

Comparative nesting ecology of the three British breeding woodpeckers



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Despite their striking plumages and loud calls, the three resident British woodpeckers, the Green *Picus viridis*, the Great Spotted *Dendrocopos major* and the Lesser Spotted *D. minor*, remain an elusive and relatively little-studied trio. Some of their nesting habits have been described by Tracy (1933, 1938) and Tutt (1951, 1956), with broader reviews by Palmer (1958), Campbell & Ferguson-Lees (1972), Sharrock (1976) and, more recently, in Cramp (1985). Considerably more research on these species has been undertaken on the Continent, and this has been continued, notably by Wesolowski & Tomiałojc (1986), Hagvar *et al.* (1990) and Török (1990).

The present paper examines many aspects of the breeding biology of the British woodpeckers, drawing largely on information given on 1,113 cards submitted to the British Trust for Ornithology's nest record scheme from its inception in 1939 up to 1989. The Natural History Museum at Tring supplied additional data on clutch size and nest sites from 53 clutches housed in the national egg collection. Details have also been taken from 57 woodpecker nests watched by the late A. Whitaker, and from 14 nests watched by the authors in the New Forest, Hampshire, and the Chiltern woodlands, Hertfordshire.

Distribution of records

Many nest-records chance across, or actively seek out, their local woodpeckers, but none has made them the subject of an intensive study. The records presented below broadly reflect, therefore, the ranges of the three woodpeckers as shown by Sharrock (1976); any weaknesses mirror areas with fewer nest-finders. The regional distributions of nest record cards for each species are shown in fig. 1.

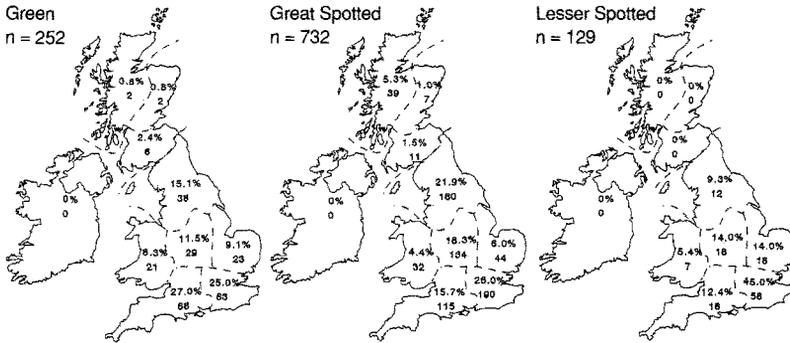


Fig. 1. Regional distribution of BTO nest record cards during 1939-89 for Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor*

The Green Woodpecker is not a scarce bird over much of England and Wales, breeding north to the Scottish borders, where it becomes increasingly local. Most of the 252 cards are from southeast and southwest England, including many from strongholds such as the New Forest, the Weald of Kent and the Forest of Dean, Gloucestershire. Northern England has been recolonised during the twentieth century (in the east from 1913 and in the west during the 1940s: Temperley & Blezard 1951), and is well represented. Scotland was first colonised in 1951 (Borders region), since when there has been a gradual spread, checked sporadically by cold winters (Thom 1986).

The Great Spotted Woodpecker breeds throughout mainland Britain, if locally in places. Most of the 732 cards come from southern counties, with the Midlands well represented. Northern England and Scotland are surprisingly well covered, bearing in mind this woodpecker's disappearance from those regions in the nineteenth century (Harvie-Brown 1908); the northward recolonisation in the present century has been variously attributed to climatic amelioration and afforestation (Thom 1986).

The Lesser Spotted Woodpecker is considerably more restricted away from southern England, being very local in West Wales and northern England and absent from Scotland; like the other woodpeckers, it has never bred in Ireland. The great majority of the 129 cards are from southeast England, with a scattering from eastern counties and the southwestern peninsula and very few from Wales and the north.

Recent estimates of breeding populations in Britain suggest 10,000-15,000 pairs of Green and 30,000-40,000 of Great Spotted Woodpeckers (Hudson & Marchant 1984), and 3,000-6,000 pairs of Lesser Spotted Woodpeckers (Cramp 1985). The nest-record samples therefore broadly reflect the relative abundance of each species.

