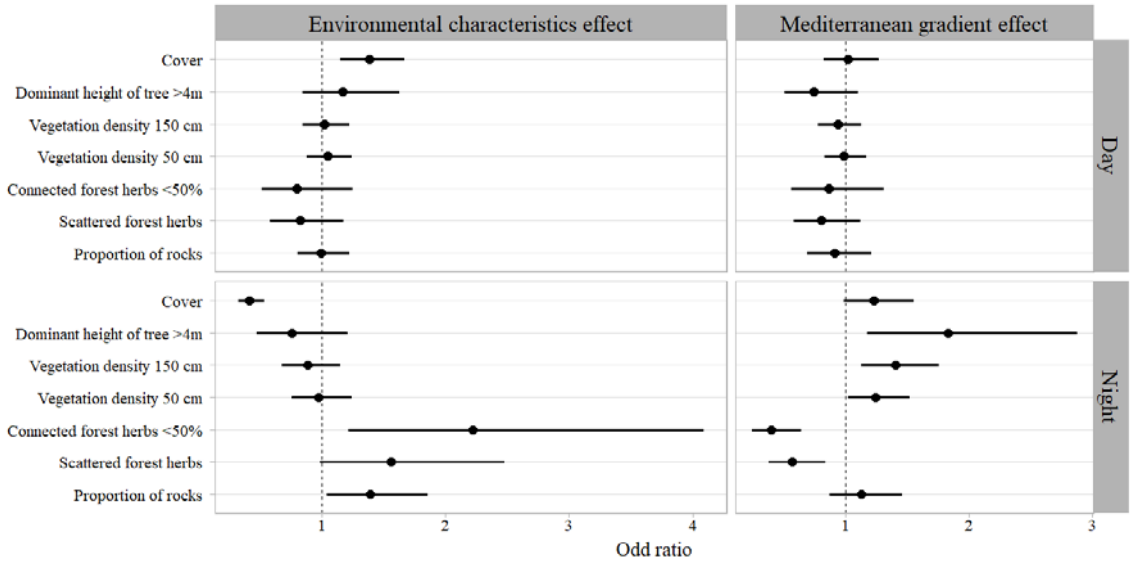

Figure 4: Odd ratios of the environmental characteristics at the local scale obtained from the selected model.

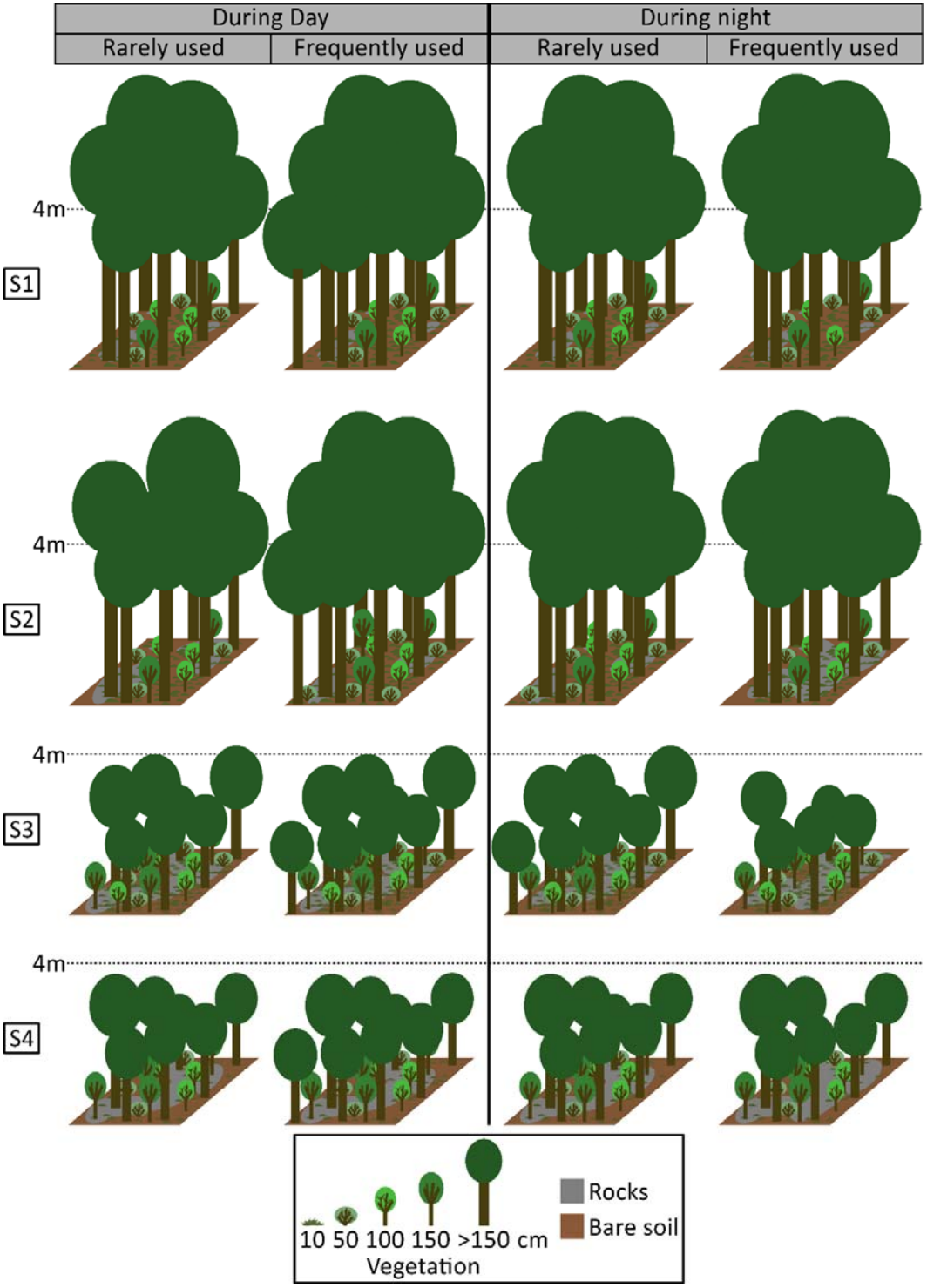
During Day
During night
Rarely used
Frequently used
Rarely used
Frequently used
4m
S1
4m
S2
4m
S3
4m
S4
10 50 100 150 >150 cm
Vegetation
Rocks
Bare soil

