

Densities and population estimates of breeding Eurasian Woodcock *Scolopax rusticola* in Britain in 2003

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Capsule The breeding Eurasian Woodcock population in Britain was estimated at 78 346 males (95% CL 61 717–96 493), with substantial differences in densities between regions and woodland type.

Aim To estimate the breeding population size of Woodcock in Britain using a dedicated survey method, to enable assessment of current status and the creation of a baseline for future monitoring.

Methods Passes of roding male Woodcock were recorded on three evening visits to 807 randomly selected sites, stratified by region and woodland size, by volunteer observers during May–June 2003.

Results Roding Woodcock were present in 35% of 1-km squares containing at least 10 ha of woodland and the mean density of males in occupied squares was 2.76 ± 0.29 birds/km² (± se). There was significant regional variation in the occurrence and density of roding Woodcock. Woodcock presence differed between woodland types at the 1-km² level and the stand level, but densities within occupied woods were similar across woodland types.

Conclusion Previous estimates of the size of the British breeding Woodcock population are far too low and the species shows much spatial variation in breeding density.

Eurasian Woodcock Scolopax rusticola breeds widely throughout Britain, with notable absences only on the highest ground in parts of Scotland and in south-west England and south Wales (Gibbons et al. 1993). However, the species is currently 'amber-listed' as a bird of conservation concern because of an apparent long-term decline in breeding numbers (-76%, 1974-1999) and range (-31% 1968/72-1988/91, Gregory et al. 2002). The species' population size is unknown and the current estimate of 5000-12 500 'pairs' (Baker et al. 2006) is based upon sightings of Woodcock made during the course of general bird surveys rather than counts from dedicated surveys (Gibbons et al. 1993). Owing to its cryptic plumage, secretive behaviour and nocturnal habits, the Woodcock is a difficult species to survey and it seems likely that the presence of breeding Woodcock in many woods may remain unnoticed during general surveys. Hence there is uncertainty about the reliability of these data and the true

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status of the species. The British Trust for Ornithology's (BTO) Common Birds Census index was certainly suggestive of a decline in breeding Woodcock numbers between 1967 and 1988, but the data were biased towards areas of higher human population density, particularly south-east England (Marchant *et al.* 1990). It is unclear whether the differences in distribution and abundance of Woodcock between the 1968–72 and 1988–91 BTO Breeding Atlas periods are, at least in part, a result of the change in methods between these two atlases.

Woodcock are likely to be sensitive to habitat change because they have specific habitat requirements, particularly during the breeding season (Hoodless & Hirons 2007). Young stands of trees with high earthworm availability and dense ground vegetation are highly utilized for feeding and brood-rearing and areas with more open ground vegetation are used for nesting (Hirons & Johnson 1987). Deciduous woodland is preferred to conifers (Clausager 1972, Hoodless & Hirons 2007), but conifer plantations are

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used for nesting up to the thicket stage (Shorten 1974), and hence forestry practice is likely to influence habitat availability and quality. Changes in agricultural practice, such as the loss of permanent pastures which constitute optimal feeding areas in winter and early spring (Hoodless & Hirons 2007), may be important because British Woodcock exhibit high fidelity to the natal area in winter (Hoodless & Coulson 1994). The species is also hunted in winter, although a high proportion of the birds shot will be continental migrants (Hoodless & Coulson 1994). Annual 'singing-ground' monitoring of the American Woodcock Scolopax minor has highlighted a long-term population decline which appears, at least in part, to be related to habitat loss and alteration on the breeding grounds (Dwyer et al. 1983, Sauer & Bortner 1991, Sepik et al. 1993).

Knowledge of the status of Woodcock as a breeding species in Britain and Ireland and of any need for conservation action is currently hindered by the lack of a specific counting method and monitoring programme. The unique display or 'roding' flight performed by males provides the best opportunity to confirm the presence of breeding birds and assess numbers. From late February to mid-July, males fly circuits above the woodland canopy at dawn and dusk in search of receptive females. During these flights males call repeatedly, producing three or four low-pitch croaks followed by a high-pitch whistle. Roding flights of individual birds seldom last more than 20 minutes and typically two to four separate flights are made each evening (Hirons & Owen 1982). The roding areas of several males may overlap and Woodcock's breeding system has been shown to be one of successive polygyny, whereby a few dominant males fertilize the eggs of most females within a given area (Hirons 1980, 1983). Counts of passes by roding Woodcock at fixed points provide the only feasible method for any largescale monitoring of breeding Woodcock populations, but their interpretation has been hindered by the fact that they represent multiple registrations of an unknown number of males. To date, analysis has therefore been limited to frequency of occurrence (Ferrand 1993, Fokin & Blokhin 2000, Ferrand et al. 2003) and only recently has the validity of using registrations of roding Woodcock for assessing numbers of males been demonstrated (Hoodless et al. 2008).