Breeding habitats

The majority of the nest records for all three woodpeckers came from low-lying localities, with some three-quarters or more of nests below 150 m (fig. 2). The highest-lying nesting locality for Green Woodpecker was at 400 m, in a wooded valley in Powys, and that for Great Spotted was at 320 m, in forest

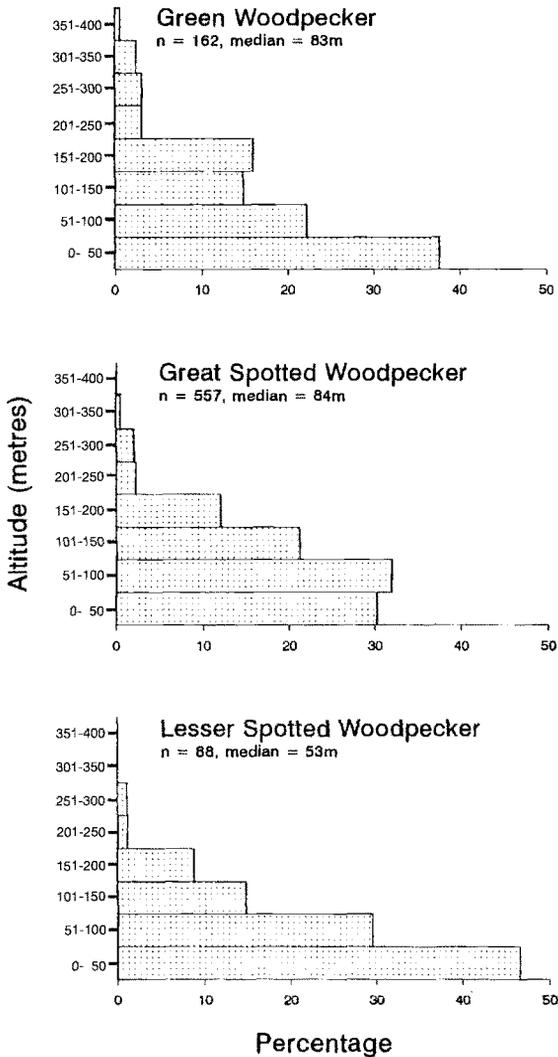


Fig. 2. Altitudinal distribution of Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain according to BTO nest record cards. Comparison of median altitudes shows that Lesser Spotted nests at lower altitudes ($\chi^2 = 10.54$; $p = 0.005$)

tracts of both the Scottish Highland Region and South Wales. Fewer Lesser Spotted Woodpeckers were found at such altitudes, the extreme being a nest in oak woodland on Exmoor, Devon, at 274 m.

All three species occupy predominantly rural habitats, with Lesser Spotted nesting comparatively more frequently in suburban areas than the other two. For each species, fewer than 1% of all nests were in urban sites (table 1). From the 1950s, Great Spotted Woodpeckers entered suburban sites such as parks and gardens (Parslow 1973). During the subsequent 20 years no significant increase

Table 1. Broad habitats occupied by Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain, as shown by BTO nest record cards

When suburban and urban categories are combined, the frequency distributions for Green and Great Spotted Woodpeckers are not significantly different ($\chi^2 = 0.43$), but Lesser Spotted is found to nest in these habitats more often than the other two species combined ($\chi^2 = 7.74$; $p < 0.01$)

	Green Woodpecker	Great Spotted Woodpecker	Lesser Spotted Woodpecker
Rural	219 (94.4%)	655 (93.2%)	110 (86.6%)
Suburban	11 (4.7%)	42 (6.0%)	16 (12.6%)
Urban	2 (0.9%)	6 (0.8%)	1 (0.8%)

was noted in the numbers seeking supplementary food in suburban gardens (Thompson 1988), although there was an increase in rural gardens, reflecting an upward trend in the size of the breeding population (Marchant *et al.* 1990).