Figure 5: Graphical interpretation of local habitats rarely or frequently used by woodcocks. “Rarely used” habitats refer to plots used ≤2 times. The habitat frequently used are plots with at least 5% of diurnal or nocturnal locations of each woodcock. The values used for graphical interpretation are available in Appendix 2, Table A4. Subareas: S1: Central Drôme, S2: Southern Drôme, S3: Ardèche gorges, S4: Hérault gorges.

Discussion

Tracking of wintering woodcocks in the southern part of their geographic range revealed different behaviors and diverse habitat selection strategies that are in marked contrast to observations from other parts of their wintering range. Our results suggest that woodcocks have adjusted their behavior to varying environmental conditions along the Mediterranean climate gradient. This emphasizes the importance of studying species across diverse habitats and under variable climatic conditions to get a complete overview of species-environment relationships.

In the northern parts of the study area, woodcocks frequently commuted between open and forested areas, which is consistent with the results of other studies (along the Atlantic coast : Duriez et al., 2005; Hoodless & Hirons, 2007; northern Spain : Braña et al., 2010), resulting in large differences in the type of habitat selected between day and night. In contrast, woodcocks in southern regions tended to remain in forested areas both day and night. However, when they were in forested areas at night (77% of the nocturnal locations in S3 and S4), they selected less covered environments, similar to woodcocks in Central European forests tracked during the breeding period (Sládeček et al., 2023), and with low grass cover. It is unlikely that this difference in forest habitat selection between day and night was caused by prey availability (Duriez, Ferrand, et al., 2005). Indeed, there is no evidence that habitats with lower forest cover provided more prey than those with high forest cover. Moreover, woodcocks selected higher rock cover at night where stony habitats are available (mainly in S3 and S4), which restricts woodcocks from probing for earthworms, their principal prey (Granval, 1986), or alternative prey (Aradis et al., 2019). Instead, nocturnal forest habitats were probably selected for protection from predators (Braña et al., 2010). Adequate overhead tree and shrub cover may shield

woodcocks from nocturnal avian predators, e.g., the Eurasian eagle-owl, *Bubo bubo* (Obuch, 2024), while relatively low tree cover allows for easier takeoff in response to ground predators. Although the selection of specific microhabitats is too small to provide precise recommendations for the management of the forest microenvironment, our study reveals some patterns. Avoidance of microhabitats that are heavily covered with continuous patches of forest herb at night could be due to the lower visibility, which makes it difficult for birds to detect approaching ground predators. The selection of habitats with higher vegetation density in the nocturnal areas of the southern subareas could indicate that the birds prioritize shelter over terrain traversability at night, which is associated with reduced feeding activity as shown by movement patterns.