We present the results of the first national survey of breeding Woodcock in Britain, the aim of which was to produce reliable baseline population estimates for England, Scotland and Wales against which future estimates could be compared.

METHODS

Site selection

Our aim was to achieve surveys at 1000 randomly selected locations (c. 1.25% of 1-km squares containing at least 10% woodland), stratified by region and by woodland area. Because roding Woodcock are generally associated with woodland, the biologically appropriate sampling unit is the stand of trees. In upland areas, Woodcock sometimes rode over open habitats and nests are found outside woodland, but roding circuits always encompass some woodland and nests are located close (< 500 m) to woodland (Hoodless 1994). In central Europe, Woodcock prefer large forests (Kalchreuter 1983) and there is evidence to suggest that in the UK Woodcock do not breed in woods smaller than 10 ha (Fuller 1982). In order to target woods to be surveyed, all 1-km squares containing at least 10% woodland were identified from the Land Cover Map 2000, available at a 1-km² resolution through the Countryside Information System (Howard & Bunce 1996). The Land Cover Map 2000 is a classification of habitats based on spectral data recorded by satellites (Fuller et al. 2002). We specified four woodland categories as 10-30 ha, 31-50 ha, 51–70 ha and 71–100 ha within the Land Cover Map 2000. Using the GIS package MapInfo 7.5 (MapInfo Corporation 2002), we sought to determine the number and size of regions that would ensure similar proportions of squares belonging to each of the four wood size classes between regions, whilst taking account of the number of potential surveyors within each BTO region.

We used a dataset containing information on the numbers of BTO members within the 118 BTO regions and combined regions until the numbers of members within each new region were as similar as possible, whilst also considering geographic continuity. It was not possible to achieve exactly the same number of members in each region because of a strong bias in BTO membership towards areas of high human population density, particularly South-East England and East Anglia. Survey site stratification resulted in 11 geographical areas each containing a similar proportion of 1-km squares of the four woodland size classes (Fig. 1). It was not possible to further stratify by type of woodland owing to pronounced geographical differences in the extent of deciduous and conifer woodland: more deciduous woodland in southern England and more conifers in northern England and Scotland.

The proportion of total BTO members within each of the 11 regions was used to calculate the number of survey squares required per region. We specified that



Figure 1. Boundaries of regions used for the Woodcock survey. Regions were selected to ensure that each had similar numbers of BTO members and similar proportions of 1-km squares belonging to each of four woodland size classes.

all selected squares had to be at least 2 km apart, to ensure the independence of counts at each survey point, because roding areas are typically 43–134 ha (Hirons 1983). The desired number of woodland squares was then randomly selected from those available within each region and size class. In the Midlands and southern England, the desired number of squares in the 51-70 ha and 71-100 ha size classes exceeded the number of available squares that met our criteria, resulting in lower overall numbers of selected squares in these size classes (Table 1). We used a random number generator to select 1-km squares for survey, ensuring that the centre of each new square was at least 3 km from the centre of all previously selected squares. Selected squares were ordered by the random number assigned to them. BTO regional organizers were asked to allocate or reject squares in random number sequence. Based on discussions with BTO regional survey organizers ('Regional Representatives') about their experiences of obtaining access permissions and the physical difficulties of gaining access to some woods, particularly at dusk, a large sample of squares (2677) relative to the desired coverage was selected.

Roding Woodcock surveys

Observers made a preliminary visit to assess each site and determine an appropriate survey point at dusk in April. Observers were asked to then make three survey visits, at least one week apart, to each site during May– June 2003. These months represent the seasonal peak of roding activity and three visits were considered appropriate to account for variability in roding activity between evenings (Hoodless *et al.* 2006). If no roding Woodcock were encountered on the preliminary visit and the first survey visit, observers were not obliged to conduct the second and third surveys, because data from a pilot study showed that at sites where no birds were seen on the first two visits, Woodcock were never seen on the last two visits.