Despite their reliance on trees for nesting, the woodpeckers occupied a remarkably wide range of habitats (table 2). Green Woodpecker nests were found in extensive tracts of mature or ancient woodland, whether deciduous or mixed broadleaved and coniferous, although only occasionally in pure conifer stands. In the breeding season, Green, unlike the other two woodpeckers, feeds extensively on the ground, where ants are a key component in a very specialised diet (Cramp 1985). Such foods are common in many conifer forests, and the afforestation programme earlier this century in Britain has been implied as one of the causes of its range expansion (e.g. Temperley & Blezard 1951). For its nests, however, the Green Woodpecker requires mature timber, often not a common feature of modern commercially managed forests. Nests were found in many open woodland environments, such as well-timbered parkland and farmland, often with copses, spinneys and mature hedgerows as a feature. Other breeding sites ranged from open-country commonland and lowland heath to elevated moorland-edge heather-grass or scree where trees were thinly dispersed. The importance of ants in the diet was reflected in the nests found in open habitats with a sunny aspect and short, closely cropped turf: old pasture, paddock, ancient forest lawn, golf courses, large gardens, clifftop grassland, downland and breckland, where grass swards may be kept low by mechanical mowing, grazing by sheep, horses or cattle, or salt-laden winds (table 2).

Most Great Spotted Woodpecker nests were in large fragments or forests of deciduous or mixed woodland (table 2); few were in mature coniferous woodland, most plantations being felled before the timber is old enough to provide ideal nesting sites. Woodland tracts were frequently in river valleys, often in streamside situations, with a few in timbered stretches along the coast and in elevated areas bordering moorland. Other habitats regularly recorded included tree-dotted parkland, orchard, bushy scrub, and a range of habitats close to man. Relatively few Great Spotted Woodpecker nests were found on farmland, exceptions usually being where there were large wooded clumps, extensive spinneys or tree-lined watercourses.

The Lesser Spotted Woodpecker nests were located almost exclusively in habitats with broadleaved trees, but covering a variety of situations: not only in deciduous woods, but along wood edges, in orchards, shelterbelts, thick hedges, and parkland dotted with established trees (table 2). Nests were also

Table 2. Breeding habitats occupied by Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain, from BTO nest record cards

Habitats follow the classification of Yapp (1955). *Other artificial habitats include, for Green, Great Spotted and Lesser Spotted, respectively: school grounds (2, 1, 2), golf course (2, 4, 0), industrial ground (1, 3, 0), cemetery (1, 0, 0), and hospital grounds (0, 2, 0)

Habitat	Green		Great Spotted		Lesser Spotted	
	No.	%	No.	%	No.	%
WOODLAND	132	56.9	545	77.3	60	49.2
<i>Deciduous</i>	54	23.3	281	39.9	36	29.5
<i>Coniferous</i>	5	2.2	12	1.7	0	-
<i>Mixed</i>	38	16.4	185	26.2	11	9.0
<i>Unspecified</i>	35	15.1	67	9.5	13	10.7
SCRUB	10	4.3	33	4.7	9	7.4
<i>Scrub</i>	6	2.6	25	3.6	3	2.5
<i>Carr</i>	4	1.7	8	1.1	6	4.9
FARMLAND	42	18.1	45	6.4	25	20.5
<i>Arable</i>	6	2.6	4	0.6	3	2.5
<i>Pasture</i>	12	5.2	12	1.7	7	5.7
<i>Mixed</i>	4	1.7	5	0.7	1	0.8
<i>Damp grazing</i>	4	1.7	3	0.4	3	2.5
<i>Orchard</i>	9	3.9	13	1.8	6	4.9
<i>Unspecified</i>	7	3.0	8	1.1	5	4.1
HEATH AND MOOR	16	6.9	16	2.3	2	1.6
<i>Lowland heath with trees</i>	8	3.5	7	1.0	0	-
<i>Upland heather/ grass moor</i>	3	1.3	3	0.4	0	-
<i>Breckland/ downland</i>	2	0.9	3	0.4	2	1.6
<i>Inland cliff/ scree</i>	3	1.3	3	0.4	0	-
WETLAND	12	5.2	24	3.4	9	7.4
<i>River-/ streamside</i>	11	4.7	22	3.1	8	6.6
<i>Marsh or fen</i>	1	0.4	2	0.3	1	0.8
GARDENS, PARKS, HABITATIONS	20	8.6	42	6.0	17	13.9
<i>Garden</i>	4	1.7	15	2.1	9	7.4
<i>Parkland</i>	10	4.3	17	2.4	6	4.9
<i>Other artificial habitats*</i>	6	2.6	10	1.4	2	1.6
TOTALS	232		705		122	

