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Habitat selection of the Eurasian woodcock in winter in relation to earthworms availability

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Abstract

The Eurasian woodcock (*Scolopax rusticola*) is a game species experiencing high hunting pressure, long-term modifications of its habitats, and with questions regarding its current conservation status. Winter is a season of highest concentration of birds and hunting pressure but woodcock precise habitat requirements are poorly known. It is crucial to assess threats and to develop sustainable management options for the conservation of woodcock populations. During three consecutive winters, we monitored 65 individual woodcocks fitted with radio-tags in Brittany, France. Habitat selection was analysed using GIS and compositional analysis, in relation to vegetation types, soil variables (humus types) and the abundance of their main prey (earthworms). Woodcocks used different habitats diurnally and nocturnally, generally preferring areas with high earthworm biomass. Diurnal habitat selection in forests was associated with humus type (preference for mulls, rich in earthworms) and dense shrub strata (better protection). Hedges with a high density of trees and shrub were also important habitat. At night, grazed meadows were the preferred habitat, containing five times higher biomass of earthworms compared to cultivated fields. Sustainable management of populations requires protection and management of habitats that incorporates food and cover. Forestry practices should preserve rich humus types and coppices by choosing tree species that ameliorate the soil and soil tilling. Changes in landscapes and intensive agricultural practices are current threats to woodcock populations: destruction of hedges, decrease of permanent grazed meadows, impoverishment of soils fauna biomasses from ploughing and chemical applications. However, woodcocks may benefit from the recent development of set-asides, grass field-borders and simplified farm practices (no-tillage and direct sowing).

Keywords: Compositional analysis; Lumbricidae; Habitat changes; *Scolopax rusticola*; Sustainable management

1. Introduction

In Europe, many wildlife populations associated with traditionally farmed landscapes declined with changes in agricultural policies and farming practices (Pain and

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Pienkowski, 1997; Aebischer et al., 2000). These large scale spatial changes in human land use reduces biodiversity (Robinson and Sutherland, 2002). For example, the changes in agricultural practices caused little bustards (*Tetrax tetrax*) and skylarks (*Alauda arvensis*) to decline drastically in most areas of Europe (Chamberlain et al., 1999; Wolff et al., 2001). Similarly, the Eurasian Woodcock (*Scolopax rusticola* L.) is likely to suffer from agricultural and forestry changes, especially in winter, when it uses habitats that are declining in Europe, especially its nocturnal habitats.

Woodcocks are mostly migratory birds, breeding in Northern and Eastern Europe and wintering in large numbers in western France (Fadat, 1991). Their conservation status is poorly known on breeding grounds. They are atypical among waders, being solitary, living inland, and nocturnal in winter (Piersma et al., 1996). Woodcocks are specialist predators of soil macrofauna: in winter, earthworms constitute about 85% of woodcocks' diurnal energy intake and probably even more at night; the rest being arthropods (insect: larvae and imagoes; myriapods) and slugs (Granval, 1987). In winter, woodcocks use three types of habitats: woodlands and hedges during the day and fields and meadows at night (Cramp and Simmons, 1983; Hirons and Bickford-Smith, 1983; Wilson, 1983; Gossmann et al., 1988; Granval and Bouché, 1993). Although wooded areas are increasing overall in the European Union, it is mostly in the form of conifer plantations (Colombet et al., 1996; Sondag, 2003). The disappearance of hedges is more dramatic. In France, 60% of hedges (740,000 km) was destroyed between 1966 and 1996 (Schmutz et al., 1996), and the trend is similar in the rest of the European Union (Pain and Pienkowski, 1997; Robinson and Sutherland, 2002). The situation for meadows and wet grasslands is similar because most of these habitats have been converted to crop fields since the late 1950s (Pain and Pienkowski, 1997; Wakeham-Dawson and Smith, 2000). Between 1975 and 1995, 12% of the natural meadows and pastures disappeared from nine European countries (Poiret, 2003). The decrease in grazing cattle and the wider use of nitrogen fertilisers enables less fertile land to be farmed, allowing farmers to convert these old meadows into arable fields or woodlands (Potter, 1997; Vickery et al., 2001).

In addition to habitat changes, woodcocks are hunted in most European countries. Hunting occurs mostly in winter, when populations are concentrated. French hunters kill 30–40% of the total harvest in Europe (about 1,200,000 woodcocks) and the interest for woodcock hunting has recently increased (Ferrand and Gossmann, 2000). Currently, there is no clear trend in woodcock populations but the very low survival rates calculated from the French ringing data base is a concern (Tavecchia et al., 2002). These threats lead conservationists to give the Eurasian woodcock a "vulnerable" status in winter (Tucker and Heath, 1994; Heath et al., 2000) although it was recently revised to "stable" (Wetlands International, 2002), following a recommendation of European management plan (Office National de la Chasse, 1998).

In this proposal, management plans must be prepared for sustainable use and conservation of woodcock populations in winter, as well as the establishment of hunting-free reserves. Designing sound management schemes requires improved knowledge of wintering ecology and behaviour of this species. The first step is to understand mechanisms that determine habitat selection in winter. Are woodcocks more constrained by the declines of pastures, hedges, or by the changes in the forestry practices? How does resource availability influence habitat selection? Previous studies of habitat selection used pointing dogs, bag statistics (Imbert, 1988), or habitats prospected during ringing (Ferrand and Gossmann, 1988; Granval and Bouché, 1993) and were biased by the behaviours of the dog, the hunter, or the ringer. Radiotelemetry can provide more rigorous and detailed data on winter habitat selection by woodcock, avoiding human biases (Kenward, 2001). Only three pilot studies, based on three radio-tracked individuals in Ireland (Wilson, 1983), five and eight individuals in Cornwall (Hirons and Bickford-Smith, 1983; Hoodless, 1994) had focused on winter habitat selection in the Eurasian woodcock.

