



Individual activity rates in wintering Eurasian woodcocks: starvation versus predation risk trade-off?

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Wintering birds face a trade-off between starvation and predation risk. In Eurasian woodcocks, *Scolopax rusticola*, habitat use may reflect this trade-off because meadows, where most birds spend the night, are characterized by a higher risk of predation and a higher biomass of food (earthworms) than the woods, used by day. We monitored activity of 34 woodcocks fitted with tiltswitch radiotags. Young birds were more active than adults, probably because they were less efficient at foraging. In general, nocturnal activity was inversely correlated with air temperature and with daylight foraging activity, suggesting some compensatory mechanism, modulated by thermoregulatory constraints. Individual activity patterns differed, and we classified woodcocks according to three main wintering strategies: 'always', 'sometimes' or 'never' visiting fields at night. The decision to fly to fields at night seemed to be taken every evening, according to the amount of daylight foraging activity in woods and the air temperature. After feeding in a rich patch of food on a mild day, woodcocks did not have to risk going to meadows. Conversely, in patches of fewer food resources or at lower temperatures or both, woodcocks could not meet all their energy requirements without going to fields at night (where there was always sufficient food) and eventually, changing their diurnal sites. Therefore, the trade-off between feeding and predation risk depends on how efficiently birds find a rich patch of food in the forest and exploit it optimally during the day.

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The main challenge for winter survival in birds is to acquire enough food and avoid predators (Cuthill & Houston 1997). In temperate latitudes, winter often represents an increase in foraging constraints in response to increased energy requirements when temperatures are

low and food scarce. As weather conditions become more severe, thermoregulatory demands increase, as does the risk of starvation (Wiersma & Piersma 1994). Hence, body reserves are often increased when food predictability and temperature decrease (Ekman & Hake 1990; Bednekoff et al. 1994; Cuthill et al. 2000). Thus, birds must take behavioural decisions to satisfy this trade-off between conflicting needs (Ludwig & Rowe 1990; McNamara & Houston 1994). Foraging choices can be affected by air temperatures, because birds become risk prone towards reward variance when expecting an energy deficit and risk averse when expecting to meet their requirements (Stephens & Krebs 1986; Caraco et al. 1990). Birds also have to trade between high foraging efficiency in a food-rich habitat and predation risk (Lima & Dill 1990). For example redshanks, *Tringa totanus*, forage in safer but poorer mudflats instead of in richer and riskier saltmarshes

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when the weather conditions are more favourable to the attack success of their predator the sparrowhawk, *Accipiter nisus* (Hilton et al. 1999). Similarly, red knots, *Calidris canutus*, are less likely to take flight in response to predators when air temperatures decline, probably as a consequence of increased thermoregulatory demand (McGowan et al. 2002).

The Eurasian woodcock, *Scolopax rusticola*, wintering in western Europe has to face these trade-offs. It has been generally believed that woodcocks use two contrasting habitats: they rest in woodlands by day and satisfy their food requirements in fields at night (Cramp & Simmons 1983; Hirons & Bickford-Smith 1983). However, the woodcock's pattern of habitat use in winter is now known to be more complicated than this, with some individuals staying in woods at night (Duriez 2003). The investigation of individual strategies of habitat use and behaviour is an important step towards an understanding of the starvation/predation trade-off. To understand what influences decision making, it is necessary to assess the potential costs and benefits associated with the different habitats (predation and hunting risks, energy losses, food availability and division of foraging effort). For woodcocks, the main benefit of going to fields, and especially meadows, is the much higher biomass of earthworms (their main food item) there than in woodlands (Granval & Bouché 1993). Conversely, energy expenditure at night in fields is correlated with air temperatures and wind speed (Wiersma & Piersma 1994; Duriez et al. 2004), and energy costs are thus likely to be higher in fields than in forest. Predation appears to be higher in fields at night than in woods (at least 75% of deaths occur in fields), probably because the main predators are nocturnal mammals (foxes, mustelids, feral cats; Duriez 2003). Because hunting is permitted only during the day, this risk occurs only when woodcocks are in woodlands. Therefore, for wintering woodcocks, the decision to leave the forest at night to go to food-rich meadows may reflect the trade-off between foraging and predation risk, depending on the foraging success during the day and the thermoregulatory costs at night.

Foraging effort is difficult to study in woodcocks because they are elusive, cryptic, solitary and active in open habitats only at night. Radiotelemetry is a useful tool to investigate the behaviours of such animals (Kenward 2001). We used activity-tiltswitch radiotags attached to woodcocks' backs to indicate the time spent active (i.e. probing for food) and consequently the foraging effort, although it was not possible to distinguish between successful and failed foraging.

We investigated the patterns of diurnal and nocturnal activity rates and the existence of different individual foraging strategies. We focus especially on the existence of diurnal foraging in winter, which has never been proved before and could have important consequences for understanding wintering strategies and habitat requirements of woodcocks, and hence for the management of this game species. We then looked at how these individual strategies can be linked to the available resources (habitat and food). Finally, we analysed the decision processes of wintering woodcocks with respect to the hypothesis of a trade-off between foraging and predation risk, and tested

for compensatory behaviour between diurnal and nocturnal activity. We predicted that individual woodcocks with a positive energy balance (i.e. able to feed efficiently in woods by day) should favour security and tend to stay in the safer habitat (woodlands), whereas individuals that cannot satisfy their requirements during the day should be more risk prone and feed in meadows at night where food is more available.

METHODS

Study Area

We collected data during December to April in two winters (2000–2001 and 2001–2002, hereafter called 2001 and 2002 winters, respectively). The study area (ca. 1800 ha) was in Brittany, western France (48°30'N, 3°28'W), and comprised the Beffou forest and the surrounding bocage. The bocage is a typical landscape in western France, with small fields separated by old woody hedges. The topography was composed of small hills (range of altitude 160–322 m) and valleys. Woodcock hunting has been prohibited in the Beffou forest since 1995 but it is allowed in the surrounding woods and hedges. The climate in Brittany in winter is rainy and windy, but mild (mean 5°C in January). Weather data (standard air temperatures, rainfalls, wind direction and speed) were collected hourly at the Météo France's station at Louargat (14 km from the Beffou forest).

Capture Methods and Radiotelemetry

We captured woodcocks at feeding sites at the beginning of the night with a spotlight and a landing net fitted to a 2–4-m pole (Gossmann et al. 1988). The age (adult >1 year old versus yearling) was determined by wing feather details and moult status (Clausager 1973; Fadat 1994). We captured 11 woodcocks (five adults and six juveniles) in winter 2001, and another 23 (eight adults and 15 juveniles) in 2002.

Each bird was fitted with a radiotransmitter (TW3: Biotrack Ltd, Warcham, U.K.) with an activity tiltswitch, consisting of a small tube containing a mercury bead (angled at 10° below the level of the bird's back). The position of the bird changed the position of the mercury bead, and the signals were consequently sent with a different pulse rate (Fig. 1). When the bird was sitting on a slope signals could be fast while resting. Therefore, we used the variations in pulse rates as indications of activity and the continuous pulse rates (slow or fast) as inactivity. In winter, activity can include feeding, preening, walking or flying. Preening probably takes only a few tens of minutes in the day (A. Le Gall, personal communication). The time spent in flight was also short (a few minutes at twilight) and could be detected by the increase in signal strength.

With an activity tiltswitch radiotag, calibration of the variation in pulse rates with the animal's behaviour is necessary (Exo et al. 1992). To do this, we tried to observe an individual and to record on a Dictaphone its

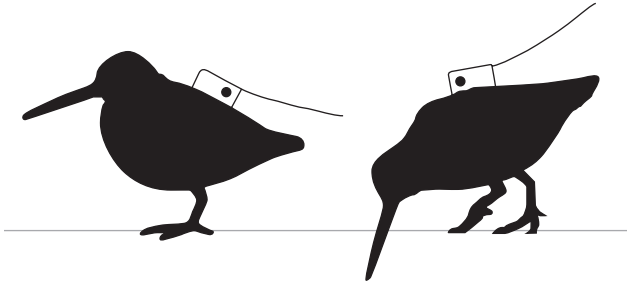


Figure 1. Illustration of the principle of activity monitoring in woodcocks using activity tiltswitch radiotags (not at scale). When the bird was resting (left), the mercury bead was at the rear of the tag and the signals were sent with a slow pulse (period of 1200 ms). When the bird was probing (right), the bead moved to the front of the tag and the signals were sent with a fast pulse (period of 800 ms).

behaviours and the signals received. Because woodcocks are cryptic and difficult to observe during the day, we decided to watch them at night, while they were actively feeding in open fields. We obtained data for only one bird more than 100 m away, which we observed for 50 min with a 30x magnifying spotting scope mounted on a tripod. During this recording, the bird alternated four feeding bouts of a mean \pm SE of 7 min 4 s \pm 7 min 5 s with four bouts of standing and vigilance of 4 min 49 s \pm 2 min 58 s. When the bird was probing, 89.0% of signals were variable pulses ($\chi^2_6 = 752.95$, $P < 0.001$). The pulse rates were constant when the bird was standing (100% of slow pulses) and when it was walking (78.9% of fast pulses).

Radiotags fitted in 2002 were more sensitive to movement than those used in 2001 (even though the models were the same, the activity switch responded more quickly to an inclination of the tag in 2002). This resulted in higher average activity values in 2002 than in 2001. We modified the analysis program (see below) to take into account this higher sensitivity, but a difference still remained between years.

Ethical Note

Woodcocks were captured, ringed and radiotagged with permission of the Centre de Recherches sur la Biologie des Populations d'Oiseaux, Muséum National d'Histoire Naturelle, Paris. Radiotransmitters weighed 12 g (mean 3.4% of body mass, range 2.9–4.2%), following the recommendations of Caccamise & Hedin (1985). They were glued on the back (hypoallergenic livestock glue, Nasco, Fort Atkinson, U.S.A.) and maintained with a single-loop harness (McAuley et al. 1993). We could not remove the harness because woodcocks cannot be recaptured before migration. However, five birds were shot by local hunters or recaptured in the following winters around the Beffou forest with the harness intact, their plumage intact and normal body mass, which indicates that radiotagged birds can survive and migrate like untagged birds. Similar glue-mounted radiotags had no effect on breeding success and return rates in the closely related great snipe, *Gallinago media* (Kalas et al. 1989).

Activity Data Recording

In 2001, 11 woodcocks were recorded one to seven times. Activity recording was initiated around 1200 hours and run for 24 h to get the activity rate during one afternoon, one full night and one morning. In 2002, 23 woodcocks were followed one to six times and 17 individuals were recorded on several successive days (3–9 days). Combining both years and all individuals, woodcock activity was recorded during 256 days and 159 nights.

Activity rates were recorded with an automatic data logger (RX-900: Televilt Positioning AB, Lindesberg, Sweden) powered by a 12-V car battery. When the signal was constant, the logger recorded the date, time (± 1 s), pulse period and signal strength every minute. Each time the signal received changed (strength or pulse period), the logger stored the new parameters (± 1 s). Two woodcocks could be recorded simultaneously, by alternation of 3-min periods, using the scan function of the logger. The data logger was connected to two types of antennas, according to the geographical and topographical location of the bird recorded. Most of the time, the logger was connected to a 9-element directional Yagi antenna, located at the highest point of the area (322 m) and in the centre of the study zone. If the bird could not be heard from this place, we took the logger closer to the bird (less than 200 m), placed it in a closed metal box and connected it to a CB car omnidirectional whip-antenna. At twilight, when the bird moved from forest to fields (or vice versa), we checked whether the signal could still be heard and we adjusted the direction of the 9-element antenna or took the logger closer to the bird.

We located each bird to the nearest 100 m or less (not too close to avoid flushing) once during the night and during the day to check the habitat type used (stand type and humus type, see below). The flight performed at twilight between woodlands and fields was called 'commuting flight'. From our experience, woodcocks did not fly to change site during the day (except when disturbed and flushed) and travelled only by walking (probably never more than 200 m). During 7 full nights in 2001, each of 23 birds (11 birds fitted with activity switch radiotags and 14 other birds fitted with traditional radiotags) was localized every 2 h on average. Of these, 80% stayed the entire night in the field chosen at the beginning of the night and 89% within a radius of 150 m. We thus assumed that woodcocks were faithful to the field chosen at the beginning of the night. Even when one bird moved during the night, the data logger recorded it because of the increase in signal strength or loss of signal, and the data from this night were excluded from the analysis.

Activity Data Treatments

Activity files were processed with a program developed by Y.T., using a programming interface of Sigma Plot 2001 for windows v. 7.1 (SPSS Inc., Chicago, U.S.A.). The beginning and the end of the night were defined as the

evening and morning civil twilights, which roughly corresponded to the twilight flight (± 10 min, according to the cloud cover; Hiron & Bickford-Smith 1983). The morning and afternoon were defined as the periods between civil twilight and the sun zenith (between 1300 and 1330 hours). In the same way, the night was divided into two parts by the same zenith value (between 0100 and 0130 hours). Civil twilights and zeniths were calculated precisely for the study zone, for each day with an astronomical calendar on the web site <http://www.bdl.fr>. For each recording, after entering the values of civil twilights and zenith, the program calculated the time spent in activity/inactivity/not recorded (signal lost or in scan) and the activity rate (%: time in activity/total time recorded) per h, per half day (or half night) and per day (or night) for each recording date. Activity rates in the morning never differed from those in the afternoon, and activity rates at the beginning of the night never differed from those at the end of the night, whatever the habitat use, category or weather (frost/normal) (paired *t* tests between beginning and end of day (or night) based on mean activity rates of individuals: all $P > 0.1$). Therefore, for analyses, we considered only the whole daylight (or night) activity rates. We estimated the activity duration per day (or night) by multiplying the activity rate (%) and the duration of the day (or night) at this date (period between the civil twilights), i.e. diurnal activity could be extrapolated from activity rates measured in the morning or the afternoon. Frosty weather might greatly influence woodcocks' behaviour and activity rates because frozen ground prevents probing. However, too few days of frost and a small sample size of recordings precluded detailed analysis of activity rates in the one frost spell encountered; hence this period was removed from the analyses.

Habitat Description

Habitat was described at two levels: stand type and humus type. In woodlands, we defined five classes of stands, based on the vegetation structure: plantations (10–15 years, 28% of study area), coppice (15–30 years, 15%), deciduous timber (30–120 years, 31%), coniferous timbers (30–120 years, 22%) and wet forests (various ages and heights, 4%). Deciduous stands (plantations, coppices and timbers) mostly contained beech, *Fagus sylvatica*, and oak, *Quercus robur* and *Q. sessiliflora*. Coniferous stands (plantations and timbers) were mostly sitka spruce, *Picea sitchensis*, common silver fir, *Abies alba*, grant fir, *A. grandis*, or Scots pine, *Pinus sylvestris*, and maritime pine, *Pinus pinaster*. Wet forests were characterized by willows, *Salix* sp., alders, *Alnus glutinosa*, and poplars, *Populus* sp. and by the presence of wet soil and typical wetland plants (greater tussock sedges, *Carex paniculata*, and common rushes, *Juncus conglomeratus*).

Because humus types depend on many factors (biotic such as vegetation, soil fauna and macrofauna; and abiotic such as nature of geological substrate, slope, hydrology), humus description can serve as an indicator of invertebrate activity in unperturbed soils (i.e. woodlands but not fields). Following Jabiol et al. (1995), we determined three

types of humus: mors (13% of samplings), moders (34%) and mulls (53%). Mors were characterized by the accumulation of litter resulting from acid substrate and scarcity of earthworms. Mulls were characterized by only a thin litter layer resulting from an active and abundant soil fauna. Moders were intermediate. Because humus could change over short distances (within 10 m) and was difficult to map, we considered the availability of humus types to be the proportion of each type of humus in a systematic sampling based on a grid of 200×200 m covering the entire forest and extended to several surrounding woods (182 points).

We divided nocturnal 'field' habitat into four classes: grazed meadows (53% of area) and ungrazed meadows (17%) (a meadow was characterized as grazed if it showed actual or recent grazing with cow dung, footprints and short vegetation), sown (13%, wheat and grass) and stubbles (17%, corn and wheat).

Earthworm Sampling

We sampled earthworms using the standardized method described by Bouché & Alliaga (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 ($30 \times 30 \times 10$ cm) to collect additional earthworms that did not respond to the chemical extraction.

We sampled earthworms 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 radiotagged woodcock (birds flushed usually returned to the same site on the following day), in the early morning (around 0900 hours) in diurnal sites (woodlands) and at dark (around 2000 hours) in nocturnal sites (fields). We selected plots by searching for signs of woodcock activity (faeces, tracks) and avoided obvious soil perturbations (tracks, paths, depressions and ridges). Meteorological conditions were noted and we did not sample during freezing weather. We also avoided sampling very wet soils (no effect of formalin application), in young wheat or grass seed plots (to prevent trampling of crops) and in ungrazed meadows (not used by woodcocks).

Because earthworm populations are highly aggregated in patches (Poier & Richter 1992; Rossi et al. 1997), formalin extraction was done on an area of six 1-m^2 plots (three 1-m^2 plots spaced 10 m apart in a triangle at the woodcock site and three other 1-m^2 plots in a randomly chosen place 50 m apart) to account for the variability in the horizontal distribution of earthworm biomass. Then, within each of the six plots, two soil cores ($30 \times 30 \times 10$ cm) were dug and hand sorted.

Because some earthworm species migrate upwards at night (Lee 1985), the earthworm biomass available to woodcocks should be higher at night than during the day. Hence, we modified the sampling procedure for nocturnal habitats slightly to take account of the earthworm biomass available to woodcocks in fields at night. After

flushing a radiotagged bird, we placed six 1-m² plots as for the daytime sampling in the 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 for hand sorting the following afternoon. On the following morning, we moved the plots 1 m away and performed the chemical extraction with formalin according to Bouché & Alliaga (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 before later identification. All individuals were identified to species, counted and weighed (± 0.01 g, fresh mass). For each sampling place, i.e. each diurnal or nocturnal site used by woodcocks, the earthworm biomass value was the mean of the six plots and was expressed as kg (fresh weight worm)/ha.

Only 44 (39%) of 113 diurnal and nocturnal sites used by woodcocks were sampled. Thus, for the 61% of sites lacking measured earthworm biomass, we used the mean value calculated for this type of habitat (for example, the combination of planting and humus types in woodlands; or field type; detailed results in Duriez 2003). Humus types can give another indication of earthworm availability in nonsampled sites. For the General Linear Mixed Models (GLMM) procedures, because the distribution of the mean earthworm biomasses was not normal, even when log transformed, we transformed them into classes (by day: class 1: <60 kg/ha; class 2: 61–90 kg/ha; class 3: 91–140 kg/ha; at night in fields: class 4: 141–700 kg/ha; class 5: 701–1000 kg/ha; class 6: >1001 kg/ha).

Statistical Analyses

Unless specified, means are reported ± 1 SD and were compared with Student's *t* tests or analyses of variance (ANOVAs). Normality of the variables was assessed with nonparametric Kolmogorov–Smirnov tests. Where data were non-normal, means were compared with nonparametric Mann–Whitney tests or Kruskal–Wallis tests. All tests were two tailed. Analyses were performed with SPSS 10.0 (SPSS 1999). To avoid pseudoreplication (Hurlbert 1984), we used the mean values for each individual, or we used GLMM with individual*age as a random variable to give the same weight to every individual, whatever the number of recordings (Littel et al. 1991). Similarly, for the decision rule, we performed a mixed logistic regression with individual*age as a random variable using the Glimmix macro in SAS v. 8 (SAS Institute 2000).

Caution was needed in comparing of the activity rates between years, because of the difference in sensitivity of radiotags. We tested the annual effect using Generalized Linear Models (GLM) with interactions between year* (other variable), which meant that we were testing whether the slopes (i.e. the patterns) differed between years (as the sensitivity of radiotags differed between years, the *Y* intercept was always different).

Habitat selection in the three strategies was compared with compositional analysis (Aebischer et al. 1993),

performed with a script written for SPSS by E. Corda (detailed methods in Duriez 2003).

RESULTS

Activity Patterns

Birds were assigned to four behavioural strategies: two birds never commuted from forest to fields at night (strategy Never), 13 sometimes commuted (strategy Sometimes), 15 always commuted (strategy Always) and three birds always used hedges (Hedge). One other individual had no assigned strategy because it was shot early in the season. We first describe the patterns of activity for all birds and then compare the three strategies of birds that stayed in woodlands by day (birds that stayed in hedges were not considered in the following analyses because of the low sample size and lack of information about earthworm biomasses in hedges).

By day, activity duration was influenced only by age, with yearlings more active than adults, and there was no variation with air temperature, earthworm biomass or humus type (Table 1). Nocturnal activity was related to age, nocturnal temperature, the previous day's humus type and diurnal activity. At night in fields, yearlings were also more active than adults and, in general, woodcocks were more active at low air temperatures and when they had shown little activity and were in a patch of poor humus during the previous day (Table 1, Fig. 2).

Activity Rates

There was no significant relation between the strategies and five individual characteristics and morphometric variables (age: $\chi^2_2 = 0.096$, $P = 0.95$; tarsus, wing and bill length, body mass at capture, ANOVAs: all $P > 0.38$). Woodcocks that spent the day in woodland and the night on fields (i.e. commuted) are hereafter referred to as WF (for Wood–Fields) and others spending the day and the night in woodlands are referred to as WW (Wood–Wood, no commuting). The total activity durations were similar among strategies of habitat use but yearlings were always more active than adults (Fig. 3). By day, activity durations for the category WW (strategies Never and Sometimes) were significantly higher than for the category WF (strategies Sometimes and Always; Fig. 4). At night, activity durations for the category WW (strategies Never and Sometimes) were lower than for the category WF (strategies Sometimes and Always; Fig. 4). In summary, when woodcocks stayed in woodlands at night, they were more active by day, but almost inactive at night (the division of the mean 60 min of activity recorded at night being almost entirely achieved around twilight, i.e. in the first or last hour of the night), whereas they were similarly active by day and at night when going to fields at night. In all strategies, yearlings were more active than adults by day but not at night in the fields.

Links Between Activity and Resources

Habitat types did not influence activity durations. Indeed, the stand types and humus types used by woodcocks

Table 1. Results of model selection from GLMM on activity duration (dependent variable) according to other variables, by day (all individuals staying in woods) and at night (only individuals in fields)

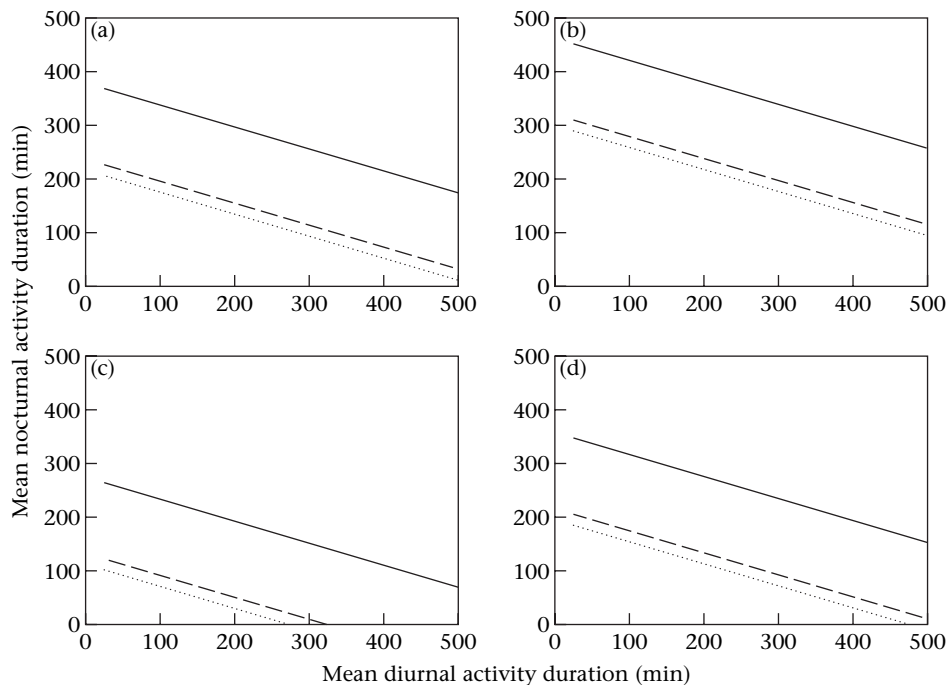
Period	R^2	Variable	df	F	P	Estimate (min)	Interpretation
Day*	0.55	Intercept				215.65	
		Age	1,26	5.50	0.027	-90.50	Adult < Yearling
Night†	0.57	Intercept				334.60	
		Night air $T^\circ\text{C}$	1,52	14.03	0.0005	-11.63	
		Activity previous day	1,52	17.21	<0.001	-0.41	
		Age	1,20	6.87	0.016	-83.27	Adult < Yearling
		Humus previous day	2,52	5.24	0.008	162.53	Mor
					20.40	Moder	
					0	Mull	

Earthworm biomasses were grouped into classes (see [Methods](#)). Data collected in frosty weather and the three individuals that stayed in hedges were excluded from the analysis because of the small sample size. Individual*age was included as a random variable (see [Methods](#)). *172 recordings for 28 individuals; variables removed from the model ($P > 0.05$): year, diurnal temperature ($T^\circ\text{C}$), diurnal earthworm biomass, humus, earthworm*age, earthworm* $T^\circ\text{C}$.

†78 recordings for 23 individuals; variables removed from the model ($P > 0.05$): year, age, nocturnal earthworm biomass, earthworm*age, earthworm* $T^\circ\text{C}$, diurnal activity*diurnal earthworm, diurnal activity* $T^\circ\text{C}$.

by day in woodlands did not differ according to the three strategies (compositional analyses: stand types: $\lambda = 0.709$, $P = 0.50$; humus types: $\lambda = 0.931$, $P = 0.79$). Activity rates did not differ between stand types in woodlands (ANOVA: $F_{4,46} = 0.39$, $P = 0.81$), or between humus types at night, birds usually remained in the same area as during the day. Field types selected at night did not differ between the strategies Sometimes and Always (compositional analysis: $\lambda = 0.929$, $P = 0.68$, for four field types). Nocturnal activity rates did not differ between field types (meadows or stubbles; ANOVA: $F_{1,32} = 0.87$, $P = 0.36$).

In our study zone, the mean earthworm biomass in meadows (928 ± 273 kg/ha, $N = 33$ samplings) was 13 times higher than in woodlands (71 ± 47 kg/ha, $N = 43$ samplings; [Duriez 2003](#)). The air temperature had a significant and positive effect on the mean earthworm biomasses collected (GLM: $F_{1,40} = 5.40$, $P = 0.025$, slope = 6.35 kg/ha per $^\circ\text{C}$ and intercept = 13.15 kg/ha, $N = 41$ in forest; $F_{1,35} = 8.93$, $P = 0.005$, slope = 63.91 kg/ha per $^\circ\text{C}$ and intercept = 336.2 kg/ha, $N = 36$ in fields). Woodcocks that did not commute (WW category) lived in diurnal sites that were slightly richer in earthworms than sites lived in by commuters (WF birds),

**Figure 2.** Nocturnal activity duration in fields at night, calculated from the GLMM in [Table 1](#), according to the activity duration of the previous day and the humus type of the previous day (—: mor; ---: moder; ...: mull). (a) Adults and (b) yearlings at a mean nocturnal air temperature of 3°C ; (c) adults and (d) yearlings at a temperature of 12°C .

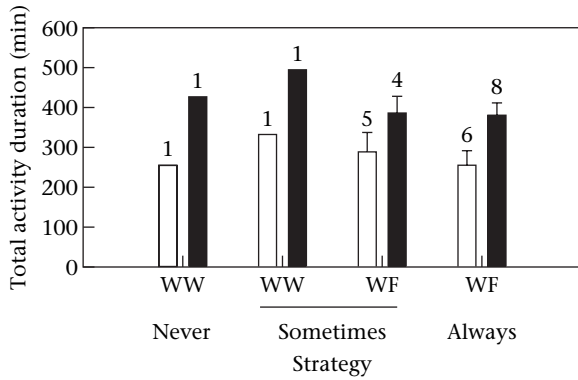


Figure 3. Mean total activity duration \pm SE (24 h: 1 day and the following night) in normal weather, according to the age (\square : adults; \blacksquare : yearlings), the strategy of habitat use (Never, Sometimes and Always commuting) and the commuting category (WW: day and night in woodland; WF: day in woodland and night on fields). The sample sizes at the top of columns are the number of individuals in each category, but note that the two individuals of the Sometimes strategy with WW commuting were also counted in the WF commuting. Results of GLMM on total activity duration on 94 days of full recording day + night in 26 individuals: $R^2 = 0.44$; age: $F_{1,22} = 11.10$, $P = 0.003$; strategy (commuting): $F_{3,67} = 0.41$, $P = 0.74$.

but the nocturnal sites (fields) used by the latter were 12 times richer than the nocturnal sites in woodland (Fig. 5).

Decision Making

The decision whether to go to fields at night or stay in the woods should be taken every evening. The decision (0 = stay in wood; 1 = go to fields) was negatively

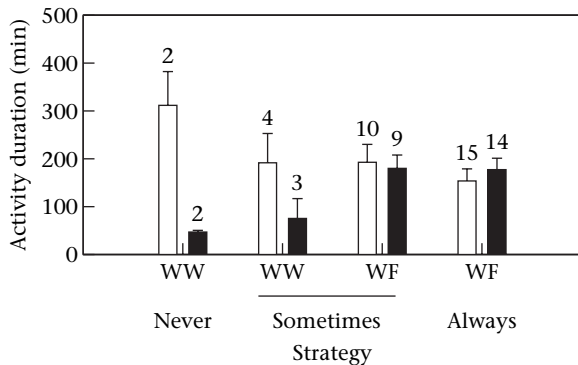


Figure 4. Mean activity durations \pm SE in normal weather according to the strategy of habitat use, (Never, Sometimes and Always commuting) by day (\square) and at night (\blacksquare). The sample sizes at the top of columns are the number of individuals. WW: day and night in woodland (day versus night: t test: $t_9 = 3.26$, $P = 0.010$); WF: day in woodland and night on fields (day versus night: t test: $t_{53} = 0.84$, $P = 0.406$). By day, 28 individuals were recorded for 171 days in total (GLMM: $R^2 = 0.53$, age: $F_{1,23} = 7.60$, $P = 0.011$; year: $F_{1,142} = 4.18$, $P = 0.043$; strategy (commuting): $F_{3,142} = 4.90$, $P = 0.003$). At night, 26 individuals were recorded for 107 nights in total (GLMM: $R^2 = 0.47$, age: $F_{1,21} = 0.37$, $P = 0.550$; year: $F_{1,80} = 2.83$, $P = 0.096$; strategy (commuting): $F_{3,80} = 4.77$, $P = 0.004$).

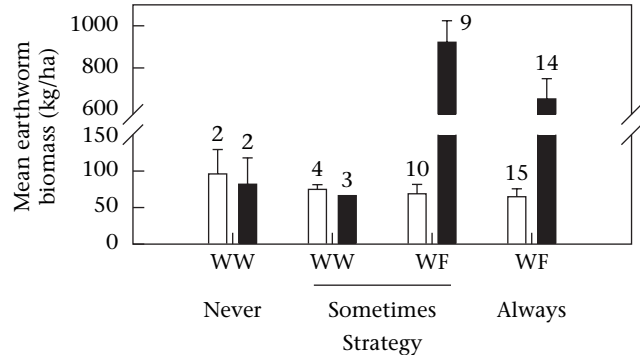


Figure 5. Mean earthworm biomass \pm SE in normal weather according to the strategy of habitat use (Never, Sometimes and Always commuting), by day (\square) and at night (\blacksquare). The sample sizes at the top of columns are the number of individuals. By day, 28 individuals were recorded for 171 days in total (GLMM: $R^2 = 0.73$, commuting: $F_{1,142} = 4.34$, $P = 0.038$; age: $F_{1,23} = 0.33$, $P = 0.568$; year: $F_{1,142} = 0.13$, $P = 0.722$; strategy (commuting): $F_{3,142} = 1.40$, $P = 0.245$). At night, 26 individuals were recorded for 107 nights in total (GLMM: $R^2 = 0.80$, age: $F_{1,21} = 0.03$, $P = 0.857$; year: $F_{1,80} = 2.00$, $P = 0.161$; strategy (commuting): $F_{3,80} = 24.57$, $P < 0.0001$).

influenced by the activity duration and the nocturnal air temperature (mixed logistic regression with Glimmix macro; Table 2). Hence, the probability of going to fields at night decreased when diurnal activity was high and when nocturnal air temperatures were mild (Fig. 6).

DISCUSSION

Winter Activity Rates

Our results are the first to show evidence for diurnal foraging by woodcocks under nonfreezing weather conditions in winter, whereas diurnal foraging seems to be the rule during summer (Cramp & Simmons 1983; Ferrand & Gossmann 1995). Individuals that stayed in the woods at night (WW) fed mainly during the day. Even birds that went to fields at night (WF) fed for an appreciable part of the day. The total feeding durations reported here seem rather low (about 5 h out of 24) but a similar average value was measured in the oystercatcher, *Haematopus ostralegus* (Zwarts et al. 1996). However our values of feeding durations considered only the time spent probing, and not the time spent walking and actively searching for food, which is also part of the foraging behaviour. This means that our activity durations probably underestimated the foraging time and gave minimum values. However, these biases should be similar in the three strategies and thus do not prevent comparisons.

By day and at night, young woodcocks were always more active than adults. Such a difference in activity duration among age classes could be due to differences in physiology or in foraging efficiency. Since the plumage insulation and the morphometric measurements did not differ between yearlings and adults (Boos 2000; Duriez et al. 2004), the hypothesis of higher energy needs in yearlings can be excluded. Furthermore, the food biomass

Table 2. Model selected from logistic regression on the decision to go to fields at night according to the activity duration and mean air temperature at night (periods of frost and last week of monitoring excluded)

Variable	df	F	P	Estimate
Intercept				12.99
Diurnal activity duration	1,67	9.89	0.0025	-0.018
Nocturnal air temperature	1,67	14.05	0.0004	-0.452

The analysis concerned 95 evenings of decisions on 26 individuals. The factors year, age, mean earthworm biomass and humus were not significant.

was not lower in the diurnal sites chosen by yearlings. Therefore, the difference in activity was probably caused by a lower foraging efficiency in young birds. This difference in foraging efficiency could be the result of taking longer to find rich patches of earthworms or poorer feeding skills with which to exploit them optimally.

At night, the increase in activity when the air temperature decreased probably resulted simultaneously from higher energy needs for thermoregulation in cold temperatures, especially in open habitats such as meadows (Wiersma & Piersma 1994), and lower availability of earthworms which burrow deeper at low temperatures. The absence of a relation between activity and air temperature by day was perhaps due to the greater protection from wind chill effects (responsible for most of the thermoregulatory demands) provided by the scrub-habitat in woods (Thompson & Fritzell 1988; Bakken 1990).

More surprising is the lack of a relation between activity rates and food biomass. The daily energy intake is the product of the instantaneous intake rate (i.e. the speed to find and consume a prey) and the time spent foraging. Although we could measure the time spent foraging, it was impossible to record the feeding success or the size of prey. In the American woodcock, *Scolopax minor*, an experimental trial showed that the number of probes per capture decreased when earthworm density increased (22 probes at 26 worms/m², i.e. probing success of 0.05,

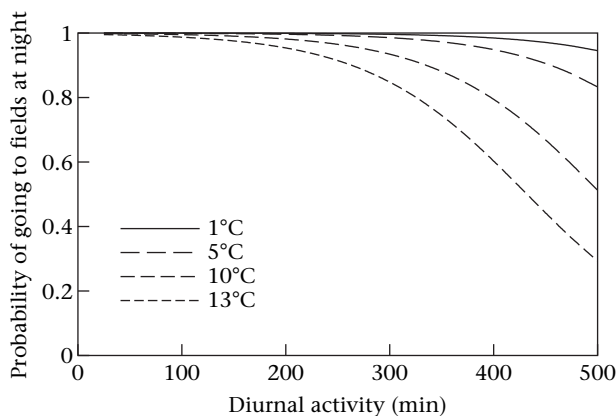


Figure 6. Probability of going to fields at night according to the diurnal activity duration and the nocturnal air temperatures (4 curves; results from the logistic regression in Table 2).

decreasing to 9 probes at 105 worms/m², i.e. probing success of 0.11; Rabe et al. 1983). Hence, we expected an increase in activity durations at low food biomasses (in mor type humus), resulting from the lower intake rate. We did not find significant differences in daylight activity in mor humus (low food biomasses) and mull humus (high food biomasses). However, it is difficult to link activity to the food quality of patches because it may vary both with intake rate (earthworm density) and with total available earthworm biomass in the area. An individual may increase its activity to be able to eat more, as well as to compensate for a low intake rate. Because of the large quantity of food available in fields at night, we consider that an increase in activity simply means an increase in the amount ingested. This probably explains why the nocturnal activity was influenced by the humus type used by day: the same time spent feeding in food-rich habitat (mull) and food-poor habitat (mor) is likely to have led to different intakes and hence different compensatory activity was required at night. We expected to find the same relation when considering classes of earthworm biomass instead of humus type, but it was not significant (Table 1), probably because humus was a better indicator of earthworm availability for a nonsampled site than the assigned mean value of earthworm biomass was. In functional response curves, demonstrated for many bird species including waders such as oystercatchers and black-tailed godwits, *Limosa limosa* (Goss-Custard et al. 1996; Gill et al. 2001), instantaneous intake rates increase with food abundance until they reach a plateau caused by the time constraint of consuming the prey (Holling 1959). In woodcocks, the constant activity durations in fields at night, whatever the earthworm biomass available, probably corresponded to the maximum intake rate. Woodcocks must also be constrained by the time to consume and digest the prey, as found in other wader species (Kersten & Visser 1996; Zwarts et al. 1996).

At night in meadows, we hypothesize that the high biomass of food available did not constrain the intake rate and that this was influenced by the energy needs resulting from the air temperature and foraging success the previous day. Indeed, the duration of nocturnal activity increased when a bird was not as active or remained in a zone of poor feeding quality, such as mor humus, the previous day. Nocturnal activity thus varied in relation to diurnal foraging success. It seems reasonable to suppose that there should be a relation between diurnal activity duration and food availability, although this was probably not statistically detectable because of small sample sizes in our data.

We did not consider the depletion of resources, which has a major influence on behaviour (Sutherland 1996). Most studies that have calculated the impact of vertebrate predators on earthworm populations from field observations and sampling suggest a minor effect of bird predation, with a depletion of 3–11% of the earthworm biomass (Judas 1989). However, Bengtson et al. (1976) found a depletion of 50% of earthworm biomass after 22 days of predation by golden plovers, *Pluvialis apricaria*, in Iceland. This intensive predation was restricted to certain fields (with short grass cover) and limited to the arctic summer when earthworms are active close to the ground

surface. Where densities of earthworms are high such as in meadows, the depletion effect is probably negligible, but it could be important where earthworm densities are lower as in woods. Logistic difficulties, the need to minimize the disturbance of birds and the removal of earthworms from sampled sites prevented us from measuring depletion rates. Ideally, we should have measured the biomasses available before the arrival of woodcocks in autumn, and measured it again after their departure. Assessments of earthworm depletion related to predation by woodcocks and measures of intake rates would be conceivable only with captive birds feeding in patches of controlled densities of earthworms. Because of the depletion and heterogeneity of earthworm patches, we compared activity durations in relation to an indicator of food quality in the diurnal habitat (i.e. humus type) instead of earthworm biomass.

Decision Rules

Since the activity durations in fields were not higher than in woods, the plateau of intake rates could be reached in the woods by day by some individuals, which were consequently not obliged to go to fields at night. The decision to go to fields was linked to activity in the diurnal site and the mean temperature at night, that is, the same variables that explained nocturnal activity durations. Because diurnal activity was probably linked to foraging success, the decision to go to fields was also indirectly related to foraging success during the day. We hypothesize that the most efficient individuals were those that could find a rich patch of earthworms in woods by day. These efficient birds could benefit from staying in the wood at night (i.e. saving energy and avoiding predation), but to do so would have to increase their daylight foraging time (i.e. activity rate) to reach their required daily food intake. This can be done only if woodland patches have enough food to allow feeding for several hours, but because densities of prey are always lower than in fields, overall daily activity time may be slightly longer. The birds that found the best patches in woods could exploit them throughout the winter (strategy Never). Other birds are likely to have found good patches that allowed them to stay in woods at night for a few days or weeks until depletion. Then they were forced to go to fields until they found another suitable patch (strategy Sometimes). This could be considered as a derivation of the marginal value theorem from optimal foraging theories, with birds foraging in poorer patches of food leaving them earlier than birds foraging in richer patches (Charnov 1976; Stephens & Krebs 1986). The birds of the Always strategy were those that did not find food-rich patches in their diurnal sites.

We believe that the decision to go to fields at night involves a trade-off between starvation and predation risks (Lima & Dill 1990). We were unable to test the direct effects of predation risk on behaviour, such as the increase in the number or the duration of pauses for vigilance, or an increase in the variance of activity (McVean & Huddlesey 1980; Lima & Dill 1990; Lima & Bednekoff 1999). However, we knew that predation rates were higher in fields (Duriez 2003), so we used habitat as a surrogate

variable for predation risk. Further work should develop experimental approaches (using predator decoys, for example) to investigate the effect of predation risk on vigilance parameters (duration of feeding bouts, number of vigilance pauses) in relation to environmental variations (moonlight, wind). Other factors such as hunting risk and territoriality must be considered in the decision to go to fields at night. However, the hunting risk cannot account for this decision directly because it occurs only during the day in woods. Hunting could have an indirect influence on the decision rules because the disturbance caused could prevent birds foraging for the necessary time and consequently force them to commute at night. Our data set cannot be used to test this hypothesis because most of the birds in this study were in a hunting-free reserve. Territoriality might prevent some individuals going to fields at night because they would lose their diurnal site. The patterns of site use are difficult to understand and it is rare to find woodcocks sharing the same site. Furthermore, some woodcocks change site very often whereas others remain faithful to one site throughout the winter (Duriez 2003). Further work is needed to determine whether territoriality exists in wintering woodcocks and whether it has an influence on the decision to commute.

The existence of these strategies was unknown before our study. The very small proportion of birds that never went to fields ($N = 2$) probably reflected the scarcity of rich feeding sites in woodlands. These two individuals spent the day in wet forests with mull humus. In the wintering population, there were probably other very efficient individuals which never went to fields at night but they were impossible to monitor, since we captured birds only in fields. For conservation purposes, the management of such rich places (shrub cover, liming, introduction of ameliorating trees; see Duriez 2003 for details on management practices) would allow more woodcocks to stay in woods at night and consequently decrease their risk of predation and energy expenditures.

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References

- Aebischer, N. J., Robertson, P. A. & Kenward, R. E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, **74**, 1313–1325.
- Bakken, G. S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. *Auk*, **107**, 587–594.
- Bednekoff, P. A., Biebach, H. & Krebs, J. 1994. Great tit fat reserves under unpredictable temperatures. *Journal of Avian Biology*, **25**, 156–160.
- Bengtson, S.-A., Nilsson, A., Nordström, S. & Rundgreen, S. 1976. Effect of bird predation on lumbricid populations. *Oikos*, **27**, 9–12.
- Boos, M. 2000. Modification des réserves énergétiques corporelles du canard colvert (*Anas platyrhynchos*) et de la bécasse des bois (*Scolopax rusticola*) au cours de leur hivernage: aspects fonctionnels liés à la biologie de ces espèces et aux conditions du milieu. Thèse de doctorat, Université Louis Pasteur.
- Bouché, M. B. & Alliaga, R. 1986. Contre une dégradation physique et chimique des sols et pour leur optimisation économique, l'échantillonnage des lombriciens: une urgente nécessité. *La Défense des Végétaux*, **242**, 30–36.
- Caccamise, D. F. & Hedin, R. S. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin*, **97**, 306–318.
- Caraco, T., Blanckenhorn, W. U., Gregory, G. M., Newman, J. A., Recer, G. M. & Zwicker, S. M. 1990. Risk-sensitivity: ambient temperature affects foraging choice. *Animal Behaviour*, **39**, 338–345.
- Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology*, **9**, 129–136.
- Clausager, I. 1973. Age and sex determination of the woodcock (*Scolopax rusticola*). *Danish Review of Game Biology*, **8**, 1–18.
- Cramp, S. & Simmons, K. E. L. 1983. *Scolopax rusticola* woodcock. In: *Handbook of the Birds of Europe, the Middle East and North Africa* (Ed. by S. Cramp & K. E. L. Simmons), pp. 444–457. Oxford: Oxford University Press.
- Cuthill, I. C. & Houston, A. I. 1997. Managing time and energy. In: *Behavioural Ecology. An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 97–120. Oxford: Blackwell Science.
- Cuthill, I. C., Maddocks, S. A., Weall, C. V. & Jones, E. K. M. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. *Behavioral Ecology*, **11**, 189–195.
- Duriez, O. 2003. Individual wintering strategies in the Eurasian woodcock *Scolopax rusticola*: energetic trade-offs for habitat selection. Ph.D. thesis, Université de Paris VI. Available at http://tel.ccsd.cnrs.fr/documents/archives0/00/00/35/09/index_fr.html
- Duriez, O., Pastout-Lucchini, L., Boos, M., Chastel, O., Fritz, H., Ferrand, Y. & Clobert, J. 2004. Low levels of energy expenditures in a nocturnal, forest-dwelling wader, the Eurasian woodcock *Scolopax rusticola*. *Ardea*, **92**, 31–42.
- Ekman, J. B. & Hake, M. K. 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. *Behavioral Ecology*, **1**, 62–67.
- Exo, K.-M., Eggers, U., Laschewski-Sievers, R. & Scheiffarth, G. 1992. Monitoring activity patterns using a micro-computer-controlled radiotelemetry system, tested for waders (Charadrii) as an example. In: *Wildlife Telemetry. Remote Monitoring and Tracking of Animals* (Ed. by I. G. Priede & S. M. Swift), pp. 79–87. Chichester: Ellis Horwood.
- Fadat, C. 1994. *La Bécasse des Bois*. Paris: Office National de la Chasse.
- Ferrand, Y. & Gossmann, F. 1995. *La Bécasse des Bois*. Paris: Hatier.
- Gill, J. A., Sutherland, W. J. & Norris, K. 2001. Depletion models can predict shorebird distribution at different spatial scales. *Proceedings of the Royal Society of London, Series B*, **268**, 369–376.
- Goss-Custard, J. D., West, A. D. & Sutherland, W. J. 1996. Where to feed. In: *The Oystercatcher: from Individual to Populations* (Ed. by J. D. Goss-Custard), pp. 105–132. Oxford: Oxford University Press.
- Gossmann, F., Ferrand, Y., Loidon, Y. & Sardet, G. 1988. Méthodes et résultats de baguages des bécasses des bois (*Scolopax rusticola*) en Bretagne. In: *3ème Symposium Européen sur la Bécasse et la Bécassine* (Ed. by P. Havet & G. Hiron), pp. 34–41. Paris: Office National de la Chasse.
- Granval, P. & Bouché, M. B. 1993. Importance of meadows for wintering Eurasian woodcock in the west of France. In: *8th American Woodcock Symposium* (Ed. by J. R. Longcore & G. F. Sepik), Page 135. Washington, D.C.: U.S. Fish and Wildlife Service.
- Hilton, G. M., Ruxton, G. D. & Cresswell, W. 1999. Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos*, **87**, 295–302.
- Hirons, G. & Bickford-Smith, P. 1983. The diet and behaviour of Eurasian woodcock wintering in Cornwall. In: *2nd European Woodcock and Snipe Workshop* (Ed. by H. Kalchreuter), pp. 11–17. Fordingbridge: International Waterfowl Research Bureau.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, **91**, 385–398.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.
- Jabiol, B., Brêthes, A., Ponge, J.-F., Toutain, F. & Brun, J.-J. 1995. *L'Humus sous Toutes ses Formes*. Nancy: Ecole Nationale du Génie Rural et des Eaux et Forêts.
- Judas, M. 1989. Predator-pressure on earthworms: field experiment in a beechwood. *Pedobiologia*, **33**, 339–354.
- Kalas, J. A., Lofdaldli, L. & Fiske, P. 1989. Effects of radio packages on great snipe during breeding. *Journal of Wildlife Management*, **53**, 1155–1158.
- Kenward, R. E. 2001. *A Manual for Wildlife Radio Tagging*. London: Academic Press.
- Kersten, M. & Visser, W. 1996. The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. *Functional Ecology*, **10**, 440–448.
- Lee, K. E. 1985. *Earthworms. Their Ecology and Relationships with Soils and Land Use*. Sydney: Academic Press.
- Lima, S. L. & Bednekoff, P. A. 1999. Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? *Animal Behaviour*, **58**, 537–543.
- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- Littel, R. C., Freund, R. J. & Spector, P. C. 1991. *SAS System for Linear Models*. 3rd edn. Cary, North Carolina: SAS Institute Inc.
- Ludwig, D. & Rowe, L. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. *American Naturalist*, **135**, 686–707.
- McAuley, D. G., Longcore, J. R. & Sepik, G. F. 1993. Techniques for research into woodcock: experiences and recommendations. In: *8th American Woodcock Symposium* (Ed. by J. R. Longcore & G. F. Sepik), pp. 5–13. Washington D.C.: U.S. Fish and Wildlife Service.
- McGowan, A., Cresswell, W. & Ruxton, G. D. 2002. The effects of daily weather variation on foraging and responsiveness to disturbance in overwintering red knots *Calidris canutus*. *Ardea*, **90**, 229–237.
- McNamara, J. M. & Houston, A. I. 1994. The effect of change in foraging options on intake rate and predation rate. *American Naturalist*, **144**, 978–1000.

- McVean, A. & Haddlesey, P.** 1980. Vigilance schedules among house sparrows *Passer domesticus*. *Ibis*, **122**, 533–536.
- Poier, K. R. & Richter, J.** 1992. Spatial distribution of earthworms and soil properties in an arable loess soil. *Soil Biology and Biochemistry*, **24**, 1601–1608.
- Rabe, D. L., Prince, H. H. & Beaver, D. L.** 1983. Feeding-site selection and foraging strategies of American woodcock. *Auk*, **100**, 711–716.
- Rossi, J. P., Lavelle, P. & Albrecht, A.** 1997. Relationships between spatial pattern of the endogeic earthworm *Polypheretima elongata* and soil heterogeneity. *Soil Biology and Biochemistry*, **29**, 485–488.
- SAS Institute** 2000. *SAS User's Guide: Statistics, Version 8*. Cary, North Carolina: SAS Institute Inc.
- SPSS** 1999. *SPSS Base 10.0 User's guide*. Chicago: SPSS Inc.
- Stephens, D. W. & Krebs, J. R.** 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Sutherland, W. J.** 1996. *From Individual Behaviour to Population Ecology*. Oxford: Oxford University Press.
- Thompson, F. R. & Fritzell, E. K.** 1988. Ruffed grouse winter roost site preference and influence on energy demands. *Journal of Wildlife Management*, **52**, 454–460.
- Wiersma, P. & Piersma, T.** 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. *Condor*, **96**, 257–279.
- Zwarts, L., Cayford, J. T., Hulscher, J. B., Kersten, M., Meire, P. M. & Triplet, P.** 1996. Prey size selection and intake rate. In: *The Oystercatcher: from Individual to Populations* (Ed. by J. D. Goss-Custard), pp. 30–55. Oxford: Oxford University Press.