

# Pre-breeding foraging and nest site habitat selection by Lesser Spotted Woodpeckers *Dendrocopos minor* in mature woodland blocks in England

Elisabeth C. Charman, Ken W. Smith, Steve Dodd, Derek J. Gruar & Ian A. Dillon

*E.C. Charman, S. Dodd, D.J. Gruar & I.A. Dillon, Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, U.K. Corresponding author's e-mail Elisabeth.Charman@rspb.org.uk*

*K.W. Smith, 24 Mandeville Rise, Welwyn Garden City, Hertfordshire, AL8 7JU, U.K.*

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Lesser Spotted Woodpeckers *Dendrocopos minor* have dramatically declined and retracted in range in Britain. Pre-breeding foraging may be critical and, although work has been carried out elsewhere in Europe our knowledge of habitat requirements for British birds is limited. We aim to describe foraging behaviour and selection of foraging locations in the pre-breeding period; and to provide descriptions of nest sites and wider habitat selection for nesting. We recorded foraging behaviour, attributes of foraging trees and nest site characteristics and compared them with random areas within woods. Small branches of live oaks at heights usually in the upper third of the tree were most frequently used for foraging. At a wider scale, areas selected contained more deadwood. Nest cavities were usually placed in the upper half of a tree, and oak was commonly used. For nesting, open areas were selected with more dead trees and a mature structure. Many of the attributes important for foraging and nesting have changed in English woodlands in the direction expected to have negative impacts on this species, except for deadwood. Further work should measure food availability in areas of differing structures. Knowledge of declining species' resource requirements allows targeted and informed management for conservation.



## 1. Introduction

The Lesser Spotted Woodpecker *Dendrocopos minor* (hereafter LSW) has undergone a massive decline in numbers (Eaton *et al.* 2011) and range (Gibbons *et al.* 1993) in Britain over the past three decades, yet our knowledge of its foraging ecology and fine-scale habitat requirements is limited (Miranda & Pasinelli 2001, Rossmanith *et al.* 2007), making conservation action difficult.

LSWs are also declining in Scandinavia and continental Europe (Nilsson *et al.* 1992, PECBMS 2011) where several studies have been carried out, primarily in Sweden and Germany, assessing habitat requirements (Wiktander 1998, Wiktander *et al.* 1992, 2001, Höntsch 2005, Hogstad 2010). However, little dedicated work has been carried out on English populations of the subspecies *comminutus*, and it is probable that habitat preferences are different across the range (Delahaye *et*

*al.* 2010). Three studies have greatly added to our knowledge of LSW habitat use in England. Charman *et al.* (2010) described broad (wood-scale) habitat requirements that can help target areas for focussed management. At this scale there appeared to be selection for open woods within a heavily wooded landscape. Smith (2007) described 16 nest sites and foraging preferences in Hertfordshire, whilst Glue & Boswell (1994), analysed nest site characteristics as recorded on 129 BTO Nest Record Scheme cards from 1939 to 1989.

Recent studies of the breeding success of LSW in England have shown that difficulties in provisioning chicks by adults can ultimately lead to brood failure through starvation, and it is suspected that the ultimate cause of this may be food availability before and during the breeding period (Charman *et al.* 2012). For most of the year, LSWs forage on deadwood invertebrates (Glutz *et al.* 1980, Cramp *et al.* 1985) which they obtain by pecking dead branches or scaling tree bark. In southern Norway, numbers of breeding LSW fluctuate in synchrony with the population of the moth *Argyresthia goedartella* (Selås *et al.* 2008), an important food source for the species in Scandinavia early in the breeding season (Olsson 1998). From the time of bud-burst the diet changes to one dominated by surface-living arthropods collected from the bark and foliage of trees (Cramp 1985, Olsson 1998). This is also the main food source for nestlings (Olsson 1998, Rossmanith *et al.* 2007, Charman *et al.* 2012).

Olsson *et al.* (1999) found evidence of a carry-over effect from the pre-breeding into the breeding season. They found that birds in territories with good feeding conditions in the pre-breeding period were able to nest early, which resulted in more fledged young per breeding attempt than birds in poorer territories, indicating the importance of examining this period in the species's life-history further.

Habitat selection at a broad scale in England has been described elsewhere (Charman *et al.* 2010). In this paper we set out to investigate foraging methods and sites in late winter/early spring in the lead up to the breeding season as well as nest sites selected in the same period. We describe the foraging habitat of LSWs at the scale of the individual foraging bird and its immediate surround-

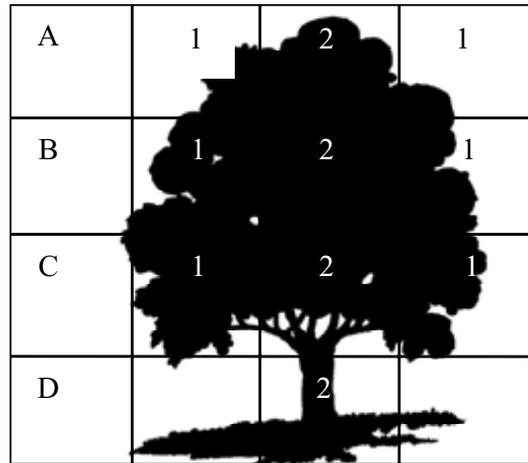


Fig. 1. Tree foraging zones. Each tree was divided into four vertical height bands A–D, of which A represents the upper quarter of the tree, B the third quarter, C the second quarter from where the first horizontal branches appear, and D the trunk, i.e., area between the main horizontal branches and the ground. The tree was also divided in two horizontal zones, of which 1 = the outer zone at each vertical height category, and 2 = the middle zone at each vertical height category, including the trunk and the ground.

ings and nest site locations at the nest tree scale and its immediate surroundings.

Specifically, we ask the following questions:

1. What are the characteristics of foraging and nest trees and how do LSWs utilise this resource?
2. What are the habitat characteristics of foraging and nesting areas of woodland?
3. Are LSWs demonstrating habitat selection in their choices of foraging and nesting sites?

## 2. Material and methods

### 2.1. Survey areas

Our study was carried out in South Yorkshire (SY) and the Hampshire/Wiltshire border (HA) in 2007 and Worcestershire (WO) from 2007 to 2009. Areas were chosen on the basis that, despite the national decline, they retained reasonable numbers of LSWs based on the 1988–91 breeding atlas

Table 1. Variables recorded for first observations of LSWs using an instantaneous sampling technique to measure individual foraging behaviour.

Variable recorded	Description
Sex	Sex of the focal individual
Tree species	Species of foraging tree
Tree DBH	Diameter at breast height (cm) of the foraging tree
Tree height	Estimated in metres
Tree status	Categorised as dead or alive
Foraging zone	Broad foraging zone on the tree – refer to Fig. 1
Foraging location	Branch or main trunk
Foraging height	Estimated height (m) of foraging
Forage branch diameter	Estimated diameter of branch (cm) where foraging
Forage branch length	Estimated length of branch (m) where observed foraging
Forage branch status	Categorised as dead or alive
Foraging technique	Scaling, pecking, gleaning

Table 2. Variables recorded at each LSW nest tree.

Variable recorded	Description
Tree species	Species of nest tree
Tree DBH	Diameter at breast height (cm) of the nest tree
Tree height	Estimated in metres
Tree status	Categorised as dead or alive
Previous woodpecker use	Old woodpecker cavities, drilling marks, bark stripping.
Cavity height	Estimated in metres
Orientation	Direction of the cavity entrance hole on 8 point directional scale.
Location	Location of cavity on the tree: trunk, branch/trunk intersection, branch
Branch length	For cavities in branches, length of branch measured in metres
Branch diameter	For cavities in branches, estimate of maximum branch diameter (cm)
Branch status	For cavities in branches, categorised as dead or alive

(Gibbons *et al.* 1993), the RSPB/FC/NE/BTO Bird Conservation Targeting Project ([www.rspb.org.uk/targeting](http://www.rspb.org.uk/targeting)) and local knowledge of County Bird Recorders. In SY, the study area centred on Sheffield city. The Wyre Forest and satellite woods formed the focal area in WO. In HA, the study area included part of the New Forest and woodlands just outside the Forest boundary. In each study area, we surveyed broadleaf dominated woodlands >20 ha but <85 ha in area within an approximate 10-km square for LSWs from 1 March until 20 April to confirm occupancy status at a wood level (SY – 17 woods surveyed/ 5 occupied, HA – 28/15, WO – 27/20). In Worcestershire, the area was increased to an approximately 15-km square to increase the sample of non-occupied woods (Charman *et al.* 2010). Surveys followed the techniques described in Charman *et al.* (2010). We minimised biases in our surveys by using a

standardised trialled survey method for LSWs (Charman *et al.* 2010), which gave a 95% probability of locating LSWs if they were present in a wood. We did not attempt to locate all LSWs in each study region; rather, we focussed on large woodland blocks where we suspected they occurred.

## 2.2. Individual foraging behaviour

When LSWs were located in 2007 & 2008, we collected foraging behaviour at the individual level using an instantaneous sampling technique (e.g. Altmann 1974, Martin & Bateson 1993, Hinsley *et al.* 2007) which uses the first observation only following initial detection. LSWs were usually first detected through their drumming or calling, followed by locating the bird in a tree. At each first

Table 3. Habitat variables collected at LSW nesting and foraging locations and random points in the woodlands. All variables in the tree structure and understorey structure groupings were tested for non linear relationships.

Grouping	Variable	Description
Tree structure	Canopy cover	Mean% cover estimated visually. The number of 2 cm squares in a 4 × 4 wire grid that were at least 50% covered by canopy foliage when viewed directly from below were counted and converted to%. Canopy was defined as foliage at least 10 m high. Measured in plots and subplots, and mean calculated.
	Maximum tree DBH	Diameter at breast height of the largest tree in the plot (cm)
	Maximum canopy height	Height of the tallest tree in the plot (m)
	Basal area	Scored according to a standardised relascope when viewed from the centre of the plot.
Understorey structure	Cover 0.5–2 m	Mean% cover at height band estimated visually as if viewed from above. Measured in plots and subplots, and mean calculated.
	Cover 2–4 m	See previous.
	Cover 4–10 m	See previous.
	Horizontal visibility	Mean% of orange bands visible out of twelve on a 2.4 m pole marked with black and orange alternating sections placed at the centre of the plot and viewed from each subplot.
Deadwood	Dead limbs	Count of all dead limbs > 20 cm in diameter attached to trees in the plot.
	Dead trees	Count of all dead trees in the plot.
Other parameters	Tree diversity	The number of species of trees present in the plot.
	Dominant tree	Categorical variable; the most numerous tree species in the plot.
	Aspect	Categorical variable; the direction of predominant slope of the plot. Measured on 8-point compass scale.
	Slope	Estimation of ground slope across the plot measured in degrees.

observation, the variables in Table 1 were recorded.

### 2.3. Descriptions of nest trees

We searched occupied woods for nesting pairs between April and June each year. Survey methods are described in more detail in Charman *et al.* (2012). At each nest tree, the variables in Table 2 were recorded.

### 2.4. Wider habitat selection for foraging and nesting

We divided the woodland blocks where occupancy by LSW had been confirmed into 1 ha squares. Squares within the surveyed area of the wood, which contained more than 25% woodland,

were numbered and random number tables used to generate a set of ten 1 ha squares in each wood for habitat measurements. Any square with a LSW record during surveys (either visual or audible) was excluded from the random square selection. The centre of the random square formed the centre of a 25 m radius area in which habitat recording took place. Most measurements were recorded from the centre of the 25 m plot, whilst others were taken from four 5 m radius subplots centred 12.5 m north, east, south and west of the centre of the edge of the larger plot (Fig. 2, Table 3). All habitat variables were measured in June and July. The same data were collected from squares where LSWs were observed foraging in March and April 2007 and 2008 and where nests were located 2007–2009. These measurements were centred on a foraging tree or nest tree. Repeat observations at the same location between or within years were excluded. We may have multiple observations of the

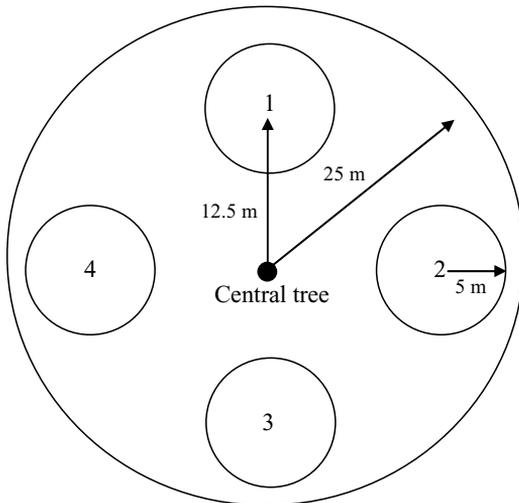


Fig. 2. Habitat measurements were taken at various scales within a 25-m radius area plot. Some measurements were recorded from the centre of the 25-m plot, and others were taken from four 5-m radius subplots centred 12.5 m north, east, south and west of the centre of the edge of the larger plot. See Table 3 for measurements and scales.

same individual using different areas of their territory. For inclusion in analyses, foraging locations must have been at least 100 m apart. In 96% of cases, LSWs were located first by call or drumming. Therefore, we do not believe that habitat influenced detection probability.

## 2.5. Statistical analyses

To address the characteristics of foraging and nest trees and how LSW utilise the resource (Question 1), we report the foraging observations and nest tree information descriptively along with tests of differences in sexes in foraging behaviour and differences in nesting sites between study areas.

Where habitat measurements were taken at the plot and subplot level (Table 3), means were calculated and these were used in analyses. Mean values and associated standard errors were calculated for each habitat variable and comparisons made between random and LSW foraging or nest areas to characterise foraging and nesting areas of woodland (Question 2).

To determine whether the features of nest or foraging sites differed from those of random

points and if LSWs were demonstrating habitat selection in their choices (Question 3), GLMMs with binomial error distribution were constructed using the `glmer` function within the LME4 package in R (R Core Development Team 2006). Separate GLMMs were constructed for foraging and nest analyses. The response variable in each model was binary (LSW foraging/nest point or random point) and wood was included as a random factor to avoid spatial pseudo-replication. The predictor variables are described in Table 3.

For model selection, comparisons using likelihood ratio tests and AIC values were used to determine if terms significantly improved the fit of the model. Those variables that did not improve the model were removed in a backwise stepwise fashion. A three-stage approach was used to reduce the number of correlated covariates entering the model. Firstly, each habitat variable was tested univariately and only those significant at  $p < 0.05$  based on likelihood ratio tests were taken forward to stage 2. In this stage, variables competed with each other in groups describing similar features to reduce collinearity and those significant at  $p < 0.05$  retained in the final stage. The groupings were “Tree structure”, comprising canopy cover, canopy height, tree DBH and basal area; “Understorey structure”, comprising cover at 0.5–2 m, 2–4 m, 4–10 m and horizontal visibility; and “Deadwood”, comprising dead limbs and dead trees. The remaining variables were not grouped. In stage 3, significant variables from stage 2 were included in one model and backward stepwise deletion used to remove variables not significant at  $p < 0.05$  in turn. Non-linear relationships were tested for those variables where it was thought they could occur (Table 3).

## 3. Results

### 3.1. Individual foraging behaviour

The foraging data consisted of 96 individual foraging observations, meeting criteria for inclusion in the analyses: 40 females, 40 males and 16 where the sex was not determined. We observed no significant differences between sexes; for test results and mean values for foraging locations, see Table 4. Overall, 80% of foraging observations were in

Table 4. Mean  $\pm$  SE values of foraging location. Results from tests of differences between sexes in values are shown.

Variable	All, mean $\pm$ SE	Males, mean $\pm$ SE	Females, mean $\pm$ SE	p
Tree DBH	41.5 $\pm$ 1.6	43.4 $\pm$ 2.2	39.6 $\pm$ 2.3	0.228
Tree height	18.9 $\pm$ 0.4	18.7 $\pm$ 0.5	19.1 $\pm$ 0.7	0.588
Foraging height	13.4 $\pm$ 0.3	13.9 $\pm$ 0.4	12.9 $\pm$ 0.5	0.134
Foraging height relative to tree height	0.7 $\pm$ 0.0	0.8 $\pm$ 0.0	0.7 $\pm$ 0.0	0.252
Foraging branch diameter	3.2 $\pm$ 0.3	2.7 $\pm$ 0.2	3.6 $\pm$ 0.6	0.154
Foraging branch length	1.4 $\pm$ 0.3	1.3 $\pm$ 0.5	1.6 $\pm$ 0.3	0.578

Oak *Quercus robur* or *petraea* ( $n = 77$ ), with Beech *Fagus sylvatica* ( $n = 5$ ), Sycamore *Acer pseudoplatanus* ( $n = 4$ ), Common Ash *Fraxinus excelsior* ( $n = 4$ ), Silver Birch *Betula pendula* ( $n = 3$ ), Common Alder *Alnus glutinosa* ( $n = 1$ ), Hawthorn *Crataegus monogyna* ( $n = 1$ ) and Small-leaved Lime *Tilia cordata* ( $n = 1$ ) as minor components. There were no significant differences between sexes in their use of foraging trees ( $\chi^2 = 3.55$ ,  $df = 5$ ,  $p = 0.616$ ). Ninety-eight percent of trees used for foraging were alive ( $n = 94$ ).

LSWs foraged exclusively on branches rather than on the trunk ( $n = 96$ ). Foraging zone on the tree was recorded for 81 cases with 45.7% at the top outer branches (Fig. 1, zone A1), 19.8% at the middle outer branches (B1), 18.5% at the top inner zone (A2), 11.1% at the middle inner zone (B2) and 4.9% at the lower outer branches (C1). In total, 70.3% of the observations were in the outer zones (zones 1) and 64.2% were in the highest category (zone A). There were no significant differences between sexes in their use of foraging zones ( $\chi^2 =$

2.48,  $df = 4$ ,  $p = 0.649$ ). 82.3% of forage branches were alive. The main foraging technique – observed when recording of this attribute was feasible – was apparent gleaning of food from the surface of branches ( $n = 46$ ). Pecking ( $n = 12$ ) and scaling ( $n = 7$ ) were also recorded but much less frequently.

### 3.2. Descriptions of nest trees

Mean height of nest trees was  $14.9 \pm 1.2$  m (range 5.5–28 m) and mean DBH was  $38.0 \pm 3.0$  cm (range 15–73 cm). Nest tree height and DBH were not significantly different between study areas ( $F_{2,24} = 1.52$ ,  $p = 0.24$ ). LSWs nested in twelve different species of tree, the commonest being oak (Fig. 3). Mean cavity height was  $9.35 \pm 0.8$  m (range 1.9–22 m). This did not differ significantly between areas ( $F_{2,24} = 2.88$ ,  $p = 0.08$ ). Cavity height was related to nest tree species ( $F_{11,15} = 3.76$ ,  $p = 0.01$ ; Fig. 3) and nest tree height ( $r = 0.692$ ,  $n = 27$ ,  $p < 0.001$ ). Analysis of nest height relative to

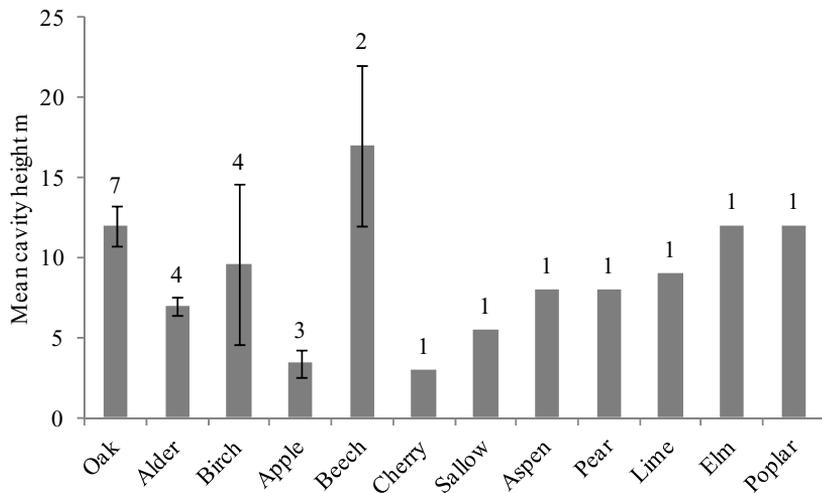


Fig. 3. Mean cavity height for nests in different tree species  $\pm$  SE where available. Bars are ordered in terms of frequency of use. Sample size is shown above each bar.

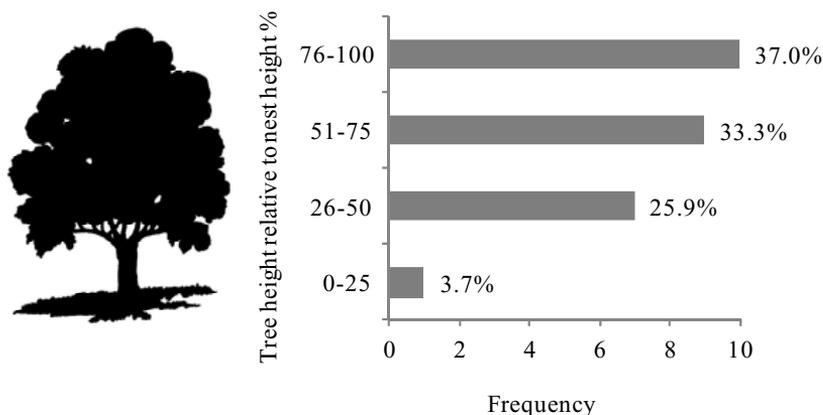


Fig. 4. The distribution of nests in terms of relative nest height (nest height divided by tree height).

tree height showed a strong tendency for nests to be high, with 70% of nests in the upper 51% of the tree (Fig. 4).

Of all nest trees, 59.1% were dead ( $n = 14$ ). Based on the four most frequent nesting tree species (oak, birch, alder and apple *Malus* spp.) there was evidence that choice of dead or alive trees was associated with tree species ( $\chi^2 = 8.57$ ,  $df = 3$ ,  $p = 0.036$ ). All birch and alder nest trees (each  $n = 4$ ) were dead. By contrast, for oak and apple nest trees, 71% ( $n = 5/7$ ) and 67% ( $n = 2/3$ ) were alive.

Of the nest cavities, 55.6% ( $n = 15$ ) were located on a branch of the main trunk, with the remainder being located directly in the trunk. In the case of trunk cavities, 83.3% ( $n = 12$ ) were in dead trees. In all cases of branch nesting, the branch was dead, although in 73.3% of these cases ( $n = 11$ ) the tree itself was alive. The mean diameter of nesting

branches was  $24.1 \pm 2.9$  cm (range 12–50) and the mean length was  $3.3 \pm 0.5$  m (range 0.5–7). In these cases, cavities were located on the underside of branches, often up against the main trunk. In 96% of cases ( $n = 26$ ) the substrate used for nesting was dead. The one exception was a cavity in the trunk of a live beech tree. Of all nest trees, 66.7% ( $n = 18$ ) had evidence of older woodpecker excavations (species unknown).

### 3.3. Wider habitat selection for foraging and nesting

#### 3.3.1. Foraging

LSWs were observed foraging at 102 different locations in 23 woods with comparable random hab-

Table 5. Mean  $\pm$  SE values of habitat variables at forage and random points and nest and random points. Values for random points are different between forage and nest pairings due to the spread of sites used in analyses. Results from tests of differences between values are shown. Values (except probability  $p$ ) are mean  $\pm$  SE.

Variable	Foraging	Random	$p$	Nesting	Random	$p$
Canopy cover	$83.8 \pm 2.2$	$79.9 \pm 1.8$	0.169	$88.4 \pm 4.9$	$76.1 \pm 2.0$	0.027
Maximum tree DBH	$62.1 \pm 2.0$	$58.7 \pm 1.3$	0.140	$55.6 \pm 0.2$	$68.7 \pm 2.4$	0.019
Maximum canopy height	$21.5 \pm 0.3$	$22.7 \pm 0.3$	0.009	$23.8 \pm 1.0$	$22.3 \pm 0.3$	0.160
Basal area	$8.1 \pm 0.4$	$9.1 \pm 0.3$	0.038	$7.1 \pm 0.7$	$9.7 \pm 0.3$	0.003
Cover 0.5–2 m	$20.9 \pm 1.9$	$29.1 \pm 1.6$	0.001	$14.2 \pm 4.2$	$23.1 \pm 1.7$	0.059
Cover 2–4 m	$21.0 \pm 1.5$	$27.3 \pm 1.3$	0.001	$17.6 \pm 3.5$	$22.6 \pm 1.4$	0.190
Cover 4–10 m	$25.7 \pm 2.1$	$35.2 \pm 1.7$	<0.001	$30.4 \pm 5.0$	$32.3 \pm 1.7$	0.714
Horizontal visibility	$70.7 \pm 1.9$	$66.3 \pm 1.7$	0.077	$81.8 \pm 5.4$	$72.1 \pm 1.8$	0.101
Dead limbs	$2.8 \pm 0.2$	$1.9 \pm 0.1$	<0.001	$1.1 \pm 0.5$	$1.6 \pm 0.1$	0.242
Dead trees	$2.5 \pm 0.3$	$1.6 \pm 0.2$	0.030	$3.6 \pm 0.8$	$1.5 \pm 0.2$	0.016
Tree diversity	$2.5 \pm 0.2$	$2.9 \pm 0.1$	0.030	$2.5 \pm 0.2$	$2.5 \pm 0.1$	0.942
Slope	$10.8 \pm 1.0$	$13.9 \pm 0.8$	0.017	$9.8 \pm 1.3$	$11.1 \pm 1.0$	0.453

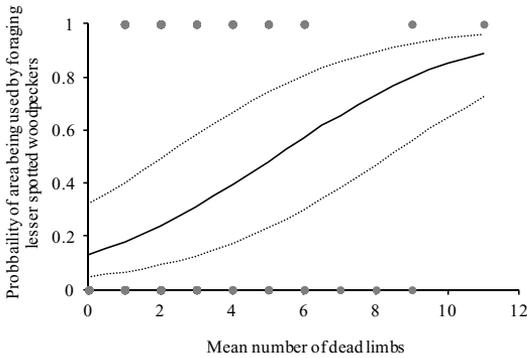


Fig. 5. The modelled relationship between the probability of an area of woodland being used by foraging LSWs the mean number of dead limbs. Lines are the logistic model fit with 95% confidence intervals. Circles are the actual data.

itat point data. Habitat data from foraging locations were compared to equivalent data from 230 random points. Mean values at foraging locations and random points with tests of the differences are presented in Table 5.

Four habitat variables were statistically significant  $p < 0.05$  at the univariate stage 1 and grouping stage 2 (Table 6a) in describing habitat selection for foraging. The probability of a LSW using an area for foraging decreased as understorey, i.e., the cover at 0.5 up to 2 metres, increased, suggesting that LSWs are selecting areas of open understorey at least up to 2 m above the ground. LSWs showed a very strong relationship with deadwood, with the probability of presence increasing as the number of dead limbs increased. They also showed a strong selection for oak trees being the dominant species in foraging areas. The final significant variable was slope, with LSWs showing a preference for flatter areas.

Only one variable, the number of dead limbs, remained to stage 3 to describe the areas selected by LSWs for foraging in our study areas (Table 6a). The relationships between the number of dead limbs and the probability of use of an area by LSWs is shown in Fig. 5. The final model performed significantly better than the null model (loglik 8.95,  $df = 1$ ,  $p < 0.001$ ).

### 3.3.2. Nesting

We compared habitat data around 22 nests in 16 woodlands with equivalent data from 160 random

points. Mean values at nest and random points, and tests of differences are presented in Table 5. Six habitat variables were statistically significant at  $p < 0.05$  at the univariate stage 1 (Table 6b) in describing habitat selection for nesting. The probability of a LSW using an area for nesting increased as canopy cover increased and tree DBH and basal density declined. Areas open in understorey up to 2.4 metres were selected as shown in the negative relationship with cover 0.5–2 m and positive relationship with horizontal visibility. There was also a strong positive relationship between the number of dead trees and the areas being used for nesting. Given the small number of nest locations, the potential to over fit the model was quickly realised and analyses could not proceed beyond stage 2. After stage 2, four variables remained which have strong association with LSW nesting locations – canopy cover, basal area, cover 0.5–2 m, and dead trees. The relationships between each of these variables individually and the probability of use of an area by LSWs for nesting is shown in Fig. 6a–d. For two of these variables, canopy cover and cover 0.5–2 m, the influence of the variable on the probability of the area being used for nesting is very small (range of influence on probability 0–20%).

## 4. Discussion

This study describes foraging behaviour and small-scale habitat selection by LSWs in mature broadleaved woodland blocks in three areas of England. LSWs use a variety of wooded habitats, and this study is not exhaustive in its coverage of these. However, we believe the results are representative of a major habitat for LSWs as they exist now, are transferable across its range in England and allow interesting comparisons to previous work from continental Europe.

### 4.1. Individual foraging behaviour

At the level of the individual bird, oak was most frequently used as a foraging tree, usually representing the dominant species in the stand. With a mean DBH of 41.5 cm and height of 19.3 m, LSWs are using large, mature trees. Mean foraging height

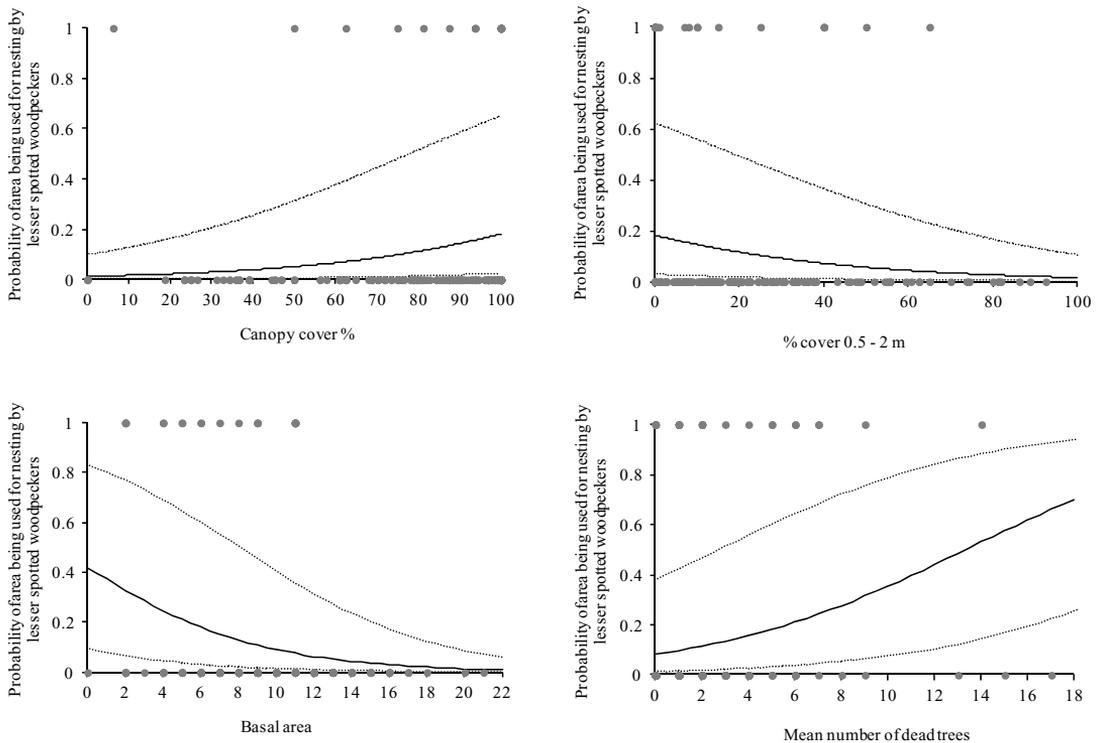


Fig. 6. The modelled relationship between the probability of an area of woodland being used by nesting LSWs and (a) canopy cover, (b) basal density, (c) cover at 0.5–2 m, and (d) mean number of dead trees. Lines are the logistic model fit with 95% confidence intervals. Circles are the actual data.

was observed to be around 13.5 m and usually towards the upper quarter of the tree. Small branches were used exclusively. Trees were almost always alive, and over 80% of branches used for foraging were alive. These results confirm previous work at this scale in another area of England by Smith (2007), comparing foraging observations of LSWs with Great Spotted Woodpeckers *Dendrocopos major* (GSW), and finding that LSWs foraged on smaller diameter branches (median 2.0 cm); higher in trees (mean 16.7 m  $\pm$  0.78) and more often on live substrate compared to GSWs.

Török (1990) has also reported an almost exclusive use of oak as a foraging tree (*Q. cerris* and *petraea*) in Hungary and the preference for live substrate. Again, most observations were on small branches at heights in excess of 12 m. Hogstad (2010) described individual foraging behaviour in subalpine woodland in central Norway, showing that in the pre-breeding period, birch, alder and sallow were preferred species for foraging pre-breeding, representing the dominant deciduous

species in the stand. In this case, the majority of trees were dead and 2–5 m in height (but see difference between sexes).

Interestingly, although tree height was low, birds still used the upper 70% of the tree for foraging relative to absolute height as found in our study. The diameter of branches used for foraging was again small. Olsson (1998) and Olsson *et al.* (2001) observed foraging in mixed forests in Sweden, showing that between August and May, LSWs feed exclusively on wood-living larvae in dead branches, mostly on live trees. Tree species preference reflected the availability of prey associated with the tree, with oak, birch, alder and lime all used to varying degrees in different years. The use of birch and alder fluctuated between years in response to populations of the larvae of the micro-moth *Argyresthia goedarthella*. Lime was particularly important, probably because of the presence of specialist longhorn beetles, *Oplasia fennica* and *Exocentrus lusitanus*.

The results from our study, and other work in

Table 6. (a) Logistic regression of relationships between habitat variables and the probability of an area being used for foraging by LSWs. The final (stage 3) model includes only the number of dead limbs. (b) Logistic regression of relationships between habitat variables and the probability of an area being used for nesting by LSWs. The stage 2 model suggests that canopy cover, basal area, cover 0.5 – 2 m and dead trees are all important determining factors associated with LSW nest sites. fc indicates failure of the model to converge.

Grouping	Variable	Stage 1, $p$ (direction)	Stage 2, $p$ (direction)	Stage 3, $p$ (direction)
(a)				
Tree structure	Canopy cover	0.212		
	Canopy c., quadratic	0.999		
	Maximum tree DBH	0.053		
	Max. tree DBH, quadratic	0.144		
	Maximum canopy height	0.070		
	Max. canopy ht., quadratic	0.102		
	Basal area	0.100		
	Basal area, quadratic	0.180		
Understorey structure	Cover 0.5–2 m	0.043 (–)	0.043 (–)	0.145
	Cover 0.5–2 m, quadratic	0.126		
	Cover 2–4 m	0.113		
	Cover 2–4 m, quadratic	0.999		
	Cover 4–10 m	0.135		
	Cover 4–10 m, quadratic	0.999		
	Horizontal visibility	0.318		
	Horizontal visib., quadratic	0.254		
Deadwood	Dead limbs	<0.001 (+)	<0.001 (+)	<0.001 (+)
	Dead trees	0.154		
Other parameters	Tree diversity	0.353		
	Dominant tree	0.030 (oak)	0.030 (oak)	0.130
	Aspect	0.149		
	Slope	0.019 (–)	0.019 (–)	0.053
(b)				
Tree structure	Canopy cover	0.016 (+)	<0.001 (+)	
	Canopy c., quadratic	fc		
	Maximum tree DBH	0.031 (–)	0.209	
	Max. tree DBH, quadratic	0.226		
	Maximum canopy height	0.101		
	Max. canopy ht., quadratic	0.424		
	Basal area	0.002 (–)	<0.001 (–)	
	Basal area, quadratic	fc		
Understorey structure	Cover 0.5–2 m	0.043 (–)	0.003 (–)	
	Cover 0.5–2 m, quadratic	0.034 (U)	0.101	
	Cover 2–4 m	0.182		
	Cover 2–4 m, quadratic	0.356		
	Cover 4–10 m	0.700		
	Cover 4–10 m, quadratic	0.999		
	Horizontal visibility	0.047 (+)	0.271	
	Horizontal visib., quadratic	fc		
Deadwood	Dead limbs	0.116		
	Dead trees	0.006 (+)	0.006 (+)	
Other parameters	Tree diversity	0.955		
	Dominant tree	0.251		
	Aspect	0.864		
	Slope	0.645		

England and elsewhere Europe, are largely in agreement in that LSWs appear to consistently use small diameter branches in the upper portion of a tree for foraging, and foraging substrate may be dead or alive. The reasons for this selection are may reflect niche separation between LSWs and GSWs (Török 1990) or LSWs may be keying into a food resource in this part of the tree. In our study, the main feeding method was gleaning, suggesting that surface-living prey is being exploited as well as dead wood larvae. The common use of live substrates supports this idea. This issue is complicated by the fact that birch, alder and lime were all present in our study areas and used by LSWs, but substantially less regularly than oak. Further work to assess food availability at different locations on foraging trees, and to establish food sources on different tree species would be essential. Further work would also be required on the presence and inter-annual variation of key LSW food sources, such as *Argyresthia goedarthella* and long-horn beetles.

Differences in foraging behaviour between sexes were earlier reported by Hogstad (2010), with females foraging more on live trees than males and in taller trees with smaller branches, suggesting partitioning to reduce inter-sexual competition for food in subalpine woods with harsh weather conditions. However, we found no significant sexual differences in this respect, possibly relating to the less extreme conditions usually faced by LSWs in England.

#### 4.2. Nest trees

We found that LSWs placed their nesting cavities most commonly in oak and in the upper half of the tree (mean height 9 m, up to 22 m). Cavities were placed in deadwood areas of trees (with one exception) and were situated either in the trunk or on a branch of the main trunk. In their analysis of nest-record data of the British Trust for Ornithology, Glue and Boswell (1994) found a wide range of tree species were used for nesting but the commonest was birch (17%), and cavity heights were around 5.4 m. Differences could be explained by lower nests in dead snags being more likely to be located in “chance” encounters by Nest Record Scheme recorders, compared with active species-

specific searching. In common with our study, the most frequent location for a nest was in a branch (39.2%) and most were in dead or decaying trees (75.2%). Smith (2007) described 16 nest sites of LSWs in Hertfordshire, England, and found that half were in dead and seven were in live trees but dead nest sites, and only one was in a live tree and live nest site. These observations confirm the importance of deadwood for nesting LSWs, in contrast with GSWs which uses live substrate more readily (Smith 2007).

Kosiński and Kempa (2007) described four nest sites in managed forests in Poland, reporting that the mean DBH of nest trees was 48 cm and mean tree height was 20 m, both larger than recorded in this study. Cavity heights were around 12 m and in the upper half of the tree. Nest sites were always dead, although the tree itself was often alive and trunks were used preferentially. Höntschi (2005) described the characteristics of 33 breeding cavities in Germany. Of these, most were in orchards (70%) and the preferred trees were apple, willow and poplar. Given the habitat, most cavities were expectedly low (3–8 m). In our study, six nests were found in orchards, with a further two associated with an orchard (all in WO). The height range of orchard nests was 1.9–8 m. Orchards are often cited as important habitat for LSWs but it is not clear whether the habitat *per se* is important or certain attributes of it. Nests located in orchards in WO were always associated with a block of mature woodland nearby, and adults were observed using this block for the majority of foraging, rather than the orchard itself. Höntschi (2001) attributed the frequent use of orchards in Germany to the amount of deadwood present, rather than any other attributes of orchards themselves.

#### 4.3. Wider habitat selection for foraging and nesting

At a wider scale, foraging locations in our study were significantly different from random locations in the same wood only in terms of the number of dead branches on live trees (variable retained in the final model). At the univariate level, a dominance of oak, flat areas and open understorey were important. Much work has been carried out describing LSW habitat selection, although caution

is required comparing results between countries as the composition of forest stands occupied by LSWs has been found to vary considerably across Europe (Delahaye *et al.* 2010).

In a similar approach to ours, Olsson *et al.* (1992) described factors determining stand use within occupied woods and habitat preferences in Sweden. LSWs were significantly more likely to be present in a stand if snag density was high (>10/ha) and the stand was older (>75 years) (the two were highly correlated). Oak dominated stands were preferred, although birch and aspen and riparian woodland was used. Olsson *et al.* (1992) suggested that the availability of snags or deadwood on live trees is an essential factor for the presence of the species. Delahaye *et al.* (2010) described fine-scale habitat selection in beech and oak forests in Belgium, finding that LSWs were significantly more likely to be detected in areas with a higher percentage cover of oak and a high density of snags and deadwood. In Finland, stands where birch dominates are used (Alatalo 1978) and in Germany oak and willow are used preferentially (Spitznagel 1990). In Germany, young stands are also used by LSWs if they contain snags and deadwood (Glutz v. Blotzheim & Bauer 1980, Spitznagel 1990). In England, the species uses a mixture of habitats including wet woodland, hedgerows, alder rich alluvial areas, birch, beech and oak stands (E. Charman, pers. obs.). Miranda and Pasinelli (2001) suggest that the species selects rough barked trees regardless of species – for example oak, maple, ash, elm, poplar – especially where 20% of the trunk was covered by moss. In a study in Austria, Riemer (2009) observed the majority of LSW registrations near riparian sidearms in softwood stands of alder, willow, poplar and in ash. Several studies show LSW selecting riparian stands and wet woodland (e.g., Spitznagel 1990, Wiktander *et al.* 1992, Höntsch 2001, Miranda and Pasinelli 2001). It is not clear whether this is a preference for the wetness of the habitat per se or rather because they are often left unmanaged and therefore may contain higher amounts of deadwood (Wiktander *et al.* 1992). Riemer (2009) suggests that the association of LSWs with water courses may be an artefact of the tree species and the amount of deadwood associated with this habitat rather than the water feature per se.

Modelling revealed that nest locations differed from random areas in the same woods in terms of canopy cover, basal area, understory and the number of dead trees. Lesser Spotted Woodpeckers were more likely to nest in areas that featured greater canopy cover and lower basal area, had an open understory structure and had a large number of dead trees. These factors suggest selection for closed canopy, older, mature areas of woodlands. To our knowledge no previous work has assessed LSW nest-habitat selection at this scale.

For both foraging and nesting, deadwood attributes emerged as strong variables determining presence. The importance of deadwood to woodpeckers is well known (Smith 1997, 2007) and other work confirms the importance for LSW (e.g., Olsson *et al.* 1992, Wiktander *et al.* 1992, Smith 2007). However, it is interesting to note that the smaller-scale observations in this study revealed that LSWs were foraging on live substrate and often nesting in live trees, albeit usually in deadwood areas of these trees. The discrepancy is most interesting for foraging. Why do LSWs select areas high in deadwood if they are using live substrate? Perhaps our measurement of deadwood was correlated with another variable important to LSWs, however other studies have found deadwood to be an important factor (e.g., Olsson *et al.* 1992). One explanation is that live oak trees, particularly mature ones, support higher numbers of dead limbs than other species (Olsson 1998) and so the apparent selection for dead limbs may actually be selection for oaks.

There may be a correlation between deadwood and the availability of invertebrates of choice for LSW. For example, mature areas of woodland high in deadwood may also be high in invertebrates. It may also represent seasonal change and LSWs switching between or exploiting various different food sources at this time of year and areas previously good for deadwood invertebrates in the winter may be good for wood surface living invertebrates in early spring.

Another possibility is that LSWs do select areas of deadwood but have switched their prey to surface-living invertebrates in response to changes in the availability of deadwood invertebrates or a reduction in the small-diameter deadwood in the canopy.

#### 4.4. Possible reasons for the population declines of LSW

LSWs have declined dramatically across England and Wales at a time when habitat has also changed. An important question, therefore, is whether – given their requirements for foraging and nesting – changes in woodland habitat are associated with declines. Amar *et al.* (2010) presented evidence of widespread changes in structure and species composition between the 1980s and 2000s from surveys of 249 British broadleaved woodlands. Overall, there have been significant decreases in canopy cover and increases in sub canopy (2–10 m) cover. Oak as a canopy species has declined significantly and dead trees have increased. These changes are consistent with reductions in active woodland management, changes in grazing pressure and interactions between the two factors. Those woodland attributes which have strong associations with LSW foraging and nest locations, with the exception of deadwood, have all changed in the direction expected to negatively impact the species.

It is therefore possible that woodlands are now less suitable for LSW foraging and nesting. However, deadwood availability has increased, and this is a very strong determining factor linking to foraging locations and nesting. Structural changes in woodland may be associated with declines in food availability, and this can be linked to over-winter survival and condition immediately prior to breeding. The availability of deadwood invertebrates or deadwood of the sort used by LSWs may have changed. Given the link between food and breeding success identified by Charman *et al.* (2012), work is required to measure food availability in stands of differing structure to establish if this could be a limiting factor.

Another hypothesis for the LSW decline in Europe is the increase in populations of GSW (Nilsson *et al.* 1992, Charman *et al.* 2010, 2012). In Sweden, Nilsson *et al.* (1992) suggested that in years with a low cone crop, GSW switch from spruce seeds to deadwood invertebrates and so compete with LSWs for food. Charman *et al.* (2010, 2012) have investigated correlations between the LSW decline and increasing populations of GSW, with little evidence suggesting a link, although the latter do predate LSWs nests. This area

could be further investigated, however interactions and their impacts are difficult to detect and ultimately may only be tested by large-scale experiments (Charman *et al.* 2012).

#### 4.5. Conclusions

We have shown clear selection of habitat attributes for foraging and nesting. This could be used to target management within woodland blocks to benefit LSWs to provide adequate habitat to meet breeding and foraging requirements. Management to improve deadwood availability and maintenance of a mature structure may also improve conditions for other declining woodland species in the UK. For example, Marsh Tits *Poecile palustris* are secondary cavity nesters which may benefit from deadwood management, and they also show a preference for mature woodlands (Broughton *et al.* 2006). Spotted Flycatchers *Muscicapa striata* also show a preference for a mature, open forests (Smith *et al.* 1987, Hinsley *et al.* 1995). Care, however, should be taken to provide a matrix of habitats to suit a variety of species. Management for LSWs should be targeted in large woodland areas, perhaps using Charman *et al.* (2010) as a guide.

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#### Pikkutikan pesintää edeltävä ruokailu- ja pesimäympäristön valinta englantilaisissa varttuneissa metsiköissä

Pikkutikka (*Dendrocopos minor*) on vähentynyt dramaattisesti ja sen elinalue on pienentynyt Britanniassa. Pesintää edeltävä ravinnonhankinta on tärkeää, ja toisaalta pikkutikan elinympäristön valinta on huonosti tunnettu Britanniassa, joskin seikkaa on tutkittu muualla Euroopassa.

Tässä tutkimuksessa kuvailemme lajin ruokailukäyttäytymistä ja ruokailuympäristön valintaa pesintää edeltävällä jaksolla, pesimäpaikkoja ja

pesimäympäristön valintaa. Havainnoimme ruokailukäyttäytymistä, ruokailupuiden laatua ja pesäpaikan piirteitä, ja vertasimme havaintoja satunnaispisteisiin samoissa metsiköissä. Pikkutikat ruokailivat useimmiten pienillä tammenoksilla puun latvakolmanneksessa. Suuremmissa mitta-kaavassa linnut valitsivat runsaslahopuustoisia paikkoja. Pesäkolot olivat useimmiten puun yläpuoliskossa, ja yleisimmin tammessa. Pesimäpaikat olivat yleensä keskimääräistä avoimempia, runsaslahopuustoisempia ja omasivat varttuneen metsän rakennepiirteitä.

Useat ravinnonhankinnalle ja pesimiselle tärkeiksi osoittautuneista piirteistä ovat brittiläisissä metsissä muuttuneet epäedulliseksi tulkittavaan suuntaan, lukuun ottamatta lahopuuta. Tulevaisuudessa täytyisi selvittää ravinnon saatavuutta rakenteeltaan erilaisissa metsiköissä. Tieto vähenevien lajien vaatimuksista edesauttaa kohdistamaan ympäristön hoitotoimia suojelun kannalta edulliseen suuntaan.

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