Habitat selection and movement patterns were generally consistent between males and females, as well as between adults and 1st winter birds, except for the selection of tree cover density at the landscape scale. During the day, males showed a significantly stronger preference for areas with denser tree cover compared to females. At night, 1st winter birds selected areas with lower tree cover density than adults. 1st winter birds might be compelled to use less favorable wintering areas (e.g., areas with higher predation risk) due to competition or inexperience (Skórka et al., 2016), while the difference between the sexes might be due to small differences in the diet (Aradis et al., 2019). While wintering, there are few dimorphisms or differences in energy requirements between sexes and age classes (Duriez et al., 2004), so few differences in physiological requirements are expected. The sample size for the habitat selection model at the local scale was probably insufficient to detect such small differences.

Although open areas were available within their home range, woodcocks rarely utilized them at night, especially in the three southernmost subareas and in drier winters. The proportion of nocturnal locations in open areas was markedly lower (S1= 53%, S2= 29%, S3 = 40%, S4= 11%) than in observations in oceanic climates in winter, where woodcocks are more frequently found in open areas at night (e.g., in England: 94% (Hoodless & Hirons, 2007), and in Brittany, France: 85% (Duriez, Fritz, Said, et al., 2005). Additionally, the analysis of woodcock movements suggested higher diurnal activity, especially in the warmest subarea, the Hérault gorges. This aligns with the hypothesis proposed by Duriez, Fritz, Binet, et al. (2005) and with the observations of Hoodless & Hirons (2007), which suggest that woodcocks shift to

diurnal activity under milder climatic conditions. First, in milder climates, the costs of thermoregulation are lower, potentially reducing the birds' overall food requirements and decreasing the need to forage in riskier open habitats at night (Duriez, Fritz, Binet, et al., 2005). Measuring the activity rate of woodcocks using accelerometry, together with recording their location, could provide valuable data to analyze both their energy expenditure and the timing and locations of their feeding under varying climatic conditions (Patterson et al., 2019; Wilson et al., 2006). The activity rate of some woodcocks was recorded during this study and confirmed that the birds in S4 were active during the day. However, we chose not to present this data as it only concerns a subset of the total number of woodcocks tagged and would require additional methods and results. Furthermore, forests may provide shelter from strong winds, which are common in Mediterranean regions and can impose significant thermoregulation costs (Duriez et al., 2004). Second, prey species in southern subareas differ from those in northern areas (Aradis et al., 2019; Granval, 1986), and food resources are not necessarily more abundant in open area, reducing the incentive for woodcocks to leave the forest. To confirm the effects of prey diversity and distribution on woodcock behavior, it would be interesting to study both the soil macrofauna in the habitats used and to refine our knowledge of woodcock diet in Mediterranean regions (Aradis et al., 2019; Granval, 1986). Assessing diet and prey availability for woodcocks is labor-intensive and requires specialists who can identify taxa at taxonomic level with sufficient resolution from different species groups. DNA-based methods could help with species identification, but are not able to provide quantitative information (Gongalsky, 2021; Hoenig et al., 2022; Smith et al., 2008). We collected data to compare food availability based on earthworm abundance (Duriez, Ferrand, et al., 2005; Granval, 1986) at random sites and at sites used by some of the GPS transmitter equipped woodcocks. Variability in earthworm abundance was high at both the utilized and randomly selected sites (results not presented in this article), so it was difficult to detect a significant difference with the protocol used. Future protocols in Mediterranean regions should include the identification of additional prey species (e.g., Coleoptera and Diplopoda, Aradis et al., 2019) to achieve greater concordance with woodcock prey in Mediterranean regions. In addition, a significant number of habitats should be included in the food resource study to account for differences in the habitat selection strategy of woodcocks wintering in different climatic regions.