In this paper, we examine diurnal and nocturnal habitat selection in winter, with a large sample of radio-tagged woodcocks. We first investigated habitat selection in a relatively undisturbed landscape, offering a large proportion of traditional habitats, with limited hunting pressure because of the hunting-free reserve status of the main forest complex. Humus type indicates how organic matter (leaf litter) is decomposed and mixed to the mineral fraction of the soil by soil fauna (Frontier and Pichod-Viale, 1993) and therefore gives information about the soil fauna present at each location. Because soil characteristics are probably important to understanding woodcock habitat selection, we also investigated the influence of humus types and earthworms availability on habitat selection by woodcocks.

2. Methods

2.1. Study site

We collected data from December to April, during three consecutive winters (1999–2000, 2000–2001 and 2001–2002, hereafter 2000, 2001 and 2002 winters, respectively). The study was conducted in the Beffou forest (48°30′N, 3°28′W) and the surrounding bocage, located in Brittany, the main wintering region for woodcocks in France (Fadat, 1991). The study area was c. 1800 ha. The topography was composed of small hills and valleys (altitude range: 160–322 m). The bocage was composed of small woods and fields (<1 ha) enclosed by old woody hedges. Woodcock hunting has been prohibited in the Beffou forest since 1995 but is allowed in the surrounding woods and hedges. Winter climate in Brittany is oceanic: rainy and windy with mild temperatures (mean 5 °C).

2.2. Capture methods and radio-tracking

We captured woodcocks at night with a spotlight and a landing net, as they fed in fields surrounding the forest (Gossmann et al., 1988). We captured 37 woodcocks in 2000 (21 adults and 16 yearlings), 48 in 2001 (15 adults and 33 yearlings) and 34 in 2002 (10 adults and 24 yearlings). Birds were aged (adult or yearling) using wing feather characteristics and moult status (Clausager, 1973). Each bird was fitted with a radio-transmitter (TW3, Biotrack®, UK), weighting 7, 9 or 12 g (2–4% of body mass) according to the battery size and presence of activity tiltswitch (Duriez et al., 2004). In winter 2000, radio-tags were secured on the back with a Teflon ribbon two-loop backpack harness (Kenward, 2001). Because seven woodcocks in 2000 were found dead of starvation after the bill caught in the upper loop of the harness, in winters 2001 and 2002, radio-tags were glued on the back and secured with a single-loop wire harness, passing around the belly and behind the wings (McAuley et al., 1993). These seven birds were not included in the rest of analyses.

Each bird was located 2–3 times per week during the day and 2–3 times per week at night in winter 2000, until departure, and 4–5 times per week in the following winters. During the day, we approached woodcocks by circling to 10 m or less. Woodcocks did not leave diurnal sites during the day or only moved by walking (usually <100 m, personal observation). At night, woodcocks were also approached by circling and located to the nearest 50 m because they were more likely to fly, especially during clear moonlight nights. However the type of field was determined each time. During seven nights in 2001, we monitored 23 birds at 2-h interval. 80% of birds stayed the entire night in the field chosen at the beginning of the night and 89% within a radius of 150 m. Subsequently we located birds once per night.

2.3. Analysis of radio-telemetry data

We recorded each location on a habitat map using a Geographic Information System (GIS; ArcView® 3.2, ESRI, Redlands, California, USA). This map was digitised from an aerial photograph taken in 1992 (scale 1/10,000, source: Institut Géographique National). For all analyses, we compared birds with similar numbers of locations. The number of locations varied according to the date of capture of the bird (December to mid January) and the date of end of monitoring (death or migration starting in the last decade of February). We only used birds with at least 7 precise diurnal/nocturnal locations (limit fixed on a natural break in the data set) during the study period which was limited to January and February (excluding December with scarce locations, and the pre-migratory period in March). Therefore, we used a total of 2834 locations concerning 65 woodcocks over the three years: 22 birds in 2000 (15 adults and 7 yearlings), 22 in 2001 (8 adults and 14 yearlings) and 21 in 2002 (7 adults and 14 yearlings). During the entire study period, we only had 3 days of frost in January 2000 and 4 days in February 2001. Because several consecutive days of freezing ground changed the behaviour and habitat selection of woodcocks (Hirons and Bickford-Smith, 1983; Wilson, 1983), we excluded from the analyses the data obtained during the days of frost because accurate analysis of habitat selection was not possible.

2.4. Habitat selection analysis

We analysed habitat selection using compositional analysis (Aitchison, 1986; Aebischer et al., 1993) where the sample size was the number of tagged individuals and radiolocations served to subsample each individual's habitat use. Since we restricted the period of study in two months in order to limit the differences in locations between individuals, we did not weighed the compositional analysis by the number (or the square-root) of radiolocations. In compositional analysis, the proportions of habitats used by each individual were compared to the proportions of habitats available. Analysis of habitat selection on the basis of home ranges was not appropriate in the case of the woodcock, because birds made flights between diurnal and nocturnal habitats. Hence "used" habitats associated with radiolocations were compared with the habitats available in the study area. "Available" habitats were calculated differently according to the type of habitat (see below). Compositional analysis is sensitive to the number of habitats tested and Aebischer et al. (1993) suggest minimising the number of different habitats. Thus we analysed first with all detailed habitats and second with pooled habitats by grouping habitats similar in structure. Compositional analysis allowed a comparison of habitat selection according to individual characteristics (age) and seasonal effects (year of study) using MANOVAs.

2.4.1. Woodlands

The "woodland" habitat included the Beffou forest (612 ha) and surrounding woodlands (c. 130 ha). The amount of available habitat of each type was calculated from the GIS map (Table 1). The stands in the Beffou forest was diverse and contained nine habitat types (Table 1). Deciduous stands (plantations, coppices and

Table 1
Description of the habitat types in the study area, comprising the Beffou forest and the surrounding woods and fields in Brittany, France

Habitat	Code	Area (ha)	%	Description
Woods				
Deciduous plantations	DP	191	*25.2*	2–4 m, 10–15 years, Abundant shrub and grass strata
Coniferous plantations	CP	21	*2.8*	2–4 m, 10–15 years, Abundant shrub and grass strata
Coppices	COP	60	*7.9*	5–10 m, 15–30 years, Abundant shrub and grass strata
Coppices-with-standard	CWS	55	*7.3*	15–30 m, 30–60 years, Abundant shrub and grass strata
Deciduous timber	DT	165	*21.8*	15–30 m, 40–120 years, Shrub and grass strata limited or absent
Mixed timber	MT	71	*9.3*	15–30 m, 40–120 years, Shrub and grass strata limited or absent
Pine timber	PT	14	*1.8*	15–30 m, 40–120 years, Shrub and grass strata limited or absent
Coniferous timber	CT	148	*19.6*	15–30 m, 40–120 years, Shrub and grass strata limited or absent
Wet forest	WF	32	*4.2*	Various height, age and shrub strata, aquatic plants, saturated soil
Total woods		756	*100*	
Fields				
Seed plots	SP	135	*13.0*	Grass or winter wheat, vegetation 5–10 cm, bare soil
Stubbles	ST	176	*17.0*	Corn or wheat (or mustard), bare soil
Young grazed meadows	YGM	47	*4.5*	<3 years, Sowing furrows still visible, regular structure, vegetation <15 cm
Dry grazed meadows	DGM	441	*42.5*	3–10 years, Sowing furrows not visible, irregular structure, vegetation <15 cm
Wet grazed meadows	WGM	58	*5.5*	Permanent, vegetation <15 cm, aquatic plants, saturated soil
Un-grazed meadows	UM	178	*17.5*	No trace of grazing, vegetation >15 cm, dry or saturated soil
Total fields		1035	*100*	
Total study zone		1791		

The area (in hectares) and % (in italics) of each habitat are given as means for each of the three years of study.

timbers) mostly contained Beech (*Fagus sylvatica*) and Oak (*Quercus robur* and *Q. sessiliflora*), and some Ash (*Fraxinus excelsior*). Coniferous stands (plantations and timbers) were mostly Sitka spruce (*Picea sitchensis*), Common silver fir (*Abies alba*), and Grant fir (*A. grandis*). 'Pine timbers' contained Scots pine (*Pinus sylvestris*) and Maritime pine (*Pinus pinaster*). In all habitats types, the shrub strata contained Yew (*Taxus baccata*), Holly (*Ilex aquifolium*), and Hazel (*Corylus avelana*). 'Wet forests' were characterised by Willows (*Salix* sp.), Alders (*Alnus glutinosa*) and Poplars (*Populus* sp.) and by the presence of typical wetland plants (Greater tussock sedges *Carex paniculata* and Common rushes *Juncus conglomeratus*). For the pooled analysis, we kept six habitat types. We kept 'deciduous timbers', 'mixed timbers' and 'wet forests', but other categories were pooled as follows: 'pine timbers' with 'coniferous timbers', 'deciduous plantations' with 'coniferous plantations' and 'coppices' with 'coppices-with-standard'.

Humus types depend on many factors: biotic (vegetation, soil fauna, macrofauna) and abiotic (nature of geologic substrate, slope, hydrology). Consequently, humus could change in short distances (within 10 m) and were very difficult to map. Thus, "available" humus variables were the proportions of each type of humus in a systematic sampling based on a 200 × 200 m grid covering the entire forest and extended to several surrounding woods (182 sampling points). Three types of humus were determined following Jabiol et al. (1995) (mors, characterised by the accumulation of litter resulting from acid substrate and scarcity of earthworms; mulls, characterised by only a thin litter layer resulting from an active and abundant soil fauna; and moders in the intermediate situation) and their proportions are given in Table 2.

Table 2
Proportions of the humus types in woodlands and hedges types in the study area in Brittany, France

Habitat type	Code	Number of points	%
Humus			
Mor		24	*13.2*
Moder		61	*33.5*
Mull		97	*53.3*
Hedges			
Wooded with strip	WS	30	*33.7*
Wooded without strip	W	27	*30.3*
Shrub with strip	SS	13	*14.6*
Shrub without strip	S	10	*11.2*
Relictual	R	9	*10.1*

The proportions of each type were considered as the same in the three years. Humus types were estimated from a systematic sampling of 182 sites and hedges were estimated from a random sampling of 89 sites (see text).

Because shrub cover is probably an important parameter to provide cover for woodcocks during the day, the proportion of shrub cover was estimated with a 10-m tape (decametre) and the presence/absence of a shrub was noted every 0.5 m. We calculated the % shrub cover for each site as the ratio of the number of points with shrubs to the total number of points (20). Shrub cover was estimated from 82 sites randomly chosen from the 182 sites used for the humus availability survey, and on 176 sites used by woodcocks (74 in 2000 and 102 in 2001).

2.4.2. Hedges

Because it was impossible to map the characteristics of every hedge in the study zone (more than 200 km of hedges), we randomly sampled 89 50-m sections of hedges to determine the availability of each type of hedge. Differences in computation of habitat availability between forest habitats and hedges (area vs. proportion) precluded any combination of the two habitats in the same analysis. Hedges were constituted by trees and shrubs growing on an embankment. Hedge had four vegetation strata: (1) the tree strata (7–20 m), mostly beeches and oaks; (2) the shrub strata (1–7 m), mostly Hazels, Gorse (*Ulex europaeus*), Broom (*Cytisus scoparius*); (3) the grass strata (<1 m); (4) an edge strata (lateral strip), which was the lateral extension of the hedge into the meadow (not on the embankment, 0.3–3 m wide) and contained mostly brambles, brackens, grass and branches and sometimes shrubs. For the pooled analysis, hedges were divided into three types: 'wooded hedges' with tree, shrub and grass strata; 'shrub hedges' with shrub and grass strata; and 'relictual hedges' with only the grass strata (Table 2). For the detailed analysis, we also analysed the presence/absence of the lateral shrub strip and we kept five types of hedges: 'wooded with strip', 'wooded without strip', 'shrub with strip', 'shrub without strip' and 'relictual' (always without strip) (Table 2).

2.4.3. Fields

Nocturnal 'field' habitat included c. 1200 land parcels. We calculated area of each type of available habitat from the GIS (Table 1). Meadows represented 70% of the fields and were divided in three types: young meadows, old dry meadows, and permanent wet meadows. A meadow was characterised as 'grazed' if it showed actual or recent grazing with cow dungs, footprints and short vegetation. Tall grass identified 'un-grazed meadows', which included meadows that had not been grazed for the six previous months, meadows for mowing and old wet set-asides. Other fields included 'seed plots' (wheat and grass) and 'stubbles' (corn and wheat). For the detailed analysis, the six habitats were: 'young grazed meadows', 'dry grazed meadows', 'wet grazed meadows', 'un-grazed meadows', 'stubbles' and 'seed plots'. For the pooled analysis, four habitats were kept: 'grazed meadows' (young, dry and wet), 'un-grazed meadows', 'stubbles' and 'seed plots'.

2.5. Earthworm sampling

We sampled earthworms using the standardised method described by Bouché and Gardner (1984) and Bouché and Aliaga (1986). This method is a combination of two complementary extraction techniques: a chemical extraction by 0.4% formalin application to expel active earthworms from the deep soil to the soil surface, and a physical extraction by hand-sorting soil cores (30 × 30 × 10 cm) to collect additional earthworms that did not respond to the chemical extraction. Earthworm sampling was performed in both diurnal and nocturnal sites used by woodcocks (i.e., woodlands and fields) from January to March 2001 and 2002. To select a plot for earthworm sampling, we flushed a radio-tagged woodcock (which usually returned to the same site on the following day), in early morning (around 09:00) in diurnal sites and at dark (around 20:00) in nocturnal sites. We avoided samplings during freezing weather, in very wet soils (no effect of formalin application), in young wheat or grass seed plots (to prevent trampling on crops) and in un-grazed meadows (not used by woodcocks).

Because earthworm populations are highly aggregated in patches (Poier and Richter, 1992; Rossi et al., 1997), earthworm formalin extraction was done on an area of 6 1-m^2 plots (3 1-m^2 spaced 10 m apart in a triangle at the woodcock place and 3 other 1-m^2 plots in a place randomly chosen 50 m apart) to take into consideration the variability of the horizontal distribution of earthworms biomass. Then, within each of the 6 plots, 2 soil cores (30 × 30 × 10 cm) were dug and hand-sorted.

Because some earthworms perform nocturnal migration and emerge from the soil at night (Lee, 1985), earthworm biomass available to woodcocks should be higher at night than during the day. Hence, we slightly modified the sampling procedure for nocturnal habitats to investigate about the earthworm biomass available to woodcocks in the first 10 cm of soil, at night in fields. After flushing a radio-tagged bird, we placed 6 1-m^2 plots similarly as for daytime sampling in forest. One soil core (30 × 30 × 10 cm) was dug in each of the 6 plots to measure the biomass of earthworms present in the first 10 cm of soil. This soil core was kept in a trash bag for future hand sorting in the following afternoon. In the following morning, we moved the plots 1 m away and performed the chemical extraction with formalin to calibrate on the standard procedure of Bouché and Aliaga (1986). The nocturnal sampling procedure and calculations are fully described in Duriez (2003).

For the two extractions (formalin and hand-sorting), the earthworms collected were preserved in 4% formalin prior to identification in the following months. All individuals were identified to species, counted and weighed to the nearest 0.01 g (fresh mass). For each sampling place, the earthworm biomass value was the mean of the 6 square plots and was expressed as kg (fresh weight worm) per hectare. We sampled a total of 38 sites in fields and 43 sites in woodlands.

2.6. Statistical analyses

Means were reported ±1 standard deviation (SD) and were compared with Student's *t*-tests or General linear models (GLM) with Tuckey's post-hoc tests, using SPSS 10.0 software (SPSS, 1999). To avoid pseudo-replication (Hurlbert, 1984), we used General Linear Mixed Models (GLMM) with individual as a random variable to give the same weight to every individual, whatever the number of recordings (Littel et al., 1991). Normality of the variables was assessed with the Kolmogorov–Smirnov tests. We wrote a program for compositional analysis for SPSS. As advised by Aebischer et al. (1993), a randomisation test based on pairwise permutations was performed to obtain an accurate *p*-value in compositional analysis.

3. Results

3.1. Earthworm biomass

In fields, earthworms were more abundant and heavier than in woodlands (number of individuals: 283 ± 199 worms·m^{-2}, $n = 43$ samplings in forest vs. 737 ± 390 worms·m^{-2}, $n = 38$ samplings in fields, $t_{53} = -6.54$, $P < 0.001$; mass per individual worm: 0.085 ± 0.176 g, $n = 12{,}464$ worms in forest vs. 0.397 ± 0.616 g, $n = 28{,}765$ worms in fields; $t_{37{,}585} = -78.87$, $P < 0.001$). Therefore, earthworm biomass was about 12 times higher in nocturnal field habitats than in diurnal woodland habitats (Fig. 1; Table 3). In diurnal woodlands, the earthworm biomass was four times higher in wet forest and coppices, and to a lesser extent in recent plantations than in the older stands (timbers) (Fig. 1; Table 3). Among the humus types, earthworm biomass tended to be higher in mulls than in moders and mors, although it was not significant (Fig. 1; Table 3). In forest, earthworm sampling was slightly influenced by the month, but not by the year nor the air temperature (Table 3).

There was no difference in earthworm biomass and its spatial distribution between the three types of meadows (young, dry and wet), but stubbles had 4–5 times less earthworm biomass than meadows (Fig. 1; Table 3). Earthworm sampling tended to be affected by air temperature, but not by the month or the year (Table 3).

3.2. Diurnal habitat selection in woodlands and hedges

We used 59 of the 65 woodcocks in the analysis of habitat selection in forest because the remaining 6 birds spent most of their time in hedges and were located less than 7 times in forest. Using the detailed classification based on nine wood stands, habitat selection index λ was not highly significant ($P = 0.037$, Table 4). The pooled classification of six forest stands showed preferences ($P < 0.001$). Plantations and coppices were the most preferred habitats by woodcocks and timbers were the least preferred. When considering soil humus types, mulls were preferred to moders and mors (Table 4). For forest stands as well as soil humus, there was no effect of year or age of woodcocks on their habitat selection (all $P > 0.1$). Mulls were present in 78% of plantations, 70% of coppices and 50% of wet forests (Fig. 2). Coniferous stands showed the highest proportion of mors (30%), but they still contained similar high proportion of mulls (30%).

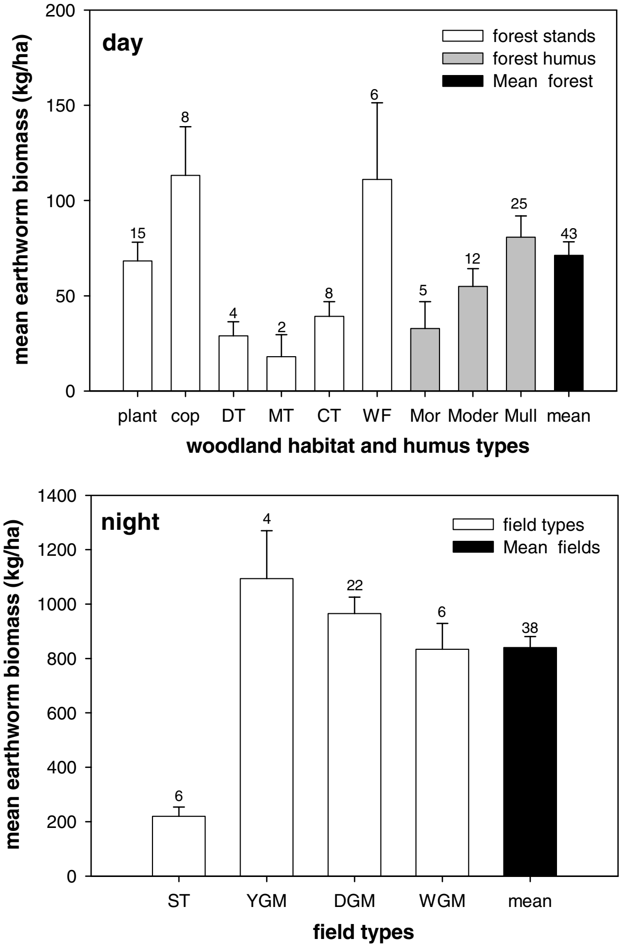

Fig. 1. Earthworm biomasses (mean ± standard error SE in kg/ha) for each diurnal (top) and nocturnal (bottom) habitat type used by woodcocks (see Table 1 for labels). Numbers on the top of bars are the number of sites sampled.

Plantations, coppices and wet forests had more shrub cover than older forest stands (Fig. 3; ANOVA $R^2 = 0.34$, $F_{5,251} = 27.26$, $P < 0.001$), and were richer in earthworms. Percent shrub cover was higher in the 175 sites used by woodcocks compared to the 82 random sites from systematic sampling (75.6 ± 27.2% vs. 57.7 ± 36.3%, respectively; GLMM on 44 individuals: $F_{1,255} = 1040.11$, $P = 0.021$).

Hedges were less frequented than woodlands: only nine individuals that were located more than seven times in hedges were analysed. In the detailed analysis, wooded and shrub hedges with lateral shrub strip were preferred over the other types (Table 4). The pooled analysis showed that wooded hedges were preferred to shrub

Table 3
Factors influencing mean earthworm biomasses in different habitats (fields and forests) and at different levels (stands or humus types)

Analysis	R^2	Factor	*F* test	df	*P*	Interpretation
Woods/fields	0.71	Habitat	175.51	1.73	<0.001	Fields > woods
		Air temperature	3.10	1.73	0.084	Increase with temperature
		Month	1.73	2.73	0.185	
		Year	0.09	1.73	0.767	
Woods stands	0.33	Stand type	3.09	5.31	0.022	Cop = WF = plant > CF = DT > MT
		Month	2.81	2.31	0.076	March > February > January
		Year	0.31	1.31	0.580	
		Air temperature	0.10	1.31	0.921	
Woods humus	0.28	Mull type	2.20	2.34	0.126	Mull > moder > mor
		Month	1.79	2.34	0.182	
		Air temperature	0.60	1.34	0.444	
		Year	0.05	1.34	0.945	
Fields	0.62	Field type	10.01	3.29	<0.001	Meadows > stubbles
		Air temperature	4.08	1.29	0.053	Increase with temperature
		Year	0.83	1.29	0.369	
		Month	0.47	2.29	0.628	

Results are from GLM and the differences among groups were tested with Tuckey's post-hoc tests.

Table 4
Results of compositional analysis on habitat selection in wintering woodcocks

Analysis	Group	*n*	Wilk's λ	*P*	Habitat ranking
Woods stands	Detailed	59	0.736	0.037	DP ≫ COP > CP > WF > PT > CWS > DT > CT > MT
	Pooled	59	0.606	<0.001	Plantation ≫ coppice ≫ WF > coniferous timber > DT > MT
Woods humus	Detailed	59	0.531	<0.001	Mull ≫ moder ≫ mor
Hedges	Detailed	9	0.067	0.004	WS ≫ SS > W > S > R
	Pooled	9	0.002	<0.001	Wooded ≫ shrub > R
Fields	Detailed	63	0.273	<0.001	DGM ≫ ST > WGM > YGM ≫ UM > SP
	Pooled	63	0.290	<0.001	Grazed meadows ≫ ST ≫ UM > SP

Diurnal habitat selection was analysed in woodlands (two levels: stands and humus) and in hedges, while nocturnal habitat selection was analysed in fields. Habitats were ranked from the most preferred to the least preferred. A significant preference between two habitats was indicated by "≫" while a non significant difference was indicated by ">" (Aebischer et al., 1993). The codes used for ranking of habitats are given in Tables 1 and 2. *P* values were given by randomisation.

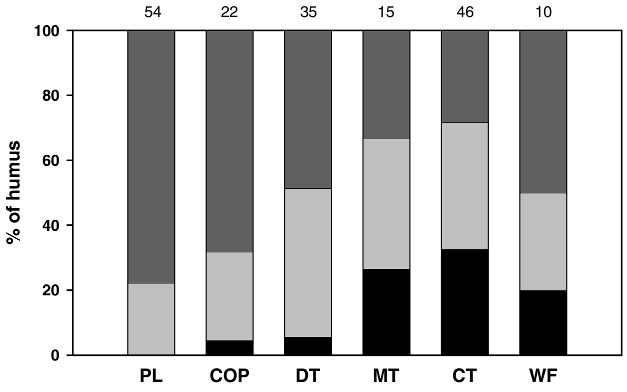

Fig. 2. Proportions of humus types in the six types of woodland habitats in the study area (black = mor, light grey = moder and dark grey = mull). The proportions of humus are calculated on the systematic sampling of 182 sites (the number of sites for each habitat are given above the columns). Legend: PL = plantation; COP = coppices; DT = deciduous timber; MT = mixed timber; CT = coniferous timber; WF = wet forest.

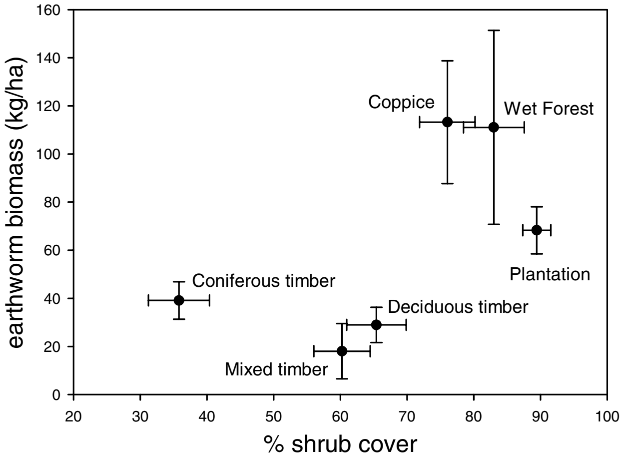

Fig. 3. Relationship between the percentage of shrub cover and earthworm biomass (means ± standard error SE) in six habitat types in woodlands. Values of percentage of shrub cover represent means ± SE of 82 random sites and 175 sites used by woodcocks.

and relictual hedges (Table 4). Year and age effects could not be tested because sample size was too small.

3.3. Nocturnal habitat selection in fields

For the nocturnal habitats analyses, 63 woodcocks were used and 2 were removed because they almost never frequented the fields. We did not consider habitat selection on nights when birds stayed in woodlands, because they were always located in the same habitat used the previous day. Nocturnal habitat selection was different from random use ($P < 0.001$) and dry grazed meadows were preferred, followed by stubbles and wet and young grazed meadows (Table 4). Un-grazed meadows and seed plots were avoided. When the three types of grazed meadows were pooled, they were the most preferred habitats. There was no effect of year or age in any of the analyses (all $P > 0.3$).

4. Discussion

4.1. Diurnal habitat selection

Among the various types of woodlands, outside frost period, woodcocks preferred young forest stands as habitats: plantations, followed by coppices and wet forests. Woodcocks avoided older stands of timber. Plantations and coppices were characterised by an important shrub strata, because more light reached the ground, while the shrub strata was scarce in timbers. The shrub strata provides overhead protection from raptors and increases cover from terrestrial predators. Preference for young habitats in winter was suspected from the hunting statistics (Imbert, 1988; Fadat, 1995) and woodcocks monitored by Wilson (1983) almost exclusively used young (20–30 years old) planted coniferous woodlands. American woodcocks (*Scolopax minor*) also preferred shrublands and young pine plantations in winter, but could adapt to a variety of habitats (Krementz and Pendleton, 1994; Krementz and Jackson, 1999).

The compositional analysis showed that mulls humus soils were preferred to moders and mors. Mulls, slightly richer in earthworms, constituted the majority of humus types in wet forests, coppices and plantations. Coniferous timbers ranked fourth in habitat selection, although they contained few earthworms. Contrary to standard coniferous forest features, rich patches of earthworms also existed in the coniferous timbers of the Beffou forest where one third of soil types were mulls. The presence of alkaline springs in coniferous stands induced these patches of mull and hazel trees. Most of the woodcocks frequenting timbers were in the vicinity of these patches and avoided mor type humus. The habitat types with highest earthworms density were also the richest in shrub cover. Therefore, we conclude that, in winter, woodcocks choose their habitat in woodlands on the basis of rich patches of food (e.g., mull humus) and on the presence of an important shrub strata. However, it is not possible with our dataset to tease apart the relative importance of these features that are probably related to prey accessibility and abundance, and to protection from predators. Insect larvae biomass and availability was not considered in this study. Although generally less abundant in woodland, their occurrence in patches in some sites that were relatively poor in earthworms might explain their selection by woodcocks. However, another study based on the same radio-tagged woodcocks showed that these birds used different foraging strategies depending on earthworm availability in their diurnal site (Duriez et al., 2004). In a site rich in earthworms, they could stay several day or weeks foraging only by day and staying in woodlands at night. But in poorer diurnal sites, they could not meet all their energetic requirements without going to fields at night (where there was always sufficient food). This result suggests that earthworm abundance may drive woodcock habitat selection and behaviour in winter while other invertebrates would play a secondary role.

Wooded hedges were preferred to shrub or relictual hedges. Moreover, hedges with a lateral strip were preferred to hedges without a strip. Because woodcocks mostly use forests for breeding and wintering, their preference for the wider and denser hedges, which resembles a miniature forest habitat, was expected. The shrub and grass strata, as well as a lateral strip, providing conditions for efficient camouflage, certainly play a role for protection against predators. Moreover, the presence of a lateral shrub strip could allow diurnal feeding opportunities. All the hedges of the study area occur on embankments. Our protocol to estimate earthworm biomass was inadequate to sample the hedges, but earthworms likely were limited or scarce because of shallow soil and the current dry soil conditions. In this context, only the strip, extending the hedge on the field (usually a meadow), likely provided food in high quantity.

4.2. Nocturnal habitat selection

Meadows (especially old dry grazed meadows) were preferred by woodcocks over fields of stubble and seed plots, as found in England and Ireland (Hirons and Bickford-Smith, 1983; Wilson, 1983; Hoodless, 1994). Because earthworm biomass (woodcock's main prey item) was four to five times higher in meadows than in the other cultivated fields, this choice probably reflected food availability. Binet (1993) found a tenfold reduction in earthworm biomass when going from a meadow to corn plot in Brittany. In addition to earthworm abundance, insect larvae was found to be an important component of the diet and habitat selection of similar-sized grassland waders (e.g., Golden plovers *Pluvialis apricaria*;

Pearce-Higgins and Yalden, 2003). Although not systematically measured, insects larvae biomass was considerably lower than earthworm biomass in our study site. Because its diet is composed of more than 80% of earthworms in winter (Granval, 1988), we believe that if woodcock habitat selection is driven by prey availability, it should be primarily towards earthworms.

Un-grazed meadows were avoided compared to the three types of grazed meadows. Grazed meadows support more earthworms than hay-meadows (Niçaise, 1996), because cattle manure serves as food for most earthworm species (Lee, 1985; James, 1992). Although we did not sample earthworms in un-grazed meadows, we did a qualitative visual inspection using a spade and found numerous earthworms there. In addition to probable but minor differences in earthworm abundance, we believe that the avoidance of un-grazed meadows is likely the result of the difference in vegetation structure (tall grass compared to short grass in grazed meadows). Ferrand and Gossmann (1995) hypothesised that the short swards of grazed meadows enable easy mobility of woodcocks and better detection of their preys and predators. Indeed predation by mammals (feral cats, foxes and mustelids) mostly happen at night in fields (Duriez et al., 2005). Such selection of short-sward grazed meadows were also found in similar-sized grassland waders like Lapwings *Vanellus vanellus* (Mason and MacDonald, 1999) and Golden plovers (Milsom et al., 1998; Whittingham et al., 2000; Pearce-Higgins and Yalden, 2003), and also passerines (Perkins et al., 2000).

Although grazed meadows were generally preferred, stubbles ranked second. Stubbles were intensively used by some individuals (5 birds used them >50% of their time, and 2 birds >90%). Stubbles probably offered an easier mobility and prey detection. Moreover, stubbles following a first cereal crop, after several years in meadows, may be rich in earthworms because of the high input of organic matter in the soil (ploughed-under grass) (Edwards and Lofty, 1977 in Lee, 1985). In 2000, a first-year wheat stubble was used every night by 2–3 woodcocks. Although the sampling protocol was not applied in 2000, the presence of hundreds of molehills in this field indicates that this plot was probably rich in earthworms, because Moles (*Talpa europaeus*) are specialist predators of earthworms (Granval and Aliaga, 1988). Fields with molehills, used as an indicator of earthworm abundance, were also significantly selected by Golden plovers (Whittingham et al., 2000).

The results of our study suggest that woodcock wintering in Brittany use meadow and stubble habitats, probably in relation to prey availability, which is a combination of sward height and prey abundance. However, it was not feasible to sample variation in prey abundance and sward height at a sufficiently fine resolution to tease these components apart. Because of the large wintering range of the woodcock (from Great-Britain to the Mediterranean coasts), our study should not be generalised too widely, although our conclusions on the influence of the availability of its primary food item should be fairly robust for such a specialised predator. Understanding woodcocks wintering strategies will require additional studies in other parts of the winter range, in similar environments, as well as in completely different habitats, for example British moorlands, pine forests in the French Landes, or Mediterranean shrublands.

4.3. Implications for conservation management

In winter, woodcock populations use a mosaic of habitats, including woodlands and fields. Currently, the few woodcock reserves only prohibit hunting in woodlands. A more effective reserve would not only limit hunting, but should manage the different habitats (diurnal and nocturnal) to provide sufficient food and shelter. The mosaic of habitats (bocage features), once common, is decreasing and/or changing today. Although woodlands are now increasing in the European Union, the recent increase of deciduous plantings follows three decades of massive introduction of coniferous trees in native plain forests. In some parts of their winter range, woodcocks are found in pine timbers because it is the only stand type available. Indeed the use of such habitats by woodcocks seems to be primarily constrained by the presence of mull soils (synonymous of high earthworm activity) and dense shrub strata. Granval and Muys (1992) reviewed that restoration of degraded forest soils is possible. Some tree species (e.g., ashes and alders) have an ameliorating effect on earthworm biomasses (Muys et al., 1992). Moderate liming without tilling can ameliorate humus if earthworms are still present (Granval and Muys, 1992). In uninhabited humus (mor), earthworm introduction could be tried (Huhta, 1979; Brun et al., 1987; Judas et al., 1997). Because beeches and oaks have relatively acid litter that favours moder humus formation (Muys et al., 1992), the plantations in the Beffou forest were limed with natural maërl (Fornasier, personal communication), which probably enhanced earthworm activity and abundance, resulting in mull type humus.

High earthworms biomass in a diurnal habitat is not sufficient to attract woodcocks if there is no cover to protect them. The shrub strata is naturally abundant in the early stages of plantations but forestry practices in France tend to suppress it after 20–30 years to manage for homogenous stands. The old practice of coppices-with-standard, providing firewood, is often abandoned. This practice was probably benefiting not only to woodcocks but also to many other forest species (mammals and birds) by providing cover and food resources (Fuller and Peterken, 1995). The optimal forest habitat for a woodcock is a mosaic of stands of various ages. Management favouring coppices and mull types humus (ameliorating trees, liming) should be used. A simple management technique would be to create numerous small clearings, allowing the natural development of shrub species (hazels, brambles), enhancing earthworm population growth as well as other invertebrates.

The conservation of traditional bocage landscapes with hedges and grazed meadows seems essential for woodcocks. Agricultural changes are of major concern for conservation of woodcock in winter and many bird species in western Europe (Robinson and Sutherland, 2002). Considering the high food potentiality in meadows for woodcocks, the loss of meadows in Europe is of concern. Moreover, changes in farming techniques could lead to damages to quality of meadows (Potter, 1997; Wakeham-Dawson and Smith, 2000; Vickery et al., 2001). Unimproved pastures were preferred to improved pastures by Lapwings and Curlews *Numenius arquata* (Barnett et al., 2004). The spreading of manures and mineral Nitrogen as fertilisers could benefit earthworms if done moderately (Cotton and Curry, 1980) but heavy or high frequencies of applications reduce invertebrate abundance (Zajonc, 1975; Gerard and Hayes, 1979; Curry, 1998). In agrosystems dominated by crops, pesticides also affect earthworms and insect populations (reviewed in Edwards, 1998), which already suffer from deep ploughing (Barnes and Ellis, 1979; Edwards, 1983; Binet, 1993). The recent development of simplified cultural techniques (no-tillage or minimum-tillage and direct sowing) shows that it is possible to yield abundant quality crops as under conventional practices, resulting from auxiliary action of abundant earthworms (Barnes and Ellis, 1979; House and Parmelee, 1985; Baker, 1998). These practices should be encouraged to protect the soil fauna and their associated predators. Set-asides, now imposed by the EU Common Agricultural Policy, are attractive to many bird species (Henderson and Evans, 2000) and would be attractive to woodcocks if they are grazed or mowed in autumn, because earthworm biomasses is higher there than in crops (Bernard et al., 1998). In agricultural landscape offering adverse soil conditions (heavy ploughing, low organic matter content, acid pH), field margins may serve as refuges for earthworms where they can spread out into agricultural fields, thereby keeping up high abundance and biodiversity (Lagerlöf et al., 2002) that favours their use by birds (Vickery et al., 2002).

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