

Wintering behaviour and spatial ecology of Eurasian Woodcock *Scolopax rusticola* in western France

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The spatial ecology of wintering Eurasian Woodcocks *Scolopax rusticola* was investigated to determine whether hunting-free forest reserves offer adequate protection to all individuals. The analysis of movements performed by 65 radiotagged Woodcocks during three consecutive winters in Brittany revealed the existence of three types of individual strategies. During daylight hours, 34% of birds remained in a unique core area (of 1.1 ha) during January and February while 18% used several core areas successively (never came back to a previously used core) and 48% alternated between several core areas (exploratory movements around several core areas visited several times). Alternating diurnal strategies seemed to result from a lower abundance of food (earthworms), whereas this was not the case in the unique core-use strategy. The successive core-use strategy was considered as a subset of the 'unique' strategy, for which birds were forced to change sites because of a lower abundance of food after depletion. During the night, 62% of birds showed alternative core-use whereas 33% lived in a unique core and the 'successive' strategy was almost absent. As food abundance was similar in the night cores used by birds under each strategy, we discuss the reasons for the nocturnal strategies in relation to individual differences in territoriality or the ability to detect predators. Both diurnal and nocturnal strategies led most of the birds to leave the reserve, and the important use of bocage and hedges by day (by 39% of birds) and meadows at night (83% of birds used meadows on more than 70% of nights), around the protected forest, call for their inclusion in management plans around reserves.

The Eurasian Woodcock *Scolopax rusticola* is a largely migratory solitary wader that winters in large numbers in western France (Cramp & Simmons 1983), and uses a mosaic of habitats in winter: woodlands (especially young deciduous stands) and hedges during the day and meadows at night (Cramp & Simmons 1983, Hirons & Bickford-Smith 1983, Wilson 1983, Gossmann *et al.* 1988, Granval & Bouché 1993). The conservation status of the Eurasian Woodcock has been the subject of several recent

investigations (Tucker & Heath 1994, Heath *et al.* 2000, Tavecchia *et al.* 2002). Although the population is now considered stable (Wetlands International 2002), there is a growing need to develop management measures for the sustainable 'use' of this species. In addition to the common concern associated with hunting in many European countries (Ferrand & Gossmann 2000, Ferrand & Gossmann 2001), Woodcock populations are threatened by changes in the landscape and by intensive agricultural practices (destruction of hedges, loss of permanent grazed meadows, impoverishment of soil fauna biomasses due to increased use of chemicals). These

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sources of threat have rarely been considered when designing management plans for the Woodcock, which mostly focus on limiting numbers killed by hunters.

Creating reserves for Woodcocks is another possible conservation measure that has rarely been considered; this would address the threats associated with both hunting and landscape change. However, to be effective, a reserve must include all the habitats used by the species concerned as well as supporting a substantial population (Hirons *et al.* 1995). Currently, the few reserves created for Woodcocks only protect important forest areas, although the species also uses small woods and hedges, where they may be subject to hunting (Duriez 2003). Moreover, in winter, half of the time budget of this atypical wader is spent foraging in agricultural fields and meadows at night. These sites are usually not managed for Woodcocks. The effectiveness of reserves depends on the patterns of movement within and between the various habitats. Quantifying these movements is necessary to identify key sectors in the landscape for further conservation schemes.

In a game species such as the Woodcock, it appears crucial to investigate in detail the spatial use of wintering quarters at the individual level. For instance, in the Eurasian Oystercatcher *Haematopus ostralegus*, the most efficient foragers stay in the more secure and richer tidal flats, while other individuals have to use fields where the predation risk is higher (Caldow *et al.* 1999). These individual differences in foraging strategies, spatial use and fitness imply that changes in the various habitats available can have different effects on population dynamics. Behaviour and spatial use by Woodcocks in winter remain poorly known. Radiotelemetry could reveal different behavioural strategies according to individual characteristics (such as age, sex or body condition) that might have important consequences for conservation (McGregor & Peake 1998, Kenward 2001). Yet only three pilot studies, based on three radiotagged Woodcocks in Ireland (Wilson 1983) and five and eight birds in Cornwall (Hirons & Bickford-Smith 1983, Hoodless 1994, respectively), have investigated Woodcock winter spatial behaviour. We describe diurnal and nocturnal movements in winter in 65 radiotagged individuals monitored in a relatively undisturbed landscape, encompassing a range of 'traditional' habitats, and with limited hunting due to the reserve status of the main forest complex. In a conservation context, we particularly wanted to answer the following questions:

1 Are there individual strategies of spatial use in the winter quarters? If so, what are the factors responsible for these strategies?

2 Are some categories of individuals likely to suffer reduced survival rates as a result of their winter behaviour?

We explore several sources of variation in individual strategies such as age, fat reserve and morphometry. We also analysed movements in relation to soil type and earthworm biomass, as these factors have been related to habitat selection in previous studies (Duriez 2003, Duriez *et al.* 2005b).

METHODS

Study site

We collected data from December to April, during three consecutive winters (1999/2000, 2000/01 and 2001/02, 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, a typical landscape in western France, consists of small woods (< 1 ha) and fields (mean 0.8 ha, range 0.07–10 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, windy and mild (mean temperature 5 °C).

Capture methods and radiotracking

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 65 Woodcocks over the three years: 22 in 2000 (15 adults and seven yearlings), 22 in 2001 (eight adults and 14 yearlings) and 21 in 2002 (seven adults and 14 yearlings). Birds were fitted with a ring and aged (adult or yearling) using wing feather details and moult status (Clausager 1973, Fadat 1995). Tarsus and bill lengths were measured (to the nearest 0.1 mm) with callipers and folded wing length was measured with a ruler. In 2002, we also measured skull and ulna lengths with callipers. Body mass was measured to the nearest gram with a Pesola spring balance. To estimate the total mass of lipids, we used the following predictive equation ($R^2 = 0.703$, $P <$

0.001) based on dissections and fat extractions of 22 Woodcocks in winter (Boos 2000):

$$\text{Total mass of lipids (in g)} = 0.548*(\text{BM}) - 1.932*(\text{SL}) - 5.213*(\text{UL}) + 336.40. \quad (1)$$

where BM is body mass (g), SL is skull length (mm) and UL is ulna length (mm).

Each bird was fitted with a radio-transmitter (TW3, Biotrack®, UK), weighing 7, 9 or 12 g (2–4% of body mass) according to the battery size and presence of an activity tiltswitch (Duriez *et al.* 2005c). Radio-tags were secured on the back with a Teflon ribbon two-loop backpack harness (Kenward 2001) in winter 2000, and glued on the back and secured with a single-loop wire harness, passing around the belly and behind the wings (McAuley *et al.* 1993) in winters 2001 and 2002.

Each bird was located two or three times per week during the day and two or three times per week at night in winter 2000, until departure. The number of radiolocations increased in the following winters up to four or five times per week by day and four or five times at night. During the day, we approached Woodcocks by circling to 10 m or less. Woodcocks did not leave diurnal sites during the day (except when disturbed) or only moved by walking (usually < 100 m, our personal observations). At night, Woodcocks were also approached by circling and located to the nearest 50 m because they were more likely to fly. During seven nights in 2001, we monitored 23 birds at 2-h intervals: 80% stayed the entire night in the field chosen at the beginning of the night and 89% of these remained within a radius of 150 m. Subsequently we located birds once per night.

Analysis of radiotelemetry data

We recorded each location on a habitat map using a Geographic Information System (GIS; ArcView® 3.2, ESRI, Redlands, CA, USA). This map was digitized from an aerial photograph taken in 1992 (scale 1 : 10 000, source: Institut Géographique National). For all analyses, we needed to compare birds with similar numbers of locations, which varied according to the date of capture of the bird (December to mid January) and the date on which monitoring ended (death or migration starting in the last 10 days of February). The study period was thus limited to January and February. During this period, the mean number of locations for each bird was 24 (range 10–36) by day and 17 (range 5–29) at night in fields. As several consecutive

days of freezing ground changed the behaviour and habitat selection of Woodcocks (Hirons & Bickford-Smith 1983, Wilson 1983), we excluded from the analyses the data obtained during the days of frost because accurate analysis of movements was not possible (only 3 days in 2000 and 4 days in 2001).

At twilight, most Woodcocks leave their diurnal sites to reach a nocturnal site by a flight hereafter called 'commuting flight'. The commuting flight index, calculated for each bird, is defined as the number of nights spent in fields as opposed to forest divided by the total number of locations at night. The study of movements was mostly based on the distances between locations, calculated using the Animal Movement extension in ArcView (Hooge *et al.* 1999).

Habitat use

Most studies of animal movements and habitat selection use home ranges, defined as the areas repeatedly traversed by individuals (Kenward 2001). This definition assumes that this area can be sampled during the movements of the individual. Woodcocks need to probe or inspect the soil visually to test food (earthworms) availability (Rabe *et al.* 1983). Our experience showed that Woodcocks usually move less than 100 m in the same day. However, the average maximum distance between two consecutive locations was 615 m (range 19–2425 m) by day. Thus, computed home ranges would include areas only flown over by birds and might comprise habitats unlikely to be used by the bird (e.g. fields by day), in the case of fragmented habitat such as the bocage (White & Garrott 1990). Another reason to consider home ranges in habitat selection analyses is the inequality of the available habitats among individuals (Kenward 2001). The potential distances covered between two consecutive days in this case mean that all the forest should be considered as available to every individual. In conclusion, we believe that analysis on the basis of radiolocations rather than home range was more appropriate for Woodcocks in winter.

We analysed habitat use by 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. The 'used' habitats were the proportions of locations in each habitat type during the 2 months of study. Habitats 'available' within the study area were calculated differently according to the type of habitat (see below). Compositional analysis allowed a comparison of habitat use according

to individual movement characteristics (core-use strategy, see later) using MANOVAS.

The 'woodland' habitat comprised six habitat types and their available areas were calculated from the GIS map. Timbers were characterized by old trees (40–120 years old; 15–30 m tall) and limited shrub and grass layers. Younger stands (coppices: 15–30 years old and 3–10 m tall; plantations: 10–15 years old and 2–4 m tall) were characterized by dense shrub and grass layers. Deciduous stands mostly contained Beech *Fagus sylvatica* and Pedunculate Oak *Quercus robur*. Coniferous stands were mostly Sitka Spruce *Picea sitchensis*, Common Silver Fir *Abies alba*, Scots Pine *Pinus sylvestris* and Maritime Pine *Pinus pinaster*. Mixed timbers were a mix of species from the last two groups. Deciduous and coniferous plantations were pooled for analysis as a single 'plantation' habitat. 'Wet forests' were characterized by willows *Salix* sp., Alder *Alnus glutinosa* and poplars *Populus* sp., and by the presence of waterlogged soil and typical wetland plants (Greater Tussock Sedge *Carex paniculata* and Common Rush *Juncus conglomeratus*).

The nocturnal 'field' habitat comprised six habitat types. Meadows represented 70% of the fields and were divided into three types: young dry meadows (< 2 years old), old dry meadows (> 2 years old) and permanent wet meadows (characterized by typical wetland plants such as Greater Tussock Sedge and Common Rush). A meadow was characterized as 'grazed' if it showed actual or recent grazing (cow dung, hoofprints and short vegetation). Tall grass identified 'ungrazed meadows', which included meadows ungrazed for the previous 6 months, meadows used for mowing and old wet set-asides. Other fields included 'sown plots' (wheat and grass) and 'stubbles' (maize and wheat).

Attributing each core (see Results for definition) to a forest stand or field type was difficult when several habitats were pooled. In such cases, we used the habitat in which most locations occurred. To analyse the use of particular habitats such as bocage or hedges by day or fields at night, we used the percentage of locations of each bird in this habitat.

Earthworm biomass

We sampled earthworms using the standardized method described by Bouché and Gardner (1984). This method is a combination of both a chemical and a physical 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 earth-

worm sampling, we flushed a radiotagged Woodcock or went to a site previously used, in early morning (around 09:00 h) in diurnal sites and at dark (around 20:00 h) in nocturnal sites. We avoided samplings during freezing weather and in very wet soils because in these conditions formalin application has no effect. Because earthworm populations are highly aggregated in patches (Poier & Richter 1992, Rossi *et al.* 1997), earthworm formalin extraction was performed on an area of six 1-m² plots to take into consideration the variability of the horizontal distribution of earthworms. Then, within each of the six plots, two 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 modified the sampling procedure slightly for nocturnal habitats to investigate the earthworm biomass available to Woodcocks in the first 10 cm of soil there. After flushing a radiotagged bird, we placed six 1-m² plots similarly as for daytime sampling in forest. One soil core (30 × 30 × 10 cm) was dug in each of the six 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 the standard procedure of Bouché and Gardner (1984). The nocturnal sampling procedure and calculations are described fully in Duriez, O., Binet, F. & Ferrand, Y. (in press).

We preserved the earthworms collected in 4% formalin prior to identification in the following months. All individuals were identified to species level, counted and weighed to the nearest 0.01 g (fresh mass). For each sampling location, the earthworm biomass value was the mean of the six square plots and was expressed as kg (fresh weight worm)/ha.

In total we sampled 40 sites in woodlands and 33 sites in fields. In the non-sampled sites, we estimated earthworm biomass on the basis of vegetation, humus or cultivation, according to mean values in control sites. The value of earthworm biomass for a given area was calculated as the mean of all the locations in that area (e.g. if the area defined contained eight locations in a plantation containing 70 kg/ha and two locations in a nearby coniferous timber containing 30 kg/ha, the earthworm value for the area was the mean of these ten locations, i.e. 62 kg/ha). The mean earthworm biomass in diurnal sites for each Woodcock during the study period was calculated as the sum

of the mean biomasses of each area multiplied by the proportions of total monitoring time spent there.

Statistical analyses

When variables were normally distributed, means were compared by means of Student’s *t*-tests or General Linear Models (GLM) with Tukey’s post-hoc tests, using SPSS 10.0 software (SPSS 1999). Otherwise, median values were compared with non-parametric Mann–Whitney tests or Kruskal–Wallis tests. To avoid pseudoreplication (Hurlbert 1984), we used General Linear Mixed Models (GLMM) with individual as a random variable to take into account repeated measurements on individuals and intra-individual variance (Littel *et al.* 1991). In the case of Poisson distributions in the dataset, we performed GLMM with individual × age as a random variable with the Glimmix macro (GLMM Glimmix) in SAS v. 8 (SAS Institute 2000). Correlations between movement parameters and individual characteristics were performed with non-parametric

Spearman rank correlations. A script for compositional analysis was written for SPSS by E. Corda. As advised by Aebischer *et al.* (1993), a randomization test based on pairwise permutations was performed to obtain an accurate *P*-value in compositional analysis. Means reported below are given ± 1 sd.

RESULTS

Individual strategies of space use

Among the 65 Woodcocks radiotagged over the three years, none disappeared from the study area; the fidelity to the wintering quarters was very high. However, the pattern of site use by Woodcocks varied greatly among individuals, which appeared to be distributed along a continuum of strategies, from the very sedentary to the very mobile. We used the distributions of distances between consecutive locations, by day and at night, to categorize these different strategies. We attributed each individual to a single category of strategy and compared them (Fig. 1). The

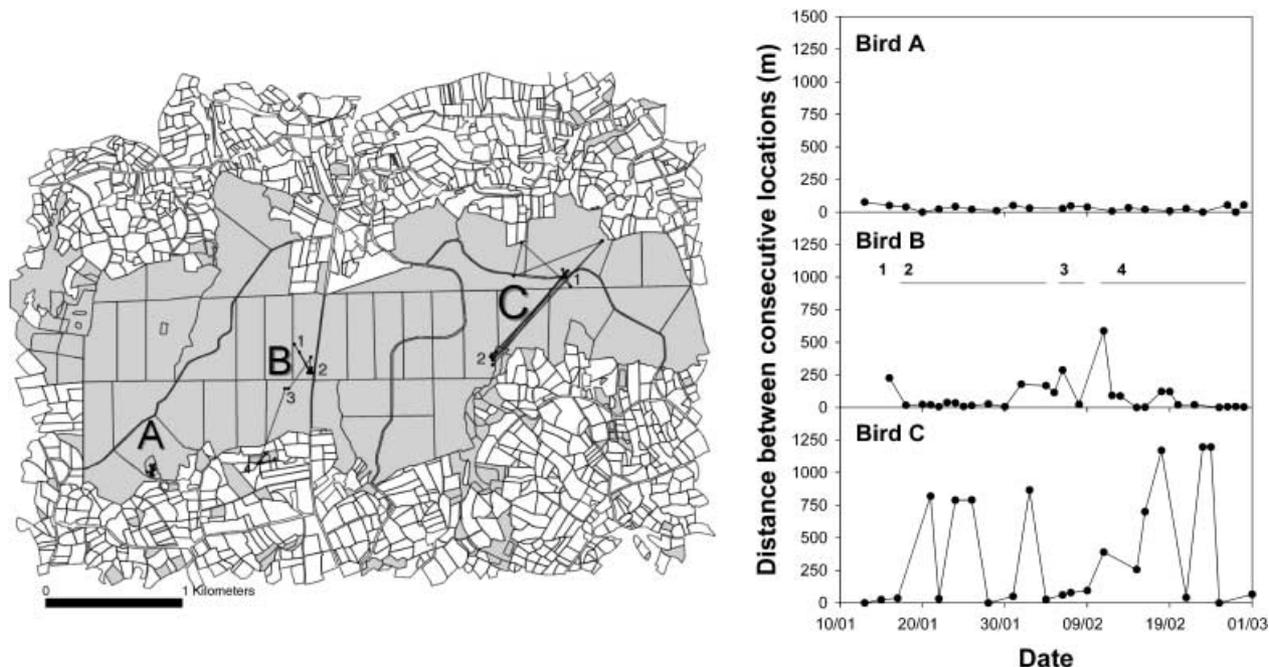


Figure 1. Examples of site use by three individuals by day (similar examples can be found at night). On the map on the left, grey plots are woodlands and white plots are fields. The lines show the movements between consecutive diurnal locations. The graphs on the right represent the variations in dates of the distances between consecutive diurnal locations (in m). Interpretation: Bird A used a ‘unique’ site by day: for ‘unique’ birds, the distance rarely exceeded 50 m. Bird B used four sites successively (the order of sites is indicated on the map and the numbers and horizontal lines on the graph indicate the duration of stay in each site): in ‘successive’ birds, the distances were low except when birds changed sites. Bird C used two main sites (numbers on map) and three temporary sites, alternately: in alternative birds, distances were often large and irregular.

mean distances between consecutive locations per individual ranged from 9 to 347 m by day and from 30 to 616 m at night. If the bird never changed site during the winter, the site use was classed as 'unique'. In this case, the distances between locations were uniformly low (e.g. bird A, Fig. 1). If the bird was faithful but, when changing site, never came back to a previously used site, the site use was termed 'successive'. In this case, the distances between locations were generally low, except for several peaks when the bird was changing site (e.g. bird B, Fig. 1). If the bird commuted regularly or irregularly between several sites, the site use was termed 'alternative' and the distances between consecutive locations were irregular, with several peaks (e.g. bird C, Fig. 1). The distributions of distances by day (median and 75% quartile of distances) were similar in 'unique' and 'successive' birds and higher in 'alternative' birds (Table 1). Hence, we hypothesized that successive use was derived from 'unique' use, related to habitat of lower quality that would not allow the bird to stay in the same place throughout the winter.

To compare movement patterns in relation to habitats and food availability for the three strategies, it was necessary to define a minimum spatial unit used by birds to be compared. We have chosen to use the 'unique' strategy as a reference, because birds of this strategy were able to winter in a unique and restricted area, which we assumed to be of high quality. This gave us the minimum reference area: because 75% of all diurnal locations were situated within 60 m of one another (Table 1), we therefore set the minimum spatial unit (called 'core') as a disc of 60 m radius (*c.* 1.13 ha). At night in fields, we followed the same procedure to define 'cores' as a disc of 120 m radius (*c.* 4.5 ha) from the characteristics of distances between locations of 'unique' strategy (Table 1). The changing core index, separately defined by day and at night, was the number of changes divided by the total number of locations.

Diurnal movements

Thirty-one birds (48%) had an 'alternative' core use, compared with 22 birds (34%) with 'unique' core use and only 12 (18%) with 'successive' core use. The frequencies of diurnal strategies did not differ between years ($\chi^2_4 = 4.36$, $n = 65$, $P = 0.85$). 'Alternative' birds frequented more cores than 'successive' birds (Fig. 2a).

By day, these three strategies were not related to habitat characteristics because forest stands were not selected differently among strategies (Table 2). 'Successive' birds stayed longer than 'alternatives' at one site (Fig. 2b). The duration of stay in the same diurnal core was influenced by the age of the individual (adults < yearlings) and, to a lesser extent, by the mean earthworm biomass, but not by the habitat (Table 3). The distances between consecutive diurnal cores used by a bird varied from 70 m to 2.43 km (Fig. 3) and were higher in 'successive' birds compared with 'alternatives', but were not influenced by the age, the duration of stay, the habitat or the mean biomass of earthworms (Table 3).

The frequencies of diurnal strategies did not differ significantly between age classes ($\chi^2_2 = 4.17$, $n = 65$, $P = 0.12$) and the changing core index was not significantly different between ages (median 0.27 in adults and 0.10 in yearlings; Mann–Whitney $U = 419.5$, $n = 65$, $P = 0.157$). Diurnal core use was not correlated with any morphometric variable (ANOVA on tarsus, bill and wing length, body mass at ringing, all $P > 0.05$, $n = 65$). However, the estimated lipid mass at ringing was 14 g lower in 'unique' birds than in 'alternative' birds (Fig. 4).

Only two birds (one 'unique' and one 'successive') out of 34 had their diurnal core visited by another individual at the same time, whereas this occurred for six out of 31 'alternative' birds ($\chi^2_1 = 2.73$, $P = 0.099$, $n = 65$ with 'unique' and 'successive' birds pooled). In these eight birds, the proportion of locations shared with conspecifics was 17% (± 14 sd, range 4–36%).

Table 1. Distributions of distances between consecutive locations in the three strategies of site use, by day and at night. Parameters measured for each strategy were the median (in m) and the 75% quartile (in m). Several individuals were pooled in each strategy (N ind.) and the number of distances analysed are given (N dist.).

Strategy	Day				Night			
	Median	75% quart.	N ind.	N dist.	Median	75% quart.	N ind.	N dist.
Unique	28	57	22	505	70	123	21	338
Successive	28	77	12	257	136	599	3	25
Alternative	57	154	31	723	135	277	39	648

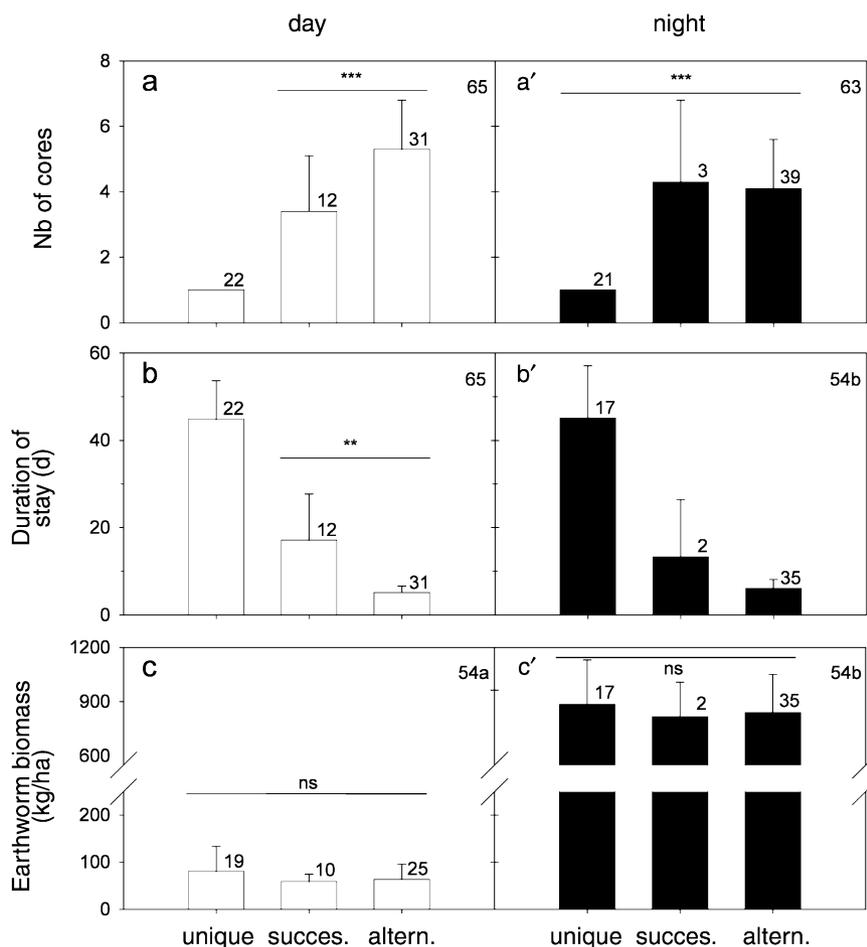


Figure 2. Patterns of movements (mean \pm sd, number of birds given above each bar) between the three types of core use ('unique', 'successive', 'alternative'), by day and at night (a and a': number of cores; b and b': duration of stay; c and c': mean earthworm biomass). Total sample size is given in the top right-hand corner (legend: a: nine birds removed because they spent > 20% of locations in hedges; b: nine birds removed because they spent < 70% of locations in fields). ANOVAs were used to compare categories linked with a horizontal line (** $P < 0.001$; ** $P < 0.01$; ns $P > 0.05$). NB: at night, tests were only performed between 'unique' and 'alternative' birds.

Table 2. Habitat selection in wintering Woodcocks according to core-use strategy. Habitat selection was analysed using compositional analysis, in woodlands by day and in fields at night. 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 '>'. P -values were given by randomization. When habitat selection was significantly different between core-use strategies, habitat preferences were given in italics for each strategy.

Analysis	Parameter	Core use	n	Wilk's λ	P	Habitat ranking ^{c,d}
Wood stands	Intercept		59 ^a	0.663	<0.001	Plant >> Cop >> Wet > Con T > Dec T > Mix T
	Core use		59 ^a	0.829	0.431	
Fields	Intercept		60 ^b	0.249	<0.001	
	Core use		60 ^b	0.797	0.005	
		<i>Unique</i>	21	<i>0.043</i>	<i><0.001</i>	<i>DGM >> HGM >> ST > YGM >> SP > UM</i>
		<i>Alternative</i>	39	<i>0.365</i>	<i><0.001</i>	<i>DGM >> ST >> HGM > YGM > UM > SP</i>

^aOnly birds with more than seven locations in woods.

^bOnly birds with more than seven locations in fields, 'successive' birds removed.

^cLegend for wood stands: Plant = plantation; Cop = coppice; Dec T = deciduous timber; Con T = coniferous timber; Mix T = mixed timber; Wet = wet forest.

^dLegend for field types: YGM = young Grazed meadow; DGM = dry grazed meadow; HGM = humid grazed meadow; UM = ungrazed meadow; ST = stubbles; SP = seed plot.

Table 3. Results of GLMM by day and at night on the duration of stay (in days) in the same core, the distance (in m) between consecutive cores, and the commuting flight distance (in m). Individual * age and year were placed as random variable. By day, habitat is forest vs. bocage. At night, habitat is meadow vs. stubble vs. seed plot and origin is forest vs. bocage.

Period	Analysis	N obs.	N birds	Parameter	df	F	P	Slope
Day	Duration of stay	319	63 ^a	Age	1,61	6.45	0.014	> 0
				Earthworm biomass	1,255	3.55	0.060	
				Habitat	1,253	0.22	0.639	
	Distance between cores	325	43 ^b	Age	1,41	0.43	0.515	
				Strategy	1,276	7.87	0.005	
				Duration of stay	1,276	2.25	0.135	
				Habitat	1,276	0.15	0.697	
				Earthworm biomass	1,238	0.55	0.461	
				Age	1,59	0.52	0.475	
Night	Duration of stay	357	63 ^c	Earthworm biomass	1,293	0.08	0.777	
				Habitat	2,292	0.59	0.553	
				Age	1,39	2.14	0.152	
	Distance between cores	324	42 ^d	Duration of stay	1,280	0.75	0.389	
				Earthworm biomass	1,280	0.04	0.835	
				Age	1,70	1.83	0.18	
	Commuting flight distance	846	65	Origin	1,780	73.54	< 0.001	

^aTwo birds living only in hedges removed because earthworm biomass was not available there.

^bTwenty-two 'unique' birds removed.

^cTwo birds that always stayed in forest at night were removed.

^dTwenty-one 'unique' birds removed and two birds only staying in woodlands at night.

Use of bocage by day

The bocage around the forest (hedges or woods) was used at least once by 25 birds (38.5%) and, for nine birds, it was the only habitat used (13.8%). Twenty

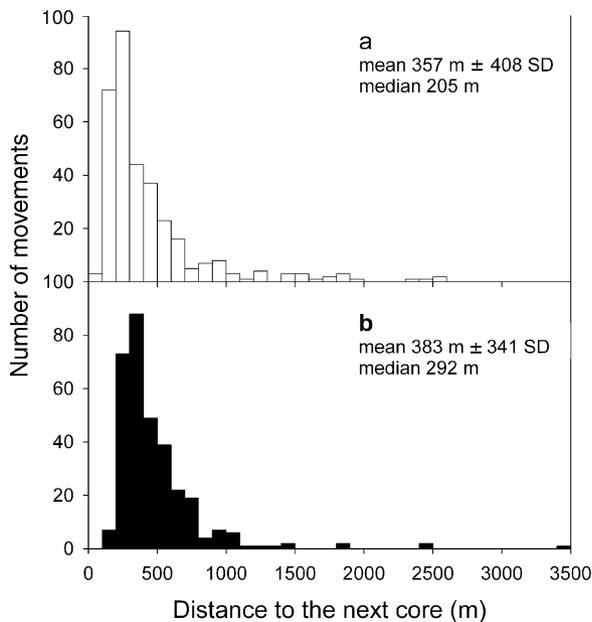


Figure 3. Distribution of distances to the next core by day (a; *n* = 330 movements) and at night (b; *n* = 324 movements).

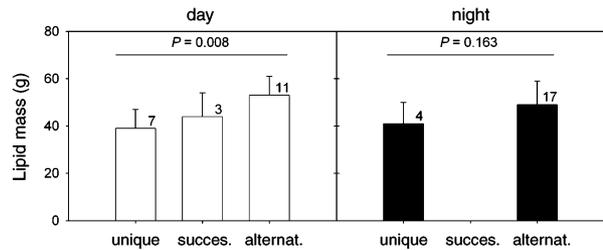


Figure 4. Estimated lipid mass (mean ± sd, number of birds given above each bar) from 21 birds monitored in 2002 between the types of core use ('unique', 'successive', alternative), by day and at night. Statistical tests (ANOVAS) were performed between types of core use.

Woodcocks (30.8%) used hedges at least once and six birds (9.2%) used hedges exclusively throughout the winter. The percentage of locations in bocage or in hedges did not differ significantly between the three types of core use (Kruskal–Wallis tests: $\chi^2_2 = 0.58$, *n* = 65, *P* = 0.75 for the percentage locations in bocage and $\chi^2_2 = 2.58$, *n* = 65, *P* = 0.28 for the percentage locations in hedges). Adults used the bocage and hedges more than young birds (Fig. 5).

Use of fields at night

The mean commuting flight index (proportion of nights on which birds left the woodland) was 0.85

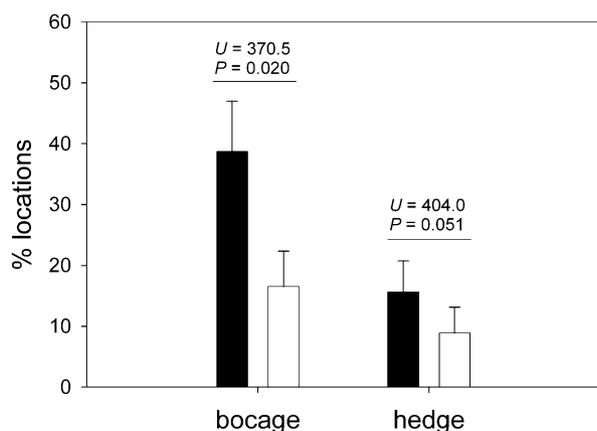


Figure 5. Percentage of locations in bocage and in hedges by day (mean \pm se) between ages ($n = 30$ adults in black and 35 yearlings in white). Mann–Whitney tests are indicated in the figure.

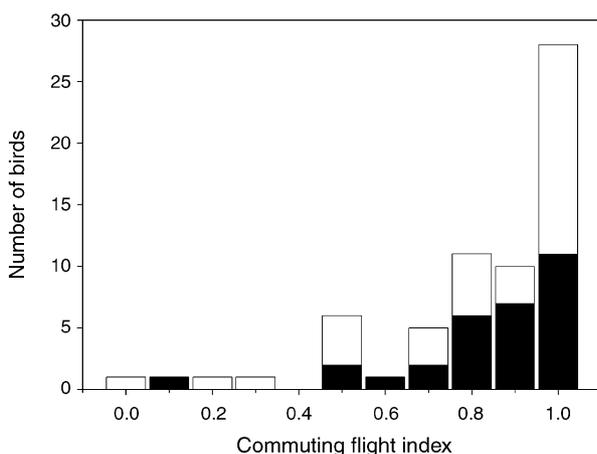


Figure 6. Distribution of commuting flight index (number of nights in fields divided by the number of nights of monitoring), according to age (black: adults; white: yearlings; $n = 65$ birds).

(± 0.23 sd) but the range between 0 and 1 indicates that it varied greatly among individuals (Fig. 6). Whereas 28 birds (43%) always left the forest at night, 26 birds (40%) left the forest between 70 and 99% of evenings, and 11 birds (17%) left the forest on fewer than 70% of evenings. The commuting flight index did not differ between age classes (Fig. 6; Mann–Whitney $U = 524$, $n = 65$, $P = 0.98$) and neither was it correlated with any morphometric parameter (Spearman rank correlations, all $P > 0.05$). In 2001, two individuals (one adult and one yearling) never left the forest at night during the period considered; they were removed for the analyses on nocturnal movements and habitat considered in the next paragraph.

The distances of commuting flights were greater when Woodcocks came from the forest than from the bocage (mean 1113 m (± 520 sd, 34–3717 m, $n = 54$ birds) vs. 259 m (± 183 sd, 6–947 m, $n = 23$ birds), respectively, $t_{73} = -10.63$, $P < 0.001$). The commuting distance was influenced by origin (bocage or forest), but not by age (Table 3).

Nocturnal movements

Thirty-nine birds (62%) had ‘alternative’ core use, 21 birds (33%) had a ‘unique’ core and only three birds (5%) had a ‘successive’ core use. There was a trend for 79% of diurnal ‘alternative’ birds to be ‘alternative’ at night, while the ‘successive’ and ‘unique’ birds by day had equal chances of behaving as ‘alternative’ or ‘unique’ at night (two-way cross-table between diurnal core use vs. nocturnal core use: $\chi^2_4 = 5.78$, $n = 60$, $P = 0.069$). There was no significant correlation between the number of cores used by day and at night, and the changing core index by day and at night (Pearson’s $r = 0.19$, $P = 0.13$ for number of cores, and $r = 0.18$, $P = 0.15$ for changing core index, $n = 63$ individuals).

The small sample size of ‘successive’ nocturnal birds precluded useful comparisons with ‘alternative’ birds concerning the duration of stay (Fig. 2b’). For the same reason, we removed the three ‘successive’ nocturnal birds in the following analyses. The frequencies of nocturnal strategies did not differ among years ($\chi^2_2 = 3.63$, $n = 60$, $P = 0.16$).

Habitat selection analysis in fields revealed that ‘alternative’ birds used stubbles significantly more often than ‘unique’ birds (Table 2). However, dry grazed meadows remained the preferred habitat for both groups. The mean earthworm biomasses in nocturnal cores during the study period did not differ between the two strategies (Fig. 2c’).

The duration of stay in the same nocturnal core was not influenced by bird age, earthworm biomass or habitat (meadows or cultivation) (Table 3). The distances between the nocturnal cores used by a bird varied from 120 m to 3.44 km (Fig. 3) and were not influenced by age, year, earthworm biomass or duration of stay in the core (Table 3). The frequencies of nocturnal strategies did not differ between age classes ($\chi^2_1 = 0.03$, $n = 60$, $P = 0.87$), and there was no difference in the nocturnal changing core index between ages (median 0.33 in adults and 0.30 in yearlings; Mann–Whitney $U = 399$, $n = 63$, $P = 0.186$). Nocturnal core use was not correlated with any morphometric variable (ANOVAS on tarsus, bill and wing length, body mass at ringing, all $P > 0.05$, $n = 60$).

Although not significantly different, the estimated lipid mass at ringing was 8 g lower in 'unique' birds than in 'alternative' birds (Fig. 4), a trend that was consistent with diurnal data.

The majority of Woodcocks shared their core with other birds at the same time at night, regardless of the core-use strategy (27 out of 39 'alternatives' (69%) and 12 out of the 21 'unique' birds (57%); $\chi^2_1 = 0.88$, $n = 60$, $P = 0.349$). Among these 39 birds that shared their field at least once with conspecifics, the proportions of locations shared by 'unique' and 'alternative' birds were similar (19% (± 16 sd, range 4–60%) in 'alternative' and 25% (± 16 sd, range 4–50%) in 'unique'; $U = 119.5$, $P = 0.196$).

DISCUSSION

Individual strategies of movements

This study is the first to illustrate the existence of individual strategies of spatial use and movements in wintering Woodcocks, observed consistently in the three years of study. The 65 Woodcocks monitored showed a general pattern of woodland use by day and fields at night, as described in the three previous studies of radiotagged Woodcocks, but with much smaller numbers of individuals (Hirons & Bickford-Smith 1983, Wilson 1983, Hoodless 1994). Hirons and Bickford-Smith (1983) and Hoodless (1994) reported a high fidelity to both diurnal covers and nocturnal fields. However, we have described a more complex pattern of movements than was previously suggested. The behaviour of Woodcocks appears similar to that of many species of dabbling duck in winter, which spend the day in nature reserves but disperse at night to feed in small ponds outside the reserve (the concept of a functional unit; Tamisier 1976, Tamisier & Tamisier 1981, Cox & Afton 1997). But similarly, some ducks frequently stay in the reserves at night, while conspecifics reach other feeding grounds in the ponds around (Guillemain *et al.* 2002).

By day, 52% of tagged Woodcocks used 'unique' or 'successive' strategies and 48% used 'alternative' strategies. We hypothesize that birds using 'unique' or 'successive' cores showed the same over-wintering strategy. We predict that these individuals stayed in the same core as long as it could offer enough food or protection against predators. The importance of diurnal feeding in wintering Woodcocks has recently been proved with activity tiltswitch radiotags (Duriez *et al.* 2005c). In a high-quality core, birds could stay all winter, whereas in less favourable cores, they would

have to move when food was depleted or when disturbance was too great. This hypothesis of fidelity until food is depleted below a threshold level is supported by the fact that birds tended to stay longer in the same diurnal core if the earthworm biomass was high, regardless of their strategy. However, the earthworm biomass in the diurnal cores of 'unique' birds was not significantly higher than it was for 'successive' and 'alternative' birds.

Birds with 'alternative' strategies, behaving like a 'floating population', changed cores several times and could come back to previously used cores. The cause of an alternative strategy could be a temporary disturbance. The effects of disturbance could not be analysed with our dataset, but our experience indicated that a bird flushed accidentally usually returned to the same site in the following days. Another cause could be a greater spatio-temporal heterogeneity in food availability in the cores used by the 'alternative' birds, and hence a lower predictability, despite an average earthworm biomass similar to that available to the 'unique' birds. Floaters have been described in several species of birds, mostly during the breeding season, as opposed to territorial breeders (Mönkkönen 1990, Sutherland 1996). The causes for a floating strategy and exploratory behaviours are various and could be attributed to social dominance (Stahl *et al.* 2001) or to a lack of suitable territory, with individuals 'queueing' for a vacant territory (Smith & Arcese 1989, Ens *et al.* 1992). Woodcocks could be forced to become 'alternative' because they could not find suitable cores to stay longer there, as suggested by the slight trend to stay longer in richer cores. By day, because there was no significant difference in habitat selection between the three types of core use, the three strategies would reflect the ability of individuals to find rich patches of food and to exploit them optimally.

Nocturnal movement strategies were characterized by the relative absence of 'successive' birds and dominant use of several alternative cores. The low number of 'successive' birds at night was perhaps due to the general richness of patches compared with woodlands (earthworm biomasses being higher in meadows than in woodlands; Fig. 2c). Because the food biomasses in the nocturnal cores of the three strategies did not differ, and the duration of stay was not linked to earthworm biomass, the causes for nocturnal strategies were perhaps the variation in individual foraging efficiency, a different sensitivity to predation risk or territoriality.

In the case of territoriality, we suggest that dominant birds might monopolize the best places and become 'unique' or 'successive', while subordinates would be obliged to move from place to place alternatively, as found in Barnacle Geese *Branta leucopsis* (Stahl *et al.* 2001). At night, the majority of birds (63%) have been found to share the same meadow or field, regardless of their strategy, but the proportion of shared locations was usually less than 25%. Indeed, by day, Woodcocks generally did not share their core areas with conspecifics, and six out of the eight birds that shared their cores were 'alternative'. Hence, territoriality might not occur at night but rather by day. At night, earthworm biomasses did not differ in the two groups but 'alternative' birds used stubbles and crops significantly more often than 'unique' birds (earthworm biomasses in crops were on average five times lower than in meadows; Duriez *et al.* 2005b). Territoriality at night was perhaps shown by the partial exclusion of 'alternatives' from the best habitats (i.e. dry meadows).

The lower estimated lipid mass in 'unique' birds by day (and, to a lesser extent, at night) could be another clue to the existence of territoriality, variation in foraging efficiency or sensitivity to predation risk. A vast literature now describes variations in body mass and energetic reserves in birds in response to environmental constraints, and especially to the trade-off between predation risk and starvation risk (Lima 1986, Rogers 1987). It has been demonstrated experimentally that small passerine birds increase their fat reserves to reduce the risk of starvation under unpredictable feeding conditions or energetic expenditures (Ekman & Hake 1990, Bednekoff *et al.* 1994, Cuthill *et al.* 2000). Additional reserves would serve as buffers against periods of low success when foraging is unpredictable, or when foragers are less efficient, as found in the European Blackbird *Turdus merula*, another solitary forager on earthworms (Cresswell 2003). Under predation risk, birds also tend to be lighter than in secure conditions (Gosler *et al.* 1995, Pravosudov & Grubb 1997). Dominant birds have also been found to have lower body mass compared with subdominants, because their better access to food reduces the need to carry such large reserves (Ekman & Lillendahl 1993, Gosler 1996, Gosler & Carruthers 1999). These contrasting results, raising the possibility of social dominance in a solitary wader such as the Woodcock, call for further investigation (date of arrival in winter quarters, signals between individuals).

In our case, if 'unique' birds were more efficient foragers (or dominant) than 'alternative' birds, their

access to rich patches of food would be enhanced and they should not need to carry these additional reserves. The less efficient (or subdominants) birds feeding in lower quality patches (i.e. 'successive' or 'alternatives') may need extra reserves as an insurance against starvation risk. Woodcocks fasting in captivity lose on average 1.6 g/h, i.e. 20 g in a 12-h day (Duriez *et al.* 2004), using mainly glucides and lipid reserves (Boos 2000). An additional 14 g of lipid in 'alternative' birds would allow them to fast for a day in a diurnal site where the food resources were too low, before changing site during the following day.

Adults were expected to be more faithful to their sites because their experience and their knowledge of the winter quarters, where they probably spent the previous winters (Wilson 1983, Gossmann *et al.* 1988), should have given them an advantage over yearlings. Our results did not show any effect of age on wintering strategy. The reasons for the absence of age effects are unclear, and require further investigation. It is possible that the high mortality of yearlings outside the reserve in the early winter (Duriez *et al.* 2005a) biased the ratio of 'unique' to 'alternative' strategies artificially in favour of the 'unique' strategy for the yearling population remaining in January and February.

Implications for management

None of our birds left the study site during the three winters. This confirmed the high fidelity to the winter quarters suspected in other studies using capture-mark-recapture data (Wilson 1983). From the analysis of 824 ringed birds recovered in the same winter over 8 years, Gossmann *et al.* (1994) found that 87% of Woodcocks were shot at a distance of less than 20 km from the ringing location. Hence, a reserve could effectively protect a population for an entire winter.

Woodcocks are particularly at risk when they are outside the main forest complex (i.e. in hedges and woods of the bocage by day and in fields and meadows at night), because terrestrial predators (foxes, cats and mustelids) are known to prospect in fields at night and to follow hedges (Harris & Woollard 1990), and 70% of cases of predation occurred in the bocage (Duriez *et al.* 2005a). Moreover, hunting occurring in the bocage by day was responsible for half of the mortality cases (Duriez *et al.* 2005a).

The use of the bocage was more important than expected. The higher use of bocage by adults could have resulted from the high interyear fidelity to

winter quarters (Wilson 1983, Gossmann *et al.* 1988) and thus a reliable knowledge of the safe parts of the wintering area. We believe that a young Woodcock that survived to its first winter in one location had a good chance of returning to the same location in subsequent years.

The relatively high fidelity to hedges and similar use of hedges by birds of the three strategies indicate that hedges are not a secondary or temporary habitat, but are of equal importance to woodlands. In our dataset, one adult bird followed in winter 2000, and which was caught again and followed in winter 2002, frequented exactly the same hedge during both winters. The use of hedges was known during the migration stopovers but underestimated in winter (Ferrand & Gossmann 1995). One benefit of living in a hedge could be energy savings as the birds travelled on average shorter distances to reach the nocturnal sites than those coming from the forest. As these fields were usually directly adjacent to the hedge used by day, this distance was probably travelled by walking. However, the costs of living in a hedge must be a lower food biomass during the day, and a higher predation risk overall.

This use of bocage around the forest means that hunting-free reserves to protect Woodcocks must integrate the woods and hedges around the protected forest complex to account for the behaviour of 'alternative' and 'successive' birds. Because most of the hedges and woods used in the bocage were within 1 km of the forest, this distance should serve as a buffer in which no hunting is allowed around the protected area (Duriez *et al.* 2005a).

In winter, it was thought that all Woodcocks frequented fields at night (Hirons & Bickford-Smith 1983, Wilson 1983, Ferrand & Gossmann 1988, Granval & Bouché 1993). Our study showed a great variability of commuting behaviour among individuals, not linked to individual features (age or morphometric variable). Every night, between 10 and 25% of the birds did not leave the woodlands. The advantage of staying in the forest at night is probably energy saving (no flight) and avoidance of predation. The overall area of meadows used at night is declining in most of the winter range of the species (Pain & Pienkowski 1997, Vickery *et al.* 2001), and changes in agricultural practices (excessive use of organic manures, nitrogen fertilizers and pesticides, replacement of meadows grazed by cattle by tall hay meadows) decrease the abundance and accessibility of earthworms (Edwards 1998). Our study showed that Woodcocks used meadows within

a mean radius of 1.2 km around the forest complex. An efficient reserve should provide optimally managed meadows within this radius.

Individual behaviours and movements must be considered in the development of sustainable management of Woodcocks. By changing cores more often than 'unique' birds, 'alternative' birds increase their risk of being shot. If our hypotheses of territoriality or foraging efficiency are correct, the management of protected forests to create favourable zones (forestry practices respecting soil macrofauna and shrub cover, reviewed in Granval & Muys (1992)) could result in more birds staying in the forest. However, the exploratory behaviour of 'alternative' birds would represent a chance for the species, because new suitable sites would be quickly discovered. Our study revealed previously unknown patterns of space use in Woodcocks in one forest in Brittany, but more studies are needed in other parts of the winter range in similar environments to verify the conclusions, as well as in different habitats, for example British moorlands, pine forests in the French Landes or Mediterranean shrublands.

This study was funded by the Office National de la Chasse et de la Faune Sauvage. Woodcocks were captured, ringed and radiotagged under the permission of the Centre de Recherches sur la Biologie des Populations d'Oiseaux, Muséum National d'Histoire Naturelle, Paris, following the conventions of the ONCFS (license no. 2000/024). We are very grateful to all those involved in the fieldwork: Y. Chaval, J.-L. Chil, S. Descamps, C. Guyot, F. Gossmann, H. Jamin, J. Le Bihan, F. Leroy, J. Marie, J.-P. Richard and S. Alary. Many thanks to F. Binet, who provided the 'earthworm' data, and G. Eon and V. Farcy for identification of 41 000 earthworms. We are grateful for the logistic facilities provided by the Conseil Général des Côtes d'Armor and J.-C. Fornasier (Office National des Forêts). This manuscript benefited from the helpful comments of H. Lormée, M. Guillemain, J. Clobert, C.-A. Bost, J. D. Goss-Custard, D. G. Krementz, S. Gillings and an anonymous referee. Many thanks to all the farmers for allowing free access to their fields.

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Received 27 January 2004; revision accepted 14 January 2005.