found in well-timbered pastures, the tree-lined banks of streams, and woodland fringing bodies of fresh water. The close association of many nest sites with fresh water was also noted in a detailed survey in Sussex (Dougharty & Hughes 1990). Those pairs studied closely were found to be generally shy and intolerant of excessive activity by man in close proximity to the nest. Nevertheless, the Lesser Spotted often frequents suburban and even urban tree-lined avenues, parks and gardens.

Nest trees

Woodpeckers require timber or a wood substitute in which to excavate their nest chamber. The main trees chosen by Britain's three woodpeckers as shown by nest record cards are listed in table 3. The Green Woodpecker turns chiefly to oak *Quercus*, ash *Fraxinus excelsior*, and less often birch *Betula*, beech *Fagus sylvatica* and elm *Ulmus*, all currently or formerly common large trees (Mitchell 1974) in its main wooded and farmland breeding haunts. Among 42 'other trees' listed for Green Woodpecker, 11 were identified: aspen

Table 3. Trees and other sites used for nesting by Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain, as shown by BTO nest record cards

	Green	Great Spotted	Lesser Spotted
Conifers	4	29	-
Willow/sallow <i>Salix</i>	7	19	14
Birch <i>Betula</i>	30	263	22
Alder <i>Alnus glutinosa</i>	15	33	17
Sweet chestnut <i>Castanea sativa</i>	4	19	4
Sycamore <i>Acer pseudoplatanus</i>	1	22	-
Beech <i>Fagus sylvatica</i>	19	37	6
Oak <i>Quercus</i>	54	108	7
Elm <i>Ulmus</i>	15	33	14
Ash <i>Fraxinus excelsior</i>	41	45	9
Fruit trees <i>Prunus</i>	11	22	17
Other trees	42	79	21
Nestbox	-	9	
Pole/post	-	2	
TOTALS	243	720	127

Populus tremula (three), hawthorn *Crataegus monogyna*, hazel *Corylus avellana* and white poplar *P. alba* (two each), hornbeam *Carpinus betulus*, and walnut *Juglans regia*. The 22 nest trees detailed in the Natural History Museum and in Whitaker's diaries endorse its affinity for a wide spectrum of the larger broadleaved, rarely coniferous, trees: oak and elm (four each), ash, willow *Salix* and alder *Alnus glutinosa* (three each), fruit trees *Prunus* (two), poplar, birch and fir *Abies*.

The Great Spotted Woodpecker appears actively to seek out suitable birches in many of the deciduous and mixed woodlands it occupies, but, like the previous species, it will excavate its nest chamber in a wide range of deciduous trees. Among 79 'other trees' listed in table 3, many were decaying stumps (see below, table 5), but 13 were specifically identified: poplar (four), hawthorn and hazel (two each), aspen, walnut, holly *Ilex aquifolium*, elder *Sambucus nigra* and common whitebeam *Sorbus aria*. The 48 trees detailed in the Natural History Museum and in Whitaker's diaries confirm this affinity for birch (25), with fewer nests in oak (nine), alder (four), elm (three), beech and fruit trees (two each), ash, white poplar and rowan *Sorbus aucuparia*.

The Lesser Spotted Woodpecker's occupation of a broad spectrum of habitats, coupled with its small size, enables it to excavate chambers in the trunks and branches of trees of smaller girth, such as willow, alder and fruit. Among 17 'other trees' listed, two were specifically identified as poplar, and one each as hawthorn and lime *Tilia*. The nine trees detailed in the Natural History Museum and in Whitaker's diaries comprise fruit and holly (two each), willow, elm, beech, oak and alder.

Great Spotted is the only woodpecker reported as using nestboxes (sometimes those meant for other species), but both Green and Lesser Spotted will also excavate purpose-built boxes filled with balsa wood, sawdust or peat (du Feu 1989). Eggs may be laid in nestboxes, but with no young fledging successfully. Other sites used by Great Spotted were a gatepost and a telegraph pole.