The winter of 2021-2022 was particularly dry, which affected soil moisture and possibly prey availability, which could explain the observed differences in habitat selection across winters. Specifically, woodcocks in the two southern subareas selected areas with higher than usual cover density both during the day and at night when soil wetness decreased. They also appeared to change their diel activity pattern, although additional analyses of activity rates and associated behavior are needed to confirm this change. Forest habitats can help to maintain soil moisture during drier periods in Mediterranean regions (Sardans & Peñuelas, 2013), ensuring an adequate food supply in forests. Furthermore, we recorded eight woodcocks relocating from the southern subarea during the winter, while woodcocks are known to be very faithful to their wintering areas throughout the winter (Ferrand et al., 2008), suggesting that this wintering area did not provide anymore the necessary conditions to meet the bird's needs, probably due to a lack of food availability. In addition, we observed that the proportion of 1st winter birds among the birds hunted or trapped was much lower in dry winters in the Southern subarea (*Réseau Bécasse - Lettre d'information n° 27*, 2018), suggesting that inexperienced 1st winter birds tend to avoid these areas when dry, while adult birds are more likely to return and remain even in such less suitable environmental conditions. One of the eight individuals relocated at the end of winter was recaptured and was in poor body condition (260 g compared to 320 g when first captured). Also, the fact that most of the tagged birds in this southern subarea (30/38 woodcocks) preferred to stay in a known location with poor food availability rather than relocate suggests that relocation comes at a significant cost compared to maintaining site fidelity. This unusual behavior of relocating during winter could serve as an early warning signal of declining habitat suitability for wintering woodcocks in Mediterranean regions. Further research is needed to identify the factors that trigger these relocations. We hypothesize that food availability is the most important factor (Duriez, Ferrand, et al., 2005; Martín et al., 2023). In addition, the relocation of wintering woodcocks may lead to a change in the local population density, which will imply a revision of population management, e.g., identification of relocation areas and local reduction of the number of birds that can be legally harvested during hunting.

The differences in movement and habitat selection strategies between the four Mediterranean subareas probably reflect differences in climate influence, structure and distribution of forests and open habitats, all of which influence the diversity and

density of prey and predators. Forests in the southernmost subareas were used for both shelter and foraging, whereas woodcocks in the northern subareas segregated feeding in open areas and resting in forests. Consequently, habitat management recommendations should be tailored to each subarea. For example, in the central and south Drôme (S1 and S2), maintaining open habitats with high earthworm densities could be beneficial, whereas in the Ardèche and the Hérault gorges, a mosaic of dense and sparse forests could be more advantageous than maintaining open areas. Overall, our results reaffirm the importance of preserving heterogeneous habitats that provide multiple options for species to persist locally under varying conditions (Oliver et al., 2010; Suggitt et al., 2018). Even within a single climatic region (<200 km apart), woodcock ecology varies considerably, highlighting the complexity of defining suitable habitat for a population. Although woodcocks are widespread and a well-studied species, our study reveals important knowledge gaps in their ecology. This highlights the misunderstanding we likely have about a variety of species because they are only studied in a small portion of their temporal and geographic range, even though animal responses to available habitat are often context-dependent (Broekman et al., 2022; Constible et al., 2010). Our results therefore highlight a well-known but often overlooked principle in species-habitat relationships: extrapolating of results beyond the geographic or temporal range of the studied population is precarious. To refine the assessment of habitat suitability, it is essential to study a sufficiently representative variety of environments within the distribution and behavior-specific habitat of a species (Roever et al., 2014).

Conclusion

The study of woodcocks wintering in the Mediterranean region shows the remarkable behavioral flexibility of this species at the climatic edges of its range. However, this flexibility makes it difficult to predict the dynamics of the woodcocks' geographic range under climate change (Oldfather et al., 2020). While behavioral adaptations appear to mitigate some challenges, their long-term effectiveness remains unclear. Our results suggest that behavioral adaptations, such as habitat use modification, are often preferred over relocation to more suitable wintering areas. Nevertheless, we lack data to determine whether these behavioral changes maintain or worsen fitness

benefits. Measuring fitness is crucial to assess whether the persistence of woodcocks in the Mediterranean regions during wintering is at risk in the near future.

The Mediterranean region is probably one of the most vulnerable areas to exceed the climatic conditions tolerable by woodcocks due to ongoing climate change. The effects of climate change in the Mediterranean region, including decreasing precipitation combined with an increase in the frequency and severity of droughts, could have a significant impact on local fauna, but are not yet well understood (Cramer et al., 2018; Ferreira et al., 2022) and present a pressing concern (Moatti & Thiébault, 2016). For instance, drought conditions can induce physiological stress (Dezetter et al., 2022), alter prey communities (Martín et al., 2023) and influence habitat use (Pearse et al., 2024). This underlines the urgent need to study species-specific ecological requirements in Mediterranean ecosystems to predict how climate change might affect species distribution and survival and to develop effective conservation strategies.

Appendices

Supplementary data to this article can be found online in Zenodo (https://doi.org/10.5281/zenodo.15056074).

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