Responses of Eurasian woodcock Scolopax rusticola to simulated hunting disturbance

Authors: Ferrand, Yves, Aubry, Philippe, Landry, Philippe, and Priol, Pauline

Original article

Responses of Eurasian woodcock *Scolopax rusticola* to simulated hunting disturbance

Yves Ferrand, Philippe Aubry, Philippe Landry & Pauline Priol

The Eurasian woodcock *Scolopax rusticola* is a valued game species in southwestern Europe, which is locally under a high hunting pressure. Disturbance due to hunting can lead to avoidance of wintering areas or have an impact on population dynamics owing to behavioural changes. We studied the impact of disturbance on 54 radio-tagged woodcocks under an experimental framework. The birds were allocated to the following three groups: simulated hunting disturbance (controlled disturbance; CD), hunted (H) and control (C). We studied the following four behavioural elements: space use, activity duration, number of commuting flights and date of spring migration departure. We found no differences in behavioural responses between the groups except for space use. A majority of CD birds used larger ranges during daytime than did H and C birds but did not change their nocturnal sites. To a large extent, this nocturnal site fidelity likely accounted for the weak disturbance effect, in so far as food intake was ensured. Our study underlines the importance of permanent meadows in the surroundings of forests to help this species to better withstand hunting disturbance.

Yves Ferrand, Philippe Aubry & Philippe Landry, Office national de la chasse et de la faune sauvage, Direction des études et de la recherche, BP 20, F-78612 Le Perray-en-Yvelines Cedex, France - e-mail addresses: yves.ferrand@oncfs.gouv.fr (Yves Ferrand); philippe.aubry@oncfs.gouv.fr (Philippe Aubry); philippe.landry@oncfs.gouv.fr (Philippe Landry)
Pauline Priol*, Fédération départementale des chasseurs du Morbihan, BP 409, F-56010 Vannes Cedex, France - e-mail: pauline_priol@yahoo.fr

*Present address: Université du Québec en Abitibi-Témiscamingue, 445 Bd. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada

Corresponding author: Yves Ferrand

Disturbance by recreational activities such as walking or hunting can lead to habitats being avoided and is often considered as a major issue in species conservation. However, the impact of disturbance can vary among species or among individuals of the same species, depending on factors such as food availability or the density of competitors (Gill & Sutherland 2000). From a behavioural point of view, disturbance has been considered similar to a predation risk, as suggested by Frid & Dill (2002) in their 'risk-disturbance hypothesis', predicting that high disturbance levels may cause population declines. For game species, this hypothesis seems to be particularly relevant as hunting disturbance can sometimes even be directly related to a high mortality risk.

Many studies on game species have addressed the effects of human disturbance; some of them directly related to hunting. For waterfowl, for example, hunting disturbance can force birds to leave a site (Madsen 1998a,b) or use unsuitable habitats (Bregnballe et al. 2004). The time budget can also be affected by disturbance with an increase in feeding activities at the expense of comfort activities (Guillemain et al. 2007). Madsen (1998a) showed that such increases in feeding time after disturbance could be needed to compensate for energy loss due to involuntary flights.

In other cases, the lack of foraging during the daytime can be compensated for by night-time feeding (Bélanger & Bédard 1990, Madsen & Fox 1995, Riddington et al. 1996). At the end of winter, most migratory bird species hit their lowest weight and need to store fat before spring migration (Piersma & Van Brederode 1990). Therefore, disturbance occurring just before migration can also be expected to impact on the date of departure as has been shown in the Icelandic black-tailed godwit *Limosa limosa islandica,* for which wintering in poor quality habitat delayed the date of spring migration departure (Gunnarsson et al. 2006).

Disturbance impact studies have usually been based on field observations of behavioural responses in a non-experimental situation. In such studies, disturbance can be caused, for instance, by pedestrians (e.g. Fernández-Juricic 2000, Gill et al. 2001, Lafferty 2001, Guillemain et al. 2007), hunters (e.g. Madsen 1998a, Paillisson et al. 2002, Béchet et al. 2004) or dogs (e.g. Langston et al. 2007). In some studies, measures such as the restriction of pedestrians to certain footpaths (Lafferty 2001, Pearce-Higgins et al. 2007) or the creation of hunting-free reserves (Madsen 1998b, Evans & Day 2002) have enabled the comparison of different levels of disturbance (e.g. Fox & Madsen 1997, Thomas et al. 2003). In other studies, modelling has been used to predict disturbance effects (e.g. Beale & Monaghan 2004, Klaassen et al. 2006, Liley & Sutherland 2007, Stillmann et al. 2007). Some of the studies which have experimentally explored disturbance effects (e.g. Lord et al. 2001, Bregnballe et al. 2009) compared different levels of disturbance (e.g. Baines & Richardson 2007) as recommended by Hill et al. (1997). The majority of studies have been carried out in open areas (mainly wetlands) and rarely in woodlands (e.g. Fernández-Juricic et al. 2004). Finally, most studies have concerned the breeding period (Hill et al. 1997), although in some taxa, disturbance is considered critical in winter, when scarce food and harsh weather conditions may cause high energy requirements (Madsen 1995, Stillmann & Goss-Custard 2002). The Eurasian woodcock *Scolopax rusticola* (hereafter woodcock) is an interesting biological model to explore disturbance effects in so far as 1) it is a forest and game species, 2) densities are locally high in winter and 3) it is a solitary species which allows a study of disturbance effects at the individual level.

In Europe, woodcocks winter mainly in the southwestern part, in the Channel, in the Atlantic and Mediterranean regions (Cramp & Simmons 1983). In France, a large proportion of woodcocks winter in Brittany (Ferrand & Gossmann 2000). In winter, the woodcock uses woodlands or hedges during the day and conduct 'commuting flights' (Duriez et al. 2005c) to open areas, mostly meadows, at night to feed mainly on earthworms, principally *Lumbricus rubellus, L. terrestris, L. centralis* and *Aporrectodea caliginosa* (Granval 1987, Hoodless 2002, Duriez et al. 2005c), depending on foraging success during the day (Duriez et al. 2005b).

In spite of an increasing interest in woodcock hunting in the southwestern part of its wintering range, studies on hunting disturbance effects are lacking. In our study, we used an experimental approach to explore effects of repeated disturbance events on woodcock wintering behaviour to provide management recommendations and to ensure sustainable use of the species. We divided radio-equipped woodcocks into undisturbed and disturbed groups. We hypothesised that compared to undisturbed control birds, disturbed birds 1) enlarge their space use, 2) commute to open areas at night more often to increase feeding activities, 3) are active for longer diurnal and/or nocturnal periods to compensate for energy loss, and 4) delay their spring migration departure because of a longer period required to deposit fat.

Material and methods

Study area

The study area (ca 2,000 ha) is located in Brittany (western France) and encompassed the Pont-Calleck State Forest (47°57'27''N, 3°21'42''W), adjacent woodlands and surrounding thickets and fields. All make up suitable habitats for the woodcock. The State Forest was composed of 80% deciduous (40-120 years old, including mainly oaks such as *Quercus robur* and *Quercus rubra* and beech *Fagus sylvatica*), and 20% of coniferous stands (15-40 years old, including mainly douglas-fir *Pseudotsuga menziesii*, sitka spruce *Picea sitchensis* and Scots pine *Pinus sylvestris*). The shrub stratum contained holly *Ilex aquifolium* and chestnut *Castanea sativa*. Adjacent woodlands were similar in composition and included various successional stages. Surrounding open areas were constituted of maize and cereal stubbles, winter wheat, ryegrass and permanent meadows (20%), oilseed rape and mustard fields. The Pont-Calleck

State Forest was a woodcock hunting-free reserve whereas adjacent woodlands were woodcock hunting areas. Hereafter, the forest will be called the 'reserve' and the adjacent woodlands the 'hunting area'. In France, woodcock is mainly hunted using one or two pointing dogs by a solitary hunter. The frequency of hunting trips is highly variable, but usually comprised 1-2 days/week/hunter.

Data collection

Our study was carried out during three consecutive winters (2003/04, 2004/05 and 2005/06). Since woodcock is a solitary, elusive and cryptic species which lives in woodlands, we used radio-telemetry in our study. From the beginning of December to the beginning of January, we captured 54 woodcocks (18 in 2003/04, 16 in 2004/05 and 20 in 2005/06) on feeding sites around the reserve in the first part of the night using a spotlight and a landing net (Gossmann et al. 1988). We chose this timing to ensure that the post-nuptial migration had ceased and that birds remained in the study area (Ferrand & Gossmann 2001). In November, woodcocks are abundant in Brittany; however, it is not possible to distinguish between migrating and wintering birds.

We aged each bird (1st year vs adult) according to wing feather details and moult status (Ferrand & Gossmann 2009a), and we sexed each bird by DNA analysis following the Sambrook et al. (1989) protocol. We fitted each bird with a VHF radio-transmitter (Biotrack® TW3; 12 g) with an activity tiltswitch. We glued the transmitter on the back of the bird using hypoallergenic livestock glue and maintained with a single-loop harness (Mac Auley et al. 1993).

We located each bird using a hand-held antenna by day (approached by circling to 10 m) and by night (approached by circling to 50 m), 5-6 times/week. We plotted the locations on a 1:2,000 map (source: Institut Géographique National) using a GIS package (ArcView® 3.3, ESRI, Redlands, USA). We calculated movement distances between locations using the Animal Movement extension (Hooge et al. 1999) in ArcView.

We recorded activity data for 24-hour periods. Recording started around 12:00 hours to get the activity rate during an afternoon, a full night and a morning. We used an automatic data logger (RX-900; Televilt Positioning AB, Lindesberg, Sweden) connected to a 4-element directional Yagi antenna, or a car omni-directional whip antenna located < 200 m from the bird. Depending on marked individuals' survival, we carried out 1-4 recordings/

bird. We processed activity files using a program specially developed under the Visual Basic programming interface of Sigma Plot 2001 V.7.1 (SPSS Inc., Chicago, USA). We defined the beginning and the end of the night as the evening and morning civil twilights, which roughly correspond to the time when the commuting flight occurs. In our analyses, we considered the daylight/night activity rates separately. 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 (see Duriez et al. 2005b for more details).

When nocturnal locations differed from diurnal locations (i.e. open areas vs forest, at a distance of > 50 m from the forest edge), the occurrence of a commuting flight was registered. We defined a commuting flight index as the proportion of nights on which birds left the woodland.

We defined disturbance as flushing a bird from its diurnal site. We allocated the radio-tagged woodcocks to three groups: controlled disturbance (CD; N = 16), hunted (H; N = 15) and control (C; N = 23). In the daytime, the radio-equipped woodcocks spread over the reserve and the hunting area, and maintained their daytime ranges throughout the study. We randomly allocated each radio-tagged woodcock staying in the reserve into CD and C birds. We classified all other birds staying in the hunting area in the daytime as H. The H birds were exposed to variable disturbance depending on hunters' activity, with no possibility of precisely registering the number of hunters, dogs, hunting hours and days. This explains the necessity of a CD group to ensure a homogeneous disturbance level. The CD birds were flushed once/day and 5 days/week (maximum number of hunting days allowed in the study area, and more generally in France, according to regional administrative decisions). Disturbance started between the 10th and 15th of January, when post-nuptial migration ceased (Ferrand & Gossmann 2001). Every winter, disturbance concluded at the end of February (closing period for woodcock hunting in France). We flushed the birds between 09:00 and 17:00 hours, as this period corresponds to the usual hunting hours. In most cases, we saw the bird in flight. In other cases, we considered disturbance as effective when the radio signal rapidly diminished.

We restricted the analysis to the period between the beginning of disturbance (mid-January) and the end of February for all behavioural responses, except the date of spring migration departure, which we

analysed for woodcocks for which we knew this date. For all woodcocks, at least 30 diurnal locations were available. For the time-budget analysis, we took into account only individual activity recordings for which at least 50% of the time (in the daytime or at night) was actually monitored. We used only data collected at least six days after radio-transmitter fitting to avoid a behavioural impact due only to tagging (Kenward 2001). Disturbance started six days after tagging to allow enough time for observing a real disturbance impact.

Data analysis

For all the statistical tests performed for our study, we did not rely on an arbitrary α-level of statistical significance and strictly interpreted the P-value as the strength of the evidence against the null hypothesis H_0, conditionally to the data at hand (a P-value is defined as the probability, calculated under H_0, of obtaining a test value as extreme as that observed in the sample; see Gibbons 2006). Whatever the magnitude of the P-value, we gave a measure of the effect size, since one always needs to carefully consider the biological significance of a result, not just the statistical significance (Yoccoz 1991).

Space use

To summarise the statistical distribution of the daily distances woodcocks travelled, we used the median as a position measurement and the interquartile range to represent dispersion, because the distances were not symmetrically distributed. Using the median as abscissa and the interquartile range as ordinate allows one to represent the birds as points in a scatterplot. For studying space use during the day and at night, we employed a Multiple Response Permutation Procedure (MRPP; Zimmerman et al. 1985, McCune & Grace 2002:188-197, Mielke & Berry 2007) to test the null hypothesis H_0 of no difference between the three groups CD, H and C. The MRPP test was based on the Euclidean distances defined in the scatterplot, with natural weighting of the groups (McCune & Grace 2002:189, Mielke & Berry 2007:20). Hence, the MRPP statistic δ was the overall weighted mean of within-group means of the pairwise Euclidean distances. No distributional assumptions are required for MRPP testing purposes. We evaluated the P-value by using a randomisation procedure (see Edgington 1995, Manly 1997, Edgington 2006). To obtain an accurate P-value, we used 10^6 random permutations as in Mielke & Berry

(2007:33-35), and the minimum attainable P-value was thus P = 0.000001. We provided an effect size measure using the 'chance corrected within-group agreement' (McCune & Grace 2002:190, Mielke & Berry 2007:31):

$$A = 1 - \frac{\delta_{obs}}{\mu}$$

with δ_{obs} being the observed value of the statistic δ measuring the within-group homogeneity (see Zimmerman et al. 1985, McCune & Grace 2002:189, Mielke & Berry 2007:14) and μ the expectation of the statistic δ under H_0. The statistic A is a chance-corrected measure of effect size, i.e. A reflects the within-group homogeneity compared to what would be expected by chance. A reaches its maximum value of 1 when the within-group homogeneity is perfect. A = 0 when the within-group homogeneity is equal to what is expected by chance. Like all chance-corrected measures, A could occasionally be slightly negative, i.e. when the within-group homogeneity is smaller than what is expected by chance. In ecology, values for A are commonly below 0.1 even when the δ_{obs} differs significantly from the expectation under H_0, and A > 0.3 is fairly high (McCune & Grace 2002:191). Furthermore, we used MRPP for testing the null hypothesis of no difference between males and females, and between yearlings and adults.

Time budgets

We recorded time budgets repeatedly for each bird (up to four times for a bird during the winter). The response variable was the duration expressed in minutes. We tested the null hypothesis of no difference between the three groups CD, H and C by using a mixed-model two-way nested ANOVA with the group as first (fixed) factor, and the bird as second (random) factor (Sokal & Rohlf 1995, Quinn & Keough 2002). We transformed the response variable using the Box-Cox transformation (Sokal & Rohlf 1995, Quinn & Keough 2002) to improve both normality and homoscedasticity. Because the design was unbalanced (the number of birds within each group was different and the number of measurements for each bird was also different), we used the sum of squares of type III (Searle 1987:459, 463) according to the recommendation of Shaw & Mitchell-Olds (1993). We provided the effect size using the partial Eta square η_p^2 (e.g. Tabachnick & Fidell 2007:55, equation 3.26).

Occurrences of commuting flights

We coded commuting flights as 1 in a binary presence/absence table for the dates (q = 20 columns) for which data were available for all the birds (N = 49 rows). We used MRPP to test the null hypothesis of no difference in the pattern of occurrences of commuting flights between the three groups CD, H and C. We used the simple matching dissimilarity (Legendre & Legendre 1998:255) calculated between the birds, on the basis of the presence/absence of commuting flights for the 20 dates.

Dates of spring migration departure

We tested the effects of the disturbance group (CD, C, H) on the date of spring migration departure using one-way ANOVA (Sokal & Rohlf 1995, Quinn & Keough 2002). No transformation was necessary to improve normality and homoscedasticity. In case of a small effect of the group on the activity duration or the date of spring migration departure, we pooled the data and tested the effect of sex or age in the same way. We provided the effect size using the correlation ratio squared, i.e. the Eta squared η^2 (e.g. Tabachnick & Fidell 2007:54, equation 3.25).

Results

Space use

For both C (N = 22) and H (N = 15) groups, the median distance between successive diurnal locations per bird was always < 150 meters (average median = 63.9 and 51.4 m, respectively, SD = 28.7 and 30.5, respectively, range: 23.1-132.8 and 0-99.7 m, respectively). For these two groups, the maximal distances between successive diurnal locations for any bird were 1.1 km and 3.24 km, respectively. For the CD group (N = 15), the distances between successive locations were in most cases very large and irregular (average median = 241.3 m, SD = 174.8, range: 48.9-731.6 m; Fig. 1). For 10 CD birds, the median was > 150 m and the maximal distance between successive diurnal locations was 4.03 km. For five CD birds, the median was < 150 m. One CD bird left the study area after 13 days of disturbance (last distance between two locations = 5,510 m). The representation of birds on a scatterplot according to their median and interquartile range of distances led us to separate CD from the C and H groups (MRPP test: P = 0.000002, A = 0.225; Fig. 2). The dispersion of birds

Figure 1. Details of diurnal movements and nocturnal locations for a controlled disturbance group woodcock (CD). No change is observed in the use of nocturnal sites in spite of the diurnal movements. (Pont-Calleck State Forest, France; winter of 2003/04).
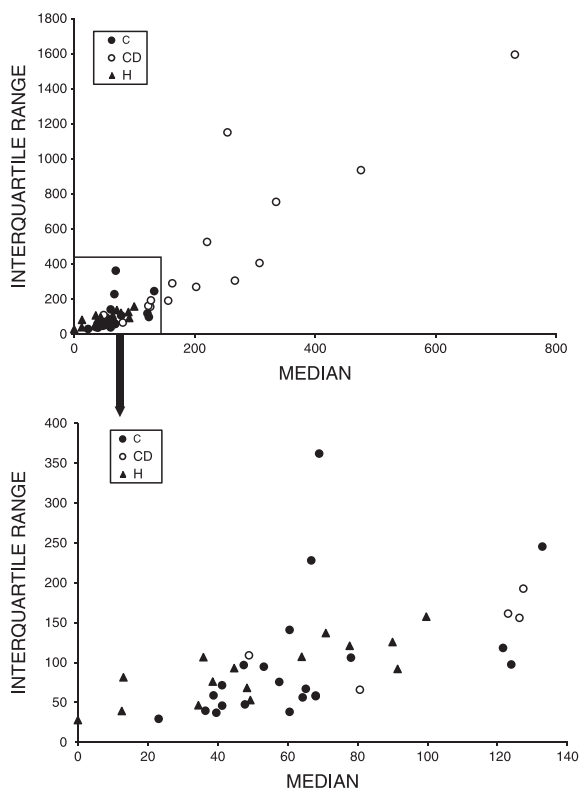
Figure 2. Median and interquartile range of distances between successive diurnal locations of control group woodcocks (C), controlled disturbance group woodcocks (CD) and hunted group woodcocks (H). (Pont-Calleck State Forest, France; winters of 2003/04, 2004/05 and 2005/06).
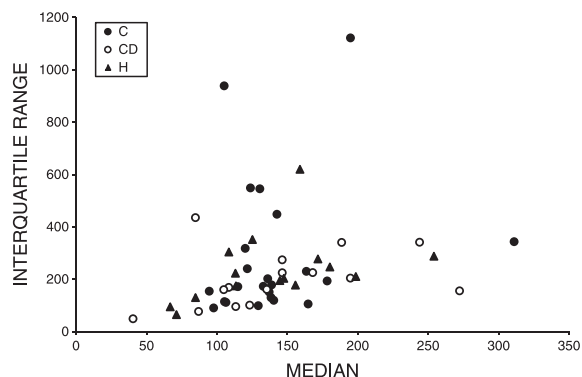

Figure 3. Median and interquartile range of distances between successive nocturnal locations of control group woodcocks (C), controlled disturbance group woodcocks (CD) and hunted group woodcocks (H). (Pont-Calleck State Forest, France; winters of 2003/04, 2004/05 and 2005/06).

on the scatterplot appeared to be not mainly related to age and sex since the levels of evidence against H_0 and the effect sizes were much lower in comparison with the disturbance groups (MRPP test: P = 0.056, A = 0.025 and P = 0.017, A = 0.044, respectively).

At night, space use appeared to be very similar among groups (MRPP test: P = 0.51, A = -0.004). In spite of the impact of disturbance on diurnal space use, CD birds did not change their nocturnal sites (see Fig. 1). The representation of birds according to their median and interquartile range of distances did not lead us to separate any group (Fig. 3). The maximal distance between successive nocturnal locations was 3.33 km.

Time budgets
The mean of diurnal activity duration was 49.0 minutes (range: 2.0-231.0) for the CD group (13 birds, 24 measures), 65.9 minutes (range: 2.7-192.9) for H group (15 birds, 26 measures) and 78.4 minutes

(range: 2.3-266.8) for C group (20 birds, 32 measures). We found no evidence of a difference between disturbance groups (P = 0.47; F = 0.76; $\eta_p^2 = 6.23\%$). We found weak evidence that diurnal activity duration differed according to age (P = 0.16; F = 2.97; $\eta_p^2 = 10.80\%$) or sex (P = 0.091, F = 2.07; $\eta_p^2 = 8.13\%$). The occurrence of a commuting flight can have an impact on the time budget in so far as birds shared their activity between day and night. However, even weaker effects were obtained for a subset of the data taking into account only diurnal data including a commuting flight, between disturbance groups (P = 0.55, F = 0.61, $\eta_p^2 = 5.77\%$), age (P = 0.49, F = 0.47, $\eta_p^2 = 2.34\%$) and sex (P = 0.30, F = 1.09, $\eta_p^2 = 4.95\%$).

The mean of nocturnal activity duration was 127.4 minutes (range: 4.8-297.8) for CD group (12 birds, 22 measures), 94.75 minutes (range: 5.0-224.8) for H group (12 birds, 25 measures) and 142.8 minutes (range: 3.3-302.9) for C group (21 birds, 31 measures).We found weak evidence that nocturnal activity durations significantly differed between groups (P = 0.14, F = 2.07, $\eta_p^2 = 12.75\%$), and no evidence with respect to age (P = 0.45, F = 0.57, $\eta_p^2 = 2.03\%$) or sex (P = 0.60; F = 0.28; $\eta_p^2 = 1.04\%$). We obtained similar results for birds that commuted from forest to fields at night, for the disturbance groups (P = 0.11; F = 2.29; $\eta_p^2 = 16.65\%$), age (P = 0.80; F = 0.07, $\eta_p^2 = 0.31\%$) and sex (P = 0.96, F = 0.00, $\eta_p^2 = 0.01\%$).

Occurrences of commuting flights
We did not find sufficient evidence that the pattern of occurrences of commuting flights differed between C

(N=21), CD (N=14) and H (N=14) groups (MRPP test: P=0.43, A=0.0007) or according to the sex (P=0.14, A = 0.008) or age (P = 0.08, A = 0.011). This allowed us to pool the data and the mean commuting flight index (proportion of nights on which birds left the woodland) was 0.88.

Dates of spring migration departure

The spring migration departure date ranged from 7 March to 6 April with an average date of 21 March (N = 46; Fig. 4A). The ANOVA revealed only weak evidence of an effect of the groups C (N=20), CD (N =13) and H (N=13) on the dates of spring migration departure (P = 0.085; F = 2.62; η^2 = 10.85%), the order of the average dates being CD < H < C. By
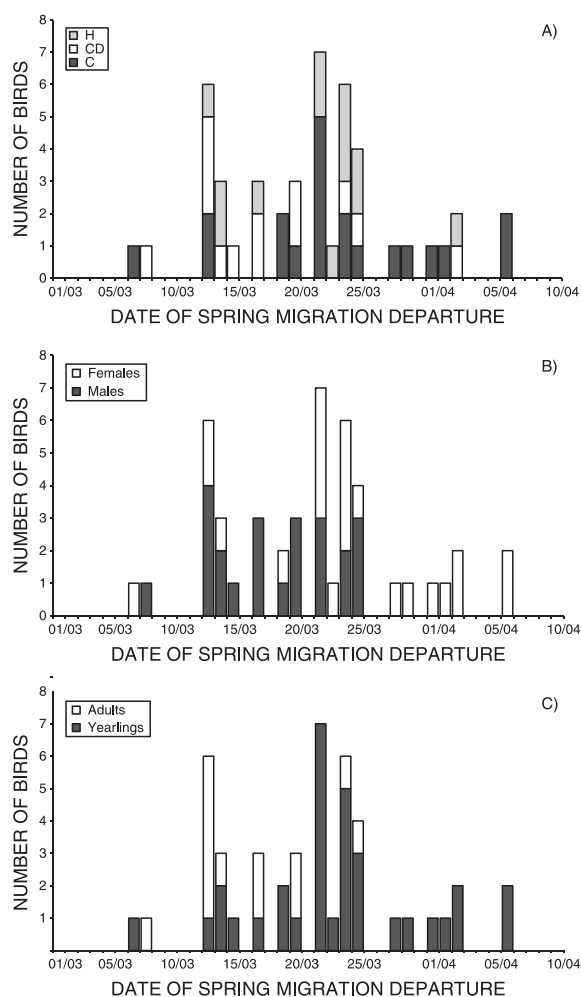

Figure 4. Distribution of dates of spring migration departure between control group woodcocks (C), controlled disturbance group woodcocks (CD) and hunted group woodcocks (H; A), between sex (B) and age classes (C). (Pont-Calleck State Forest, France; winters of 2003/04, 2004/05 and 2005/06).

contrast, there was more evidence that 1) males (N= 23) departed before females (N= 23) (mean dates:18 March and 24 March, respectively; Fig. 4B; P = 0.003; F = 9.58; η^2 = 17.87%), 2) adults (N = 13) departed before 1st year birds (N=33) (mean dates: 16 March and 23 March, respectively; Fig. 4C; P = 0.001; F = 11.96; η^2 = 21.37%).

Discussion

Disturbance effects

From our experimental study, the impact of simulated hunting disturbance on woodcock wintering behaviour seemed to be relatively weak. As expected, disturbance increased the space use. However, we found no impact on diurnal and/or nocturnal activity durations, occurrences of commuting flights, and only a weak effect on spring migration departure.

The main impact was a larger space use during the daytime for the CD woodcocks, one of which left the study area. Such large movements were not observed at night. By contrast, whatever the location of the diurnal site, the CD woodcocks kept a previous nocturnal site where most of their feeding occurred (Duriez et al. 2005b). This site fidelity was surprising considering the large distance sometimes separating diurnal and nocturnal sites (> 1.5 km), although closer nocturnal sites were available. Like many other bird species, wintering woodcocks face a trade-off between starvation and predation risk (Duriez et al. 2005b), and previous experience of suitable nocturnal sites with high food resources could encourage birds to continue using these sites. Exploring new nocturnal sites could also increase energy expenditures, which could be detrimental to the birds in the winter period. The nocturnal site fidelity probably explained, to a large extent, the weakness of the disturbance effect in so far as food intake was ensured. Of the woodcocks, four always remained in their diurnal sites in spite of a high level of disturbance. This indicated that the responses to disturbance can vary greatly among individuals, probably in relation to the quality of the occupied site and/or information acquired by the individuals at their sites (Gill et al. 2001).

We found no difference in the occurrence of commuting flights between disturbed and undisturbed birds. Since the main purpose of these flights is feeding in meadows, this shows that disturbance did not force woodcocks to reach nocturnal feeding sites more frequently. Nevertheless, extra diurnal flights

of disturbed birds over large distances could imply a higher energy expenditure (as shown for the brent goose *Branta bernicla bernicla*; Riddington et al. 1996), a decrease in time available for foraging in less suitable sites (as reviewed by Frid & Dill 2002), and we could expect a higher nocturnal activity rate to compensate for this, as has been found for the sanderling *Calidris alba* (Burger & Gochfeld 1991) and the snow goose *Chen caerulescens atlantica* (Bélanger & Bédard 1990).We did not observe this in our study, likely because the high available earthworm biomass in meadows (about 1 ton/ha; Granval & Bouché 1993) does not constrain the instantaneous intake rate and easily allows woodcocks to compensate for a loss of diurnal foraging.

We found only a weak difference between disturbance groups; however, the order of spring migration departure seemed to be related to the disturbance level, i.e. the higher the disturbance level, the earlier the average date of departure. This suggests that even a high disturbance level does not impair preparation for migration, which is in contrast to the negative effect observed by Madsen (1995) for the pink-footed goose *Anser brachyrhynchus*. This could be related to the low energetic requirements of woodcock (Duriez et al. 2004) and/or a capacity to quickly increase energetic reserves as suspected by Duriez (2003). As an example, the whimbrel *Numenius phaeopus*, a similar-sized wader to the woodcock, is known to increase its daily food intake to 1.5 times the winter level a few weeks before spring migration departure (Zwarts 1990). As suggested by Klaassen (2002), another hypothesis could be to consider woodcock as an income breeder owing to its small size and relatively short flight range (< 3,000 km for the majority of woodcocks; Ferrand & Gossmann 2009b). In this case, energetic requirements before migration are rather low and only assigned to flight cost.

Simulation of hunting disturbance

In our study, the disturbance aimed to simulate hunting (without shooting). To apply a standardised protocol, we did not use hunting dogs to flush the birds. This seemed to be appropriate in so far as birds could be tracked using radio-telemetry and pursued till they flushed, i.e. as a hunting dog could have done it. Moreover, owing to radio-telemetry, the approach to the bird is usually direct, which is the most disturbing approach (Frid & Dill 2002). For standardisation, the birds were flushed once/day. This situation could be considered artificial compared

with a hunting situation. During hunting, some birds may be flushed several times while others are never flushed. We considered that the regularity (5 days/week) and the duration of the experiment (1.5 month) were sufficient to generate disturbance at a level at least as high as hunting. We showed that H birds staying in the hunting area did not seem to change their behaviour as compared to undisturbed C woodcocks. Since we showed that CD birds increased their space use, this suggests that the controlled disturbance level used in our study was likely higher than the level of disturbance caused by hunting.

However, our study period did not correspond entirely to the woodcock hunting period which really starts at the beginning of November in Brittany. During the two first hunting months, the hunting pressure (number of hunters/day) is higher than in January-February, i.e. our study period (Ferrand & Gossmann 2000). In November-December, both migrating and wintering woodcocks are hunted. Migratory birds stay in the forest during a short period and should not be concerned by disturbance. In contrast, woodcocks that have already reached their wintering sites could be more sensitive. Nothing allows us to assume that the behaviour of wintering woodcocks facing disturbance differs in January-February compared with November-December.

Wintering woodcock behaviour

Our results suggest that the behaviour of the studied population was consistent with wintering woodcock populations in Brittany as described in Duriez et al. (2005c). Space use (for C birds), occurrences of commuting flight, date of spring departure (23 February - 10 April for O. Duriez, unpubl. data) were not different from expectations. The only exception was the time budget with about 200 minutes of activity in our study as compared to 300 minutes reported by Duriez et al. (2005c). This might have resulted from higher availability of food resources in our study area. Weather conditions may have increased the availability of earthworms and/or decreased energy expenditures (Wiersma & Piersma 1994, Duriez et al. 2004) and, therefore, may have reduced the daily period required to feed. During the three winters of our study, no exceptional weather conditions were registered (see http://www.cdc.noaa.gov - Air temperature/Composite anomalies).

Management implications

In terms of woodcock habitat management, we

26

emphasise the role of nocturnal feeding habitats. Indeed, as shown by Goss-Custard et al. (2006) for the oystercatcher *Haematopus ostralegus*, the impact of disturbance appears much lower with good feeding conditions. Consequently, we recommend that a special effort be made to maintain grazed meadows in the surroundings of forests in woodcock wintering areas because the earthworm biomass in meadows is five times higher than in cultivated fields (Duriez et al. 2005a). Maintenance of permanent meadows may help woodcock to better withstand disturbance.

Our study addressed disturbance effects on a local scale, for one habitat type and in rather mild weather conditions. This could be different in other wintering conditions, especially with regard to habitat. In Mediterranean regions, for example, woodcock food resources are scarcer than in Brittany and the behavioural responses to disturbance could be different. Additional experiments in different habitats and food resource levels seem to be necessary to estimate the impact of disturbance at a population level, as recommended by Sutherland (2007) and Gill (2007).

References

Baines, D. & Richardson, M. 2007: An experimental assessment of the potential effects of human disturbance on black grouse *Tetrao tetrix* in the North Pennines, England. - Ibis 149 (s1): 56-64.

Beale, C.M. & Monaghan, P. 2004: Human disturbance: people as predation-free predators? - Journal of Applied Ecology 41: 335-343.

Béchet, A., Giroux, J.F. & Gauthier, G. 2004: The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. - Journal of Applied Ecology 41: 689-700.

Bélanger, L. & Bédard, J. 1990: Energetic cost of man-induced disturbance to staging snow geese. - Journal of Wildlife Management 54: 36-41.

Bregnballe, T., Madsen, J. & Rasmussen, P.A.F. 2004: Effects of temporal and spatial hunting control in waterbird reserves. - Biological Conservation 119: 93-104.

Bregnballe, T., Speich, C., Horsten, A. & Fox, A.D. 2009: An experimental study of numerical and behavioural responses of spring staging dabbling ducks to human pedestrian disturbance. - Wildfowl, special issue 2: 131-142.

Burger, J. & Gochfeld, M. 1991: Human activity influence and diurnal and nocturnal foraging of sanderlings (*Calidris alba*). - The Condor 93: 259-265.

Cramp, S. & Simmons, K.E.L. 1983: *Scolopax rusticola* woodcock. - In: Cramp, S. & Simmons, K.E.L. (Eds.); Handbook of the Birds of Europe, the Middle-East and North Africa. Vol. 3. Waders to Gulls. Oxford University Press, Oxford, UK, pp. 444-457.

Duriez, O. 2003: Individual wintering strategies in the Eurasian woodcock *Scolopax rusticola*: energetic trade-offs for habitat selection. - PhD thesis, University of Paris 6, France, 253 pp.

Duriez, O., Ferrand, Y., Binet, F., Corda, E., Gossmann, F. & Fritz, H. 2005a: Habitat selection of the Eurasian woodcock in winter in relation to earthworms availability. - Biological Conservation 122: 479-490.

Duriez, O., Fritz, H., Binet, F., Tremblay, Y. & Ferrand, Y. 2005b: Individual activity rates in wintering Eurasian woodcocks: starvation versus predation risk trade-off? - Animal Behaviour 69: 39-49.

Duriez, O., Fritz, H., Saïd, S. & Ferrand, Y. 2005c: Wintering behaviour and spatial ecology of Eurasian woodcock *Scolopax rusticola*, in western France. - Ibis 147: 519-532.

Duriez, O., Pastout-Lucchini, L., Boos, M., Chastel, O., Fritz, H., Ferrand, Y. & Clobert, J. 2004: Low levels of energy expenditure in a nocturnal forest-dwelling wader, the Eurasian woodcock *Scolopax rusticola*. - Ardea 92: 31-42.

Edgington, E.S. (Ed.) 1995: Randomization tests. 3rd edition, revised and expanded. - Marcel Dekker, New York, New York, USA, 406 pp.

Edgington, E.S. 2006: Randomization tests. - In: Kotz, S., Balakrishnan, N., Read, C.B., Vidakovic, B. & Johnson, N.L. (Eds.); Encyclopedia of statistical sciences. John Wiley & Sons, Hoboken, New Jersey, USA, pp. 6845-6852.

Evans, D.M. & Day, K.R. 2002: Hunting disturbance on a large shallow lake: the effectiveness of waterfowl refuges. - Ibis 144: 2-8.

Fernández-Juricic, E. 2000: Local and regional effects of pedestrians on forest birds in a fragmented landscape. - The Condor 102: 247-255.

Fernández-Juricic, E., Vaca, R. & Schroeder, N. 2004:

Spatial and temporal responses of forest birds to human approaches in a protected area and implications for two management strategies. - Biological Conservation 117: 407-416.

Ferrand, Y. & Gossmann, F. 2000: La Bécasse des bois - Enquête nationale sur les tableaux de chasse à tir. Saison 1998-1999. - Faune Sauvage 251: 96-105. (In French).

Ferrand, Y. & Gossmann, F. 2001: Elements for a woodcock (*Scolopax rusticola*) management plan. - Game and Wildlife Science 18: 115-139.

Ferrand, Y. & Gossmann, F. 2009a: Ageing and sexing series 5: Ageing and sexing the Eurasian woodcock *Scolopax rusticola*. - Wader Study Group Bulletin 116: 75-79.

Ferrand, Y. & Gossmann, F. 2009b: La Bécasse des bois - Histoire naturelle. - Effet de lisière-éditeur, Saint-Lucien, France, 222 pp. (In French).

Fox, A.D. & Madsen, J. 1997: Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. - Journal of Applied Ecology 34: 1-13.

Frid, A. & Dill, L.M. 2002: Human-caused disturbance stimuli as a form of predation risk. - Conservation Ecology 6(1): 11. Available at: http://www.mmc.gov/drakes_estero/pdfs/conservationecology_02.pdf (Last accessed on 3 August 2012).

Gibbons, J.D. 2006: P-values. - In: Kotz, S., Balakrishnan, N., Read, C.B., Vidakovic, B. & Johnson, N.L. (Eds.); Encyclopedia of statistical sciences. John Wiley & Sons, Hoboken, New Jersey, USA, pp. 6845-6852.

Gill, J.A. 2007: Approaches to measuring the effects of human disturbance on birds. - Ibis 149(s1): 9-14.

Gill, J.A., Norris, K. & Sutherland, W.J. 2001: Why be-havioural responses may not reflect the population consequences of human disturbance. - Biological Conservation 97: 265-268.

Gill, J.A. & Sutherland, W.J. 2000: Predicting the consequences of human disturbance from behavioural decisions. - In: Gosling, L.M. & Sutherland, W.J. (Eds.); Behaviour and Conservation. Cambridge University Press, Cambridge, UK, pp. 51-64.

Goss-Custard, J.D., Triplet, P., Sueur, F. & West, A.D. 2006: Critical thresholds of disturbance by people and raptors in foraging wading birds. - Biological Conservation 127: 88-97.

Gossmann, F., Ferrand, Y., Loidon, Y. & Sardet, G. 1988: Méthodes et résultats de baguages des bécasses des bois (*Scolopax rusticola*) en Bretagne. - In: Havet, P. & Hirons, G. (Eds.); Actes du 3ème Symposium Européen sur la Bécasse et les Bécassines, Paris, France, pp. 34-41. (In French).

Granval, P. 1987: Régime alimentaire diurne de la Bécasse des bois (*Scolopax rusticola*) en hivernage: approche quantitative. - Gibier Faune Sauvage 4: 125-147. (In French).

Granval, P. & Bouché, M.B. 1993: Importance of meadows for wintering Eurasian woodcock in the west of France. - In: Longcore, J.R. & Sepik, G.F. (Eds.); Proceedings of the Eight American woodcock Symposium, Washington, U.S. Fish and Wildlife Service, Biological Report 16: 135.

Guillemain, M., Blanc, R., Lucas, C. & Lepley, M. 2007: Ecotourism disturbance to wildfowl in protected areas: historical, empirical and experimental approaches in the Camargue, Southern France. - Biodiversity Conservation 16: 3633-3651.

Gunnarsson, T.G., Jennifer, A.G., Atkinson, P.W., Gél-inaud, G., Potts, P.M., Croger, R.E., Gudmundsson, G.A., Appleton, G.F. & Sutherland, W.J. 2006: Population-scale drivers of individual arrival times in migratory birds. - Journal of Animal Ecology 75: 1119-1127.

Hill, D., Hockin, D., Price, D., Tucker, G., Morris, R. & Treweek, J. 1997: Bird disturbance: improving the quality and utility of disturbance research. - Journal of Applied Ecology 34: 275-288.

Hoodless, A. 2002: Eurasian woodcock *Scolopax rusticola*. - In: Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (Eds.); The migration atlas: movements of the birds of Britain and Ireland. British Trust for Ornithology, UK, pp. 319-322.

Hooge, P.N., Eichenlaub, W. & Solomon, E. 1999: The animal movement program, Version 2.0. - Anchorage, USA: USGS, Alaska Biological Science Center. Available at: http://gcmd.nasa.gov/records/USGS_animal_mvmt.html (Last accessed on 3 August 2012).

Kenward, R.E. 2001: A Manual for Wildlife Radio Tagging. 2nd edition. - Academic Press, London, UK, 311 pp.

Klaassen, M. 2002: Relationships between migration and breeding strategies in arctic breeding birds. - In: Berthold, P., Gwinner, E. & Sonnenschein, E. (Eds.); Avian migration. Springer, Berlin, Germany, pp. 237-249.

Klaassen, M., Bauer, S., Madsen, J. & Tombre, I. 2006: Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. - Journal of Applied Ecology 43: 92-100.

Lafferty, K.D. 2001: Disturbance to wintering western snowy plovers. - Biological Conservation 101: 315-325.

Langston, R.H.W., Liley, D., Murison, G., Woodfield, E. & Clarke, R.T. 2007: What effects do walkers and dogs have on the distribution and productivity of breeding European Nightjar *Caprimulgus europaeus*? - Ibis 149(s1): 27-36.

Legendre, P. & Legendre, L. 1998: Numerical Ecology. - Elsevier, Amsterdam, The Netherlands, 853 pp.

Liley, D. & Sutherland, W.J. 2007: Predicting the population consequences of human disturbance for Ringed Plovers *Charadrius hiaticula*: a game theory approach. - Ibis 149(s1): 82-94.

Lord, A., Waas, J.R., Innes, J. & Whittingham, M.J. 2001: Effects of human approaches to nests of northern New Zealand dotterels. - Biological Conservation 98: 233-240.

Mac Auley, D.G., Longcore, J.R. & Sepik, G.F. 1993: Techniques for research into woodcock: experiences and recommendations. - In: Longcore, J.R. & Sepik, G.F. (Eds.); Proceedings of the Eight American woodcock

Symposium, Washington, USA, Fish and Wildlife Service, Biological Report 16: 5-13.

Madsen, J. 1995: Impacts of disturbance on migratory waterfowl. - Ibis 137(s1): 67-74.

Madsen, J. 1998a: Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. - Journal of Applied Ecology 35: 386-397.

Madsen, J. 1998b: Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. - Journal of Applied Ecology 35: 398-417.

Madsen, J. & Fox, A.D. 1995: Impacts of hunting disturbance on waterbirds - a review. - Wildlife Biology 1(4): 193-207.

Manly, B.F.J. 1997: Randomization, bootstrap and Monte Carlo methods in biology. - Chapman & Hall, London, UK, 424 pp.

McCune, B. & Grace, J.B. 2002: Analysis of ecological communities. - MjM Software Design, Gleneden Beach, Oregon, USA, 300 pp.

Mielke, P.W. & Berry, K.J. 2007: Permutation methods. A distance function approach. 2nd edition. - Springer Verlag, New York, New York, USA, 439 pp.

Paillisson, J.M., Reeber, S. & Marion, L. 2002: Bird assemblages as bio-indicators of water regime management and hunting disturbance in natural wet grasslands. - Biological Conservation 106: 115-127.

Pearce-Higgins, J.W., Finney, S.K., Yalden, D.W. & Langston, R.H.W. 2007: Testing the effects of recreational disturbance on two upland breeding waders. - Ibis 149(s1): 45-55.

Piersma, T. & Van Brederode, N.E. 1990: The estimation of fat reserves in coastal waders before their departure from Northwest Africa in spring. - Ardea 78: 221-236.

Quinn, G.P. & Keough, M.J. 2002: Experimental design and data analysis for biologists. - Cambridge University Press, Cambridge, UK, 556 pp.

Riddington, R., Hassall, M., Lane, S.J., Turner, P.A. & Walters, R. 1996: The impact of disturbance on the behaviour and energy budgets of Brent Geese *Branta b. bernicla*. - Bird Study 43: 269-279.

Sambrook, E., Fritsch, F. & Maniatis, T. 1989: Molecular Cloning: a laboratory manual. 2nd edition. - Cold Spring Harbor Press, New York, New York, USA, 1659 pp.

Searle, S.H. 1987: Linear models for unbalanced data. - John Wiley & Sons, New York, New York, USA, 536 pp.

Shaw, R.G. & Mitchell-Olds, T. 1993: ANOVA for unbalanced data: an overview. - Ecology 74: 1638-1645.

Sokal, R.R. & Rohlf, F.J. 1995: Biometry. The principles and practice of statistics in biological research. 3rd edition. - Freeman, New York, New York, USA, 887 pp.

Stillmann, R.A. & Goss-Custard, J.D. 2002: Seasonal changes in the response of oystercatchers *Haematoopus ostralegus* to human disturbance. - Journal of Avian Biology 33: 358-365.

Stillmann, R.A., West, A.D., Caldow, R.W.G. & Le V. dit Durell, S.E.A. 2007: Predicting the effect of disturbance on coastal birds. - Ibis 149(s1): 73-81.

Sutherland, W.J. 2007: Future directions in disturbance research. - Ibis 149(s1): 120-124.

Tabachnick, B.G. & Fidell, L.S. 2007: Using multivariate statistics. 5th edition. - Pearson Education, Boston, Massachusetts, USA, 980 pp.

Thomas, K., Kvitek, R.G. & Bretz, C. 2003: Effects of human activity on the foraging behavior of sanderlings *Calidris alba*. - Biological Conservation 109: 67-71.

Wiersma, P. & Piersma, T. 1994: Effects of microhabitats, flocking climate and migratory goal on energy expenditure in the annual cycle of red knots. - The Condor 96: 257-279.

Yoccoz, N.G. 1991: Use, overuse, and misuse of significance tests in evolutionary biology and ecology. - Bulletin of the Ecological Society of America 72: 106-111.

Zimmerman, G.M., Goetz, H. & Mielke, P.W. 1985: Use of an improved statistical method for group comparisons to study effects of prairie fire. - Ecology 66: 606-611.

Zwarts, L. 1990: Increased prey availability drives premigration hyperphagia in whrimbrels and allows them to leave the banc d'Arguin, Mauritania, in time. - Ardea 78: 279-300.