73-75. Above, female Green Woodpecker *Picus viridis*, Devon, June 1974 (Eric & David Hosking); left, male Lesser Spotted Woodpecker *Dendrocopos minor*, Leicestershire, June 1989 (S. C. Brown); below, male Great Spotted Woodpecker *D. major*, London, May 1986 (Eric & David Hosking)



Table 4. Heights of nests of Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain, from BTO nest record cards

A comparison of median heights shows that Great Spotted occupies the highest levels: Green 4.0 m, Great Spotted 4.9 m, Lesser Spotted 4.0 m ($\chi^2 = 22.04$; $p = 0.0001$)

	Total nests					Mean height
	0-4 m	4.1-8 m	8.1-12 m	12.1-24 m		
Green Woodpecker	243 (50.6%)	123 (25.0%)	97 (19.9%)	17 (3.5%)	6 (1.2%)	4.6
Great Spotted Woodpecker	720 (39.3%)	283 (14.8%)	343 (17.8%)	66 (3.4%)	28 (1.4%)	5.3
Lesser Spotted Woodpecker	127 (6.2%)	65 (3.2%)	37 (1.9%)	17 (0.8%)	8 (0.4%)	5.4

Nest heights

All three woodpeckers may rarely excavate as low as 1 m above ground, including in unusual sites such as fence posts. Most nests are found by 'warm searching' and any bias towards low nests, although unknown, is not thought to be great. Green Woodpecker generally excavates at between 2 and 6 m, Great Spotted at 3-7 m and Lesser Spotted at 2-8 m (table 4). A comparison of median nest heights, however, showed that Great Spotted most often occupies the higher sites: Green 4.0 m (range 0.6-15.2 m), Great Spotted 4.9 m (range 0.9-21.3 m) and Lesser Spotted 4.0 m (range 0.4-18.3 m). A tendency for the larger species to nest lower down in trees is also reflected in Whitaker's findings, with mean heights of 4.8 m (S.E. \pm 0.7) for 21 Green Woodpecker nests, 5.2 m (S.E. \pm 0.3) for 46 Great Spotted, and 5.5 m (S.E. \pm 0.5) for ten Lesser Spotted. Other sources give Green Woodpecker as generally nesting at 1-5 m, Great Spotted at 3-5 m and Lesser Spotted at 2-8 m (Dementiev & Gladkov 1951; Sharrock 1976; Glutz & Bauer 1980).

The three species appear to select different relative heights in trees, which could help reduce competition. The height of the nest hole as a percentage of the total height of the tree, where known, was 46.6% (range 12.5-93.3%; $n = 15$) for Green Woodpecker, 65.1% (range 20.0-93.8%; $n = 56$) for Great Spotted, and 83.9% (range 73.3-97.1%; $n = 5$) for Lesser Spotted.

In addition, the mean diameter of trunk or branch used for the nest chamber decreases with the size of the woodpecker, again reducing competition. In cases where the thickness of the trunk or branch was measured, the mean diameter for Green Woodpecker was 39.4 cm (range 31-46 cm; $n = 4$), for Great Spotted 28.6 cm (range 15-41 cm; $n = 8$), and for Lesser Spotted 19.9 cm (range 10-43 cm; $n = 7$).

Nest site

Many observers noted the site of the nest chamber in terms of 'trunk', 'branch' or 'stump' (including such synonyms as 'limb', 'bole', 'stem' etc.). Again, woodpecker size appeared to influence the frequency with which various positions in a tree were used (table 5). The larger Green and Great Spotted Woodpeckers nested more often in trunks, and the smaller Lesser Spotted in branches. Stumps appear to provide an important source of nesting places, especially for the two 'spotted' woodpeckers. When excavated in the main trunk, nest chambers were commonly sited under the junction of a branch, invariably a dead one, and also where the trunk or ascending limb had snapped off through lightning or storm damage.