Observers were asked to conduct surveys in the largest wood within the random square, but were permitted to move up to 400 m outside the square to find a suitable observation point if the wood was partly overlapped by the survey square. This happened in 49 cases and meant that in practice the minimum distance between all survey points was at least 1.2 km. Surveys were undertaken from ride intersections, glades or felled areas within mature woodland. They commenced 15 minutes before sunset and lasted 60 minutes. On average this timing ensures detection of 83% of Woodcock passes (Hoodless et al. 2006). On each occasion that a Woodcock was seen or heard, a separate registration was noted with the time to the nearest minute. Observers were encouraged to familiarize themselves with the Woodcock's roding call prior to undertaking surveys. The total number of Woodcock registrations during each survey was defined as the sum of all Woodcock seen and heard, plus those only seen or only heard. Wet or windy evenings (with continuous rain or wind speed exceeding Beaufort force 3) were avoided. Preliminary work showed that, provided these conditions were met, numbers of registrations were unaffected by cloud cover, wind or drizzle (Hoodless et al. 2006).

Habitat classification

Woodland habitat was classified at two scales: the 1-km OS grid square and the stand level. At the 1-km square

level, survey squares containing woodland that was > 70% deciduous or coniferous based on Land Cover Map 2000 data were classified as such and the remaining squares were classed as mixed. For stand level classification, observers recorded the dominant and sub-dominant tree species and the dominant and sub-dominant species of ground vegetation at four points 50 m from the count location in cardinal directions. This information was used to classify conifer plantations according to the tree species and deciduous woods into those of basic (National Vegetation Classification (NVC) types W8, W9), neutral (W10, W11) or acid (W16, W17) soils or beech woodland (W12, W14) or wet woodland (W1, W4, W6, W7) on the basis of characteristic NVC species (Rodwell 1991, Hall et al. 2004). Woodland was defined as mixed at the stand level where conifers were planted in an intimate mixture with deciduous species, such as Beech Fagus sylvaticus with a spruce *Picea* spp. nurse crop. At this level, woodland was also defined as mixed if the 1-km square classification was mixed woodland and the ratio of conifer: deciduous tree species records, or vice versa, was at least 25%:75%.

Data analysis and population estimates

Data checks were made to ensure that surveys commenced at the appropriate time. Where observers continued to count birds for more than 60 minutes, the data were truncated. The wood size class was reclassified according to the new 1-km square at the 49 random sites where observers located their observation point outside the allocated square. Some data from self-selected sites where landowners, foresters or gamekeepers wanted to participate were accepted for inclusion in habitat analyses, but population estimates were based solely on randomly selected sites. Data for 28 self-selected sites which were within 1.2 km of a random site were excluded.

The number of individual male Woodcock (W) at each survey site was estimated from the maximum number of registrations (R) using the equation $W = 0.74R^{0.708}$, based on a calibration involving identification of individuals at 43 sites using spectrograms of calls (Hoodless *et al.* 2008). This relationship appears to be widely applicable because there were no differences in slope or intercept between broad regions (north-east England and Scotland compared to central southern England) or habitats (coniferous, mixed, deciduous woodland). The maximum number of registrations was used because this was considered to provide a better estimate of the total number of males at a site than the mean count, owing to variation in roding activity between nights (Hoodless *et al.* 2006). The estimated number of males at each survey point was assumed to be equivalent to the density in the 1-km survey square, because the mean of roding areas measured by Hirons (1980) was 88 ha.

National and regional Woodcock population estimates were calculated by expansion, based on the mean density per stratum used in the survey stratification i.e. wood size class within region. Thus, the national population estimate, $W_{\rm np}$, was derived by combining density estimates from all 44 strata:

$$W_{\rm np} = \sum_{\rm s} (W_{\rm s} \times N_{\rm s})$$

where W_s is the mean number of male Woodcock per km^2 per region-wood size class stratum, s, and N_s is the number of 1-km squares in each stratum. Confidence limits were calculated by boot-strapping independently within each stratum using the method described by Sarndal *et al.* (1992). This involved creating a 'pseudopopulation' containing *n* replicates of each observation, where *n* was the nearest integer to the expansion raising factor (the inverse of the proportion of squares surveyed) for the stratum. Confidence limits were computed from 1000 boot-strap samples, of the same size as the sample of squares surveyed, taken from the 'pseudopopulation'. These calculations were conducted using the 'svstratified' procedure, for analysing a stratified random survey, in GENSTAT 9.1 (Lawes Agricultural Trust 2006).

Regional Woodcock presence and density in occupied 1-km squares were calculated from weighted stratum means because these reflect the expected presence or density across each region, whereas estimates based on raw stratum means would simply represent the sample of squares surveyed. Regional presence, P_r , was calculated from the four wood size class strata in each region as

$$P_{\rm r} = \Sigma (P_{\rm s} \times WT_{\rm s})$$

where P_s is the mean presence per region-wood size class stratum, s, and WT_s is the stratum weight (number of available 1-km squares in the stratum divided by the total number of squares containing at least 10 ha of woodland in the region). Regional density in occupied squares, D_r , was calculated as

$$D_{\rm r} = \Sigma(D_{\rm s} \times ((P_{\rm s} \times WT_{\rm s}) / \Sigma(P_{\rm s} \times WT_{\rm s})))$$

where *Ds* is the mean density in occupied squares per region-wood size class stratum, s. The standard error of the regional density in occupied squares, *SE*, was

 $SE_{r} = \sqrt{\Sigma} \left(V_{s} \times ((P_{s} \times WT_{s}) / \Sigma (P_{s} \times WT_{s}))^{2} \right)$

where V_s is the variance associated with D_s .

Variation in Woodcock presence between regions and wood size classes was examined using a generalized linear model (GLM) with binomial errors, the number of occupied woods per region-wood size class stratum being the dependent variable and the number of woods surveyed the binomial denominator. Woodcock density in occupied squares was analysed using analysis of variance (ANOVA), with mean males/km² per stratum as the dependent variable and region and wood size class as factors. Comparisons of Woodcock presence and density between habitats used GLMS with binomial errors and anovas, respectively, with numbers of woods or mean densities per woodland type within wood size class within region as the units of analysis. Region, wood size class and woodland type were included as factors and only the main effects were tested. GLMs were performed in GENSTAT 9.1 and all other statistics were calculated in SYSTAT 9 (SPSS Inc. 1999).

RESULTS

Dataset attributes

Counts of roding Woodcock were made at a total of 907 points, 807 of which were in randomly selected woods and 100 of which were self-selected. Of the randomly selected woods where Woodcock were present, 82% were visited three times and 93% were visited at least twice. Woods surveyed once, twice and three times were distributed evenly between wood size classes $(\chi_6^2 = 6.11, P = 0.411)$ and between regions (amalgamated to Scotland, northern England, Midlands, southern England to ensure expected values > 5; $\chi_6^2 = 11.34$, P = 0.079). Comparison of the number of random squares surveyed with the number selected within each region-wood size class stratum revealed an overall difference from the stratification in the proportions of squares surveyed (χ^2_{43} = 84.34, P < 0.001). The main difference between regions was proportionately low coverage of squares in South-West England, whilst comparison of wood size classes showed that a lower proportion of squares containing 10-30% woodland was surveyed than selected and a higher proportion of

Table 1. Numbers of randomly selected 1-km squares in each of the 11 regions and four wood size classes used in the survey stratification and numbers of these that were surveyed for roding Woodcock. Percentages are the proportions of the total number of squares selected or surveyed within each region or wood size class.

	Squares selected		Squares surveyed	
Region/wood size class	Number	%	Number	%
Northern Scotland	100	3.7	27	3.3
Southern Scotland	152	5.7	35	4.3
Northern England	155	5.8	55	6.8
Eastern England	139	5.2	56	6.9
North Midlands	327	12.2	128	15.9
Wales	144	5.4	46	5.7
South Midlands	252	9.4	65	8.1
East Anglia	243	9.1	80	9.9
South-East England	563	21.0	152	18.8
Central South	280	10.5	110	13.6
South-West England	322	12.0	53	6.6
10–30% woodland	756	28.2	181	22.4
31–50% woodland	756	28.2	226	28.0
51–70% woodland	709	26.5	213	26.4
71–100% woodland	456	17.0	187	23.2
Total	2677		807	

squares containing 71–100% woodland was surveyed (Table 1). This meant that the national population size had to be calculated from estimates for each region-wood size class stratum.

Woodcock distribution and population estimates

Roding Woodcock were present at 340 random survey sites (42%). Weighting by the availability of 1-km squares within each region-wood size class stratum gave a national estimate of 35% presence in squares containing at least 10 ha of woodland. The frequency of occurrence differed between wood size classes (class 1: 27%, class 2: 36%, class 3: 45% and class 4: 62%) and regions (GLM wood size class: $F_{3,30} = 17.88$, P < 0.001, region: $F_{10,30} = 5.45$, P < 0.001). The occupancy of woods was highest in Northern Scotland, where Woodcock were recorded in 69% of woods, and was lowest in the South Midlands, with birds recorded in just 11% of woods (Table 2). Closer examination of occurrence at individual sites reveals several distinct aggregations of breeding Woodcock in large forests, such as Kielder Forest, Dalby and Newtondale Forests, Thetford Forest, Forest of Dean and New Forest, and heavily wooded regions, such as Derbyshire and Nottinghamshire, West Sussex and north Hampshire

(Fig. 2). Breeding Woodcock generally had a more widespread distribution in Scotland and northern England (north of a line between the Wash and the River Mersey) than in southern England and Wales.

Of woods with Woodcock, 70% had fewer than five males and the highest number of males at any wood was 10 (41 registrations). Woodcock density in occupied woods differed between regions, ranging from 0.87 males/km² in Wales to 4.10 males/km² in East Anglia (ANOVA region: $F_{10,30} = 3.66$, P = 0.003, Table 2). There was no difference between wood size classes (ANOVA wood size class: $F_{3,30} = 2.73$, P = 0.061). Mean density in occupied woods within each region was not correlated with Woodcock presence ($r_0 = 0.42$, P = 0.202).

The national Woodcock population was estimated as 78 346 males (95% confidence interval: 61 717–96 493). Population sizes were estimated to be similar in



Figure 2. Presence (filled circles) and absence (open circles) of breeding Woodcock in 2003, based on surveys of roding males in 807 randomly selected 1-km squares that contained at least 10 ha of woodland. No surveys were conducted on Orkney or Shetland.

Scotland (39 251 males, 95% CL: 24 173–56 632) and England (37 328 males, 95% CL: 30 101–44 089), with only 1 767 males (95% CL: 541–3 259) in Wales (Table 2). The estimate for Northern Scotland should be treated with caution because there are a large number of 1-km squares with less than 30% woodland in this region, but only three squares were surveyed in this stratum, resulting in an estimate based on a large number of imputed squares and with large confidence limits. In England, the total number of breeding males in the three regions north of a line between the Wash and the River Mersey (19 119 males) was estimated to be similar to that in the five regions to the south of this line (18 210 males).

Densities in different habitats

The presence of Woodcock differed significantly between 1-km²-level wood types, with males present more frequently in mixed woodland than in deciduous or coniferous woods (GLM wood type: $F_{2,97} = 19.96$, P < 0.001, wood size class: $F_{3,97} = 13.73$, P < 0.001, region: $F_{10,97} = 5.15$, P < 0.001, Table 3). There was a gradation in mean density in occupied woods from coniferous (lowest) to deciduous (highest), but the difference was not statistically significant (ANOVA wood type: $F_{2,81} = 2.90$, P = 0.061, wood size class: $F_{3,81} = 2.50$, P = 0.066, region: $F_{10,81} = 3.91$, P < 0.001, Table 3).

Woodcock presence also varied according to stand type, with males seen roding most frequently over pine *Pinus* spp. stands within coniferous woods and over wet woodland stands in deciduous woods (GLM stand type: $F_{9,225} = 5.35$, P < 0.001, wood size class: $F_{3,225} = 8.45$, P < 0.001, region: $F_{10,225} = 4.95$, P < 0.001, Table 3). Male density did not differ significantly between stand types in woods where roding males were present (ANOVA stand type: $F_{9,145} = 1.75$, P = 0.082, wood size class: $F_{3,145} = 1.90$, P = 0.133, region: $F_{10,145} = 1.65$, P = 0.098).

DISCUSSION

Population estimates

Our population estimate of 78 350 roding males in Britain far exceeds the most recent estimate of 5000–12 500 'pairs' in 2000 (Baker *et al.* 2006). It also greatly exceeds both the 1968–72 and the 1988–91 Breeding Atlas estimates of 19 000–47 000 and 8500–21 500 'pairs' respectively (Sharrock 1976, Gibbons *et al.* 1993). Our estimates of breeding

Table 2. Regional, country and national presence of roding Woodcock, mean numbers of registrations and mean densities in occupied squares, and Woodcock population size estimates (males, with 95% confidence intervals). Mean Woodcock presence, registrations and densities in occupied squares are weighted by the number of available 1-km squares within each region-wood size class stratum. The overall density is the presence multiplied by the density in occupied squares.

Region	Squares surveyed	Presence (%)	Registrations ± se	Density (males/ km2) ± se	Population estimate (males)	Lower 95% CL	Upper 95% CL
Northern Scotland	27	68.5	5.90 ± 1.65	2.39 ± 0.55	24 088	14 640	34 633
Southern Scotland	35	35.9	10.94 ± 5.18	3.52 ± 1.28	15 163	6110	28 075
Northern England	55	46.2	8.94 ± 1.51	3.32 ± 0.44	7169	4192	10 469
Eastern England	56	52.7	12.05 ± 3.77	3.91 ± 0.98	6811	3011	11712
North Midlands	128	27.9	9.50 ± 1.22	3.51 ± 0.33	5139	2998	7612
Wales	46	21.4	1.34 ± 0.12	0.87 ± 0.04	1767	541	3259
South Midlands	65	10.6	3.87 ± 0.59	1.71 ± 0.18	1123	520	1820
East Anglia	80	27.3	12.43 ± 3.11	4.10 ± 0.82	3485	1747	5794
South-East England	152	23.0	7.01 ± 1.35	2.73 ± 0.41	4782	2480	7785
Central South	110	42.1	8.10 ± 1.08	3.07 ± 0.31	6586	4506	9124
South-West England	53	13.2	4.42 ± 1.70	1.81 ± 0.49	2234	774	4147
England	699	26.9	8.53 ± 0.74	3.11 ± 0.20	37 328	30 101	44 089
Scotland	62	53.8	7.40 ± 1.93	2.73 ± 0.54	39 251	24 173	56 632
Wales	46	21.4	1.34 ± 0.12	0.87 ± 0.04	1767	541	3259
National total	807	35.2	7.45 ± 1.03	2.76 ± 0.29	78 346	61 717	96 493

Table 3. Roding Woodcock presence and mean density in occupied squares in relation to woodland type at the 1-km² level and the stand level. The overall density is the presence multiplied by the density in occupied squares.

1-km² level			Stand level			
Wood type	Presence (%) ± se	Density (males/km²) ± se	Stand type	Presence (%) ± se	Density (males/km²) ± se	
Coniferous	42 ± 4	2.78 ± 0.24	Pine Fir/larch Spruce Mixed conifers	59 ± 5 40 ± 10 23 ± 6 42 ± 7	$3.19 \pm 0.37 2.69 \pm 0.68 1.68 \pm 0.66 3.28 \pm 0.49$	
Mixed Deciduous	62 ± 3 37 ± 2	3.05 ± 0.20 3.55 ± 0.21	Mixed Acid Neutral Basic Beech Wet	$ \begin{array}{r} 46 \pm 4 \\ 66 \pm 7 \\ 54 \pm 4 \\ 37 \pm 5 \\ 29 \pm 6 \\ 69 \pm 8 \end{array} $	$\begin{array}{c} 3.17 \pm 0.36 \\ 3.29 \pm 0.42 \\ 3.32 \pm 0.33 \\ 3.50 \pm 0.45 \\ 3.75 \pm 0.53 \\ 4.72 \pm 0.47 \end{array}$	

Woodcock density are crude and likely to be minima because the roding counts were assumed to be representative of the whole of a 1-km square. In reality, the counts may not have detected all the roding activity by males in squares with more than 70% woodland. Nevertheless, our survey method and density calculations are easy to apply and repeatable, and hence the current survey data form a baseline against which future monitoring will enable assessment of changes in numbers.

The 1968–72 and 1988–91 Breeding Atlas estimates were obtained by assuming 10–25 pairs per 10-km square with probable or confirmed breeding and the discrepancy between these estimates and our estimate seems to be partly because this guess of pair density is too low. Given that 35% of 1-km squares in Britain contain more than 10 ha of woodland, our data suggest that an average of 34 males per 10-km square ($35 \text{ km}^2 \times 35\%$ presence $\times 2.76 \text{ males/km}^2$ in occupied 1-km squares) is more realistic. Even this may be too low because for an atlas estimate this figure would be applied to 10-km squares where Woodcock are known to be present and hence the presence within constituent 1-km squares containing more than 10 ha of woodland might be higher than the 35% which we have had to assume. A figure of 34 males per 10-km square with probable or confirmed breeding still gives Atlas population estimates lower than our current estimate. Our survey coverage was far less extensive than that of the Atlases and this is also likely to be a source of error. Poor survey coverage in Scotland resulted in a country estimate with a large confidence interval. Consequently, this estimate should be treated with caution, although its lower confidence limit is 24 200 males and use of this figure for Scotland still gives a population estimate for Britain of 63 300 males. Historically, Woodcock have only very rarely bred in Devon and Cornwall (Sharrock 1976, Gibbons et al. 1993, Holloway 1996) and consequently uptake of random squares by surveyors was extremely low in these counties. We are therefore likely to have overestimated Woodcock presence and hence breeding numbers in South-West England. Nevertheless our estimate for this region was only 2234 males and, even if the true number is half this, our national population estimate remains little altered.

Our overall estimate of breeding Woodcock presence of 35% in 1-km squares with at least 10 ha of woodland suggests that there remains much potential habitat, in the form of large woods, which currently supports no birds. Thirty-day spring diurnal home ranges of both sexes are about 60 ha (Hoodless & Hirons 2007) and hence the absence of breeding Woodcock from small woods and an increased frequency of occurrence in 1-km squares containing higher proportions of woodland is to be expected. However, absence from squares with at least 50 ha of woodland presumably reflects unsuitable habitat structure or local population decline.

Comparison with surveys in central Europe

Better monitoring across the Woodcock's European breeding range is an important part of ensuring sustainable harvesting of this widely hunted species (Ferrand & Gossmann 2001). The 2003 Woodcock survey was the first step towards improved monitoring in Britain. However, similar surveys have been undertaken in several central European countries for a varying number of years. Although sampling designs and the duration of counts differ between countries, the basic field method is the same and appears to be adequate for assessing annual variation in abundance and trends (Ferrand *et al.* 2003).

At 35%, Woodcock presence in Britain was slightly higher than that recorded in France (20–30% during

1991–2000, n = 706-823 sites; Ferrand & Gossmann 2000, Ferrand et al. 2003) and in western Switzerland (19-31% during 1991-2000, n = 54-85 sites; Estoppey)2001), whose breeding populations are estimated as 10 000-30 000 males and 1130-1630 males, respectively (Thorup 2006). In contrast, in Russia which is believed to be the main stronghold for the species in Europe, with a breeding population of 6-7 million males (Thorup 2006), Woodcock were present at 85-95% of random sites surveyed during 2000-2004 (n = 210-236; Fokin et al. 2004). Comparison of Woodcock abundance is more difficult, because numbers of counts and count duration differ between schemes. Nevertheless, mean numbers of registrations at occupied sites were broadly similar (Britain 7.5 (1 h count), Switzerland 5.1 (up to 1.5 h), Belarus 10.5-11.6 (2 h), Russia 9.1–11.5 (2 h); Estoppey 2001, Fokin et al. 2004, Mongin et al. 2006) and indicative that breeding densities in Russia were not vastly higher than elsewhere in Europe.

Regional and habitat-related distribution and abundance

Our survey highlighted regional differences in both Woodcock occurrence and density within occupied squares. With the exception of Central South, regional presence in Northern and Eastern England and in Scotland was approximately twice that of the regions in southern England and Wales. In the south, the highest male densities were in Hampshire, West Sussex and Norfolk. Certain large forests or regions of extensive woodland appear to be important strongholds for breeding Woodcock and may act as reservoirs for dispersal into surrounding areas following years of high productivity. Ensuring appropriate management of these forests will be an important step towards securing breeding Woodcock populations into the future. Comparison of our data on Woodcock distribution with those from the 1988-91 Breeding Atlas (Gibbons et al. 1993) is limited by the difference in survey methods and the relatively poor coverage in our survey. However, the distribution indicated by the two surveys is in broad agreement, with the exception that in 2003, despite good coverage, no roding males were detected in Galloway Forest, an area of high abundance during 1988–91. The 2003 survey is also suggestive of possible losses of breeding Woodcock in Cambridgeshire, Northamptonshire and Leicestershire since 1988–91.

The current paucity of roding Woodcock in southwest Scotland and Wales is likely to be related, at least in part, to the maturation of many of the conifer forests in these regions. Conifers tend to be used by breeding Woodcock only up to the thicket stage (Shorten 1974, Hoodless & Hirons 2007), which is reached after about 20 years, and the main expansion of coniferous afforestation in Britain took place during 1950–1990 (Forestry Commission 2003). Dependent on future forestry policy, it is possible that in northern and western parts of Britain breeding Woodcock numbers may fluctuate in relation to the cycle of forest restocking over a period of approximately 50 years.

Woodcock presence at the 1-km² level was considerably higher in mixed woodland than in predominantly deciduous or coniferous woodland. This may reflect a greater diversity of stand types in mixed woodland and hence a greater likelihood of some parts of these woods being of suitable age and structure for nesting and for feeding and brood rearing. The magnitude of difference between densities in occupied squares was small relative to that of the difference in percentage occurrence between wood types at both the 1-km² level and the stand level. Because the Woodcock typically breeds at low density relative to many other woodland birds, the frequency of occurrence in a particular type of woodland probably better reflects the frequency and duration for which that wood type provides habitat of structure suitable for breeding.

Our use of roding counts to examine habitat preferences at the stand level is, at best, crude and should be treated with caution because roding areas are large relative to the size of stands in many woods. We have assumed that males display most intensively over nesting habitats but the only evidence for this is the association between counts of roding males and numbers of nesting females found by Hirons (1988). Woodcock displayed more frequently over pine stands than those of fir Abies spp./Douglas-fir Pseudotsuga spp. and larch Larix spp., which in turn had a greater frequency of displaying birds than spruce stands, suggesting that the structure of pine stands remains suitable for breeding for longest. Sitka Spruce Picea sitchensis has been the main tree species grown in Britain's upland forests owing to its exceptional growth rate, but this results in a dense canopy (Rook 1992). In deciduous woods, the higher frequency of roding over stands with vegetation typical of acidic soils than over those with vegetation typical of basic and neutral soils was surprising given that earthworms are such an important component of the Woodcock's diet (Hoodless & Hirons 2007). The reason may be that W16 and W17 NVC types have a tendency to become dominated by dense birch Betula pendula/B. pubescens and bracken Pteridium aquilinum, whose structures result in high use by Woodcock for feeding and nesting, respectively (Hoodless & Hirons 2007). The low relative frequency of roding males over Beech stands confirmed the findings of intensive studies indicating that the structure and food availability of Beech stands is often unsuitable for breeding (Hirons & Johnson 1987). The high frequency of roding males over wet woodland stands probably reflects high accessibility of food, but use of this type of woodland may vary between years because 2003 was a particularly warm, dry summer.

Rationale for counting roding males

As with other cryptic, crepuscular and lekking species, such as Great Bittern *Botaurus stellaris*, Corncrake *Crex crex*, European Nightjar *Caprimulgus europaeus* and Black Grouse *Tetrao tetrix*, counts of males provide the most feasible way of monitoring breeding Woodcock numbers at large scales. It is now apparent from individual recognition based on calls that counting registrations of roding males is a valid approach to estimating the number of males displaying in a wood (Hoodless *et al.* 2008).

Our survey method should provide a robust measure for monitoring trends in breeding male abundance and for estimating the size of the breeding population at a large scale. We are likely to have underestimated total male Woodcock densities and population sizes because some males may not have displayed during May and June. In radiotracking studies, Ferrand (1983) found that some males only roded sporadically and Hirons (1983) found that a small proportion (8-13%) over four years) of males did not rode at all. The proportion of non-roding males may vary between sites or years and to some extent buffer change in the size of local breeding Woodcock populations, but it is unlikely to have an appreciable effect upon population and trend estimates at a national scale. The limitations of monitoring just the male component of the Woodcock population should be borne in mind, because adult sex ratios in populations of many wild birds are unequal (Donald 2007) and in a polygynous species female survival is likely to be more important than that of males in determining the persistence of breeding populations.

Design of future surveys

The 2003 Woodcock survey suffered from a bias in survey effort related to human population density, as

reflected by BTO membership. We were aware during the stratification process that this was likely to be the case, particularly in South-East England and the North Midlands (Table 1), but decided to try to maximize participation by making the best use of the volunteer effort available. Even so, the proportional uptake of randomly selected survey squares was lower in the two Scottish regions than in Wales and in all of the English regions apart from South-West England (Table 1). This is not surprising given that many upland squares were relatively inaccessible compared to lowland squares. The relative standard errors (se/mean) of the country estimates were 10% for England, 21% for Scotland and 40% for Wales. To reduce the relative standard errors for Scotland and Wales to 10% in future surveys, sample sizes of 271 and 360 1-km squares would be required, respectively. It is apparent that professional fieldworkers are likely to be needed to improve coverage in future surveys and this will be particularly important in Scotland, which may hold half the British breeding Woodcock population.

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