Table 5. Position in tree of nests of Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain, from BTO nest record cards

Disregarding box nests, the frequencies of Green and Great Spotted nests in trunk, branch and stump were not significantly different ($\chi^2 = 5.61$), but Lesser Spotted nested significantly more often in stumps than the other two species combined ($\chi^2 = 28.16$, $p < 0.01$)

	Total nests	Trunk	Branch	Stump	Box
Green Woodpecker	82	53 (64.6%)	16 (19.5%)	13 (15.9%)	—
Great Spotted Woodpecker	312	155 (49.7%)	66 (21.1%)	82 (26.3%)	9 (2.9%)
Lesser Spotted Woodpecker	74	18 (24.3%)	29 (39.2%)	27 (36.5%)	—

'Degree of decay' of the nest tree is not easy to define objectively. The various proportions of nests in 'hard' (mature or live) as against 'soft' (dead or decaying) timber are given in table 6. Where the timber was described as 'living', 'mature' or 'sound', this was defined as 'hard wood'; where described as 'old', 'dead', or 'broken branches', or where damage was implied, it was defined as 'soft'. The latter category was probably under-represented, as trees which appear sound externally may conceal a rotten centre. Green and Great Spotted Woodpeckers nested equally frequently in live and dead trees, whereas Lesser Spotted in comparison tended to select timber showing a greater degree of decay. The stronger-billed larger species would appear better equipped for excavating harder wood. Hagvar *et al.* (1990) in Norway and Osborne (1982) in Britain also found that the larger species excavated harder wood. Osborne also speculated that the Lesser Spotted's ability to exploit live orchard trees, which may be excavated more easily than certain larger timber, may free it from total dependence on dead wood. The availability of easily worked decayed timber may also be more important to this smaller woodpecker than species or height of tree.

Table 6. Relative soundness of trees used for nesting by Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain, from BTO nest record cards

For definition of terms, see text. Green and Great Spotted nested equally frequently in live and dead wood ($\chi^2 = 1.18$; n.s.), Lesser Spotted more often using decayed wood ($\chi^2 = 32.73$; $p < 0.01$)

	Total nests	NATURE OF WOOD	
		Mature/live	Dead/decaying
Green Woodpecker	213	117 (54.9%)	96 (45.1%)
Great Spotted Woodpecker	720	365 (50.7%)	355 (49.3%)
Lesser Spotted Woodpecker	129	32 (24.8%)	97 (75.2%)

Nest chamber

Exploratory boring of future chambers may start in the previous autumn, but most excavation observed commenced in earnest in March and April. Trees were sometimes re-used in subsequent years, in rare cases for more than a decade: 41 trees held previous borings, involving six Green, 26 Great Spotted and nine Lesser Spotted Woodpeckers. Fresh borings were generally made below existing excavations, and less often above or beside (as rotting descends). Only occasionally was the same nest chamber used in the following year (18 cases in all). Natural cavities in trees were rarely used: once by Green and twice by Great Spotted.

The size of the nest chamber tends to increase with the size of the species.

Where chamber depths were measured, the mean figures were 38.1 cm for Green, 28.3 cm for Great Spotted and 21.4 cm for Lesser Spotted (table 7). Cramp (1985) gave depths of, respectively, 30-50 cm, 25-35 cm and 10-18 cm. The shape of the entrance hole varied between round and oval for all species, and the mean hole diameters were 5.3 cm for Green, 5.8 cm for Great Spotted, and 3.9 cm for Lesser Spotted (table 7). Cramp (1985) gave respective diameters of 6 cm, 5-6 cm and 3-3.5 cm. As the incubation and, more importantly, the fledging periods progress, nest holes may become enlarged and change shape through accidental damage by the parents, young and intruders. This was applicable particularly to Great Spotted Woodpeckers nesting in decayed birches.

All three woodpeckers generally laid their eggs on wood chips, which could form a layer several centimetres deep (5 cm in the case of one Lesser Spotted) on the floor of the chamber. Less often the eggs were laid on bare wood, and just occasionally the white glossy eggs became stained by the wood.

Table 7. Depth of nest chamber and diameter of nest hole of Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain, as shown by BTO nest record cards

	CHAMBER DEPTH (cm)			HOLE DIAMETER (cm)		
	No.	Range	Mean	No.	Range	Mean
Green Woodpecker	17	20-107	38.1	5	4.4-5.7	5.3
Great Spotted Woodpecker	11	20-46	28.3	5	4.8-7.6	5.8
Lesser Spotted Woodpecker	4	10-25	21.4	5	3.5-5.1	3.9

Laying season

The date of laying of the first egg was recorded either by direct observation or by calculating back from a point when the age of the clutch or brood was known. Where only a single visit was made to eggs or young in an active nest of unknown development, it was assumed to be halfway through the incubation or fledging periods respectively (see below for mean values). First-egg dates, grouped in five-day periods, are shown in fig. 3.

Of the three, the Green Woodpecker laying season was the longest, spanning 104 days from the earliest date of 18th March (Hampshire, 1957, and Dorset, 1977) to the latest of 29th June (Essex, 1988). Great Spotted came next, covering 70 days from 30th March (Lancashire, 1976) to 7th June (Northamptonshire, 1984). Lesser Spotted had the most synchronised season, spanning just 41 days from 17th April (Essex, 1988) to 27th May (Hertfordshire, 1986), although the smaller sample size may have influenced the figures. Cramp (1985) indicated periods for the three species of, respectively, early April to July, mid April to the end of June, and mid April to early July.

For all three species, there were cases of repeat nesting attempts when eggs were lost during the laying or incubation stages. No cases of second broods were documented.

Clutch sizes

Clutch sizes were analysed using only cards showing the same number of eggs in active nests on consecutive visits at least 48 hours apart, or where a visit to

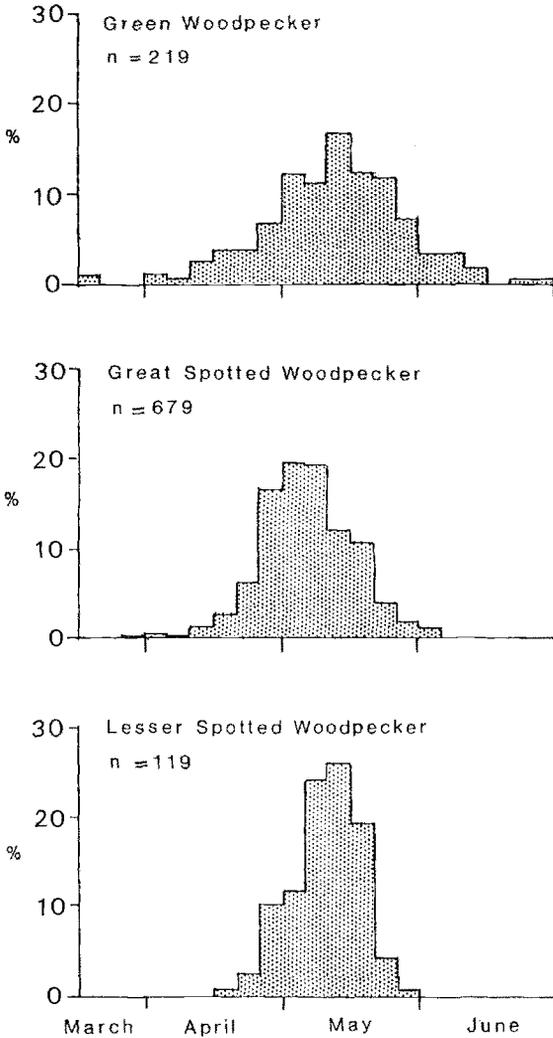


Fig. 3. Laying seasons of Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain during 1939-89 as shown by first-egg dates taken from BTO nest record cards

a nest containing eggs was followed by a visit when hatched young did not exceed the number of eggs. Clutch sizes from a combination of nest record cards and Natural History Museum data are shown in table 8. The commonest sizes were five or six eggs for both Green and Great Spotted, and five for Lesser Spotted. Cramp (1985) gave normal clutch sizes of, respectively, 5-7 (extremes 4-9; rarely, 11), 4-7 (3-8) and 4-6 (3-8).

Brood sizes

These were taken from nest histories where the young were two-thirds or

Table 8. Clutch sizes of Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain

	CLUTCH SIZE								Total	Mean
	2	3	4	5	6	7	8	9		
GREEN WOODPECKER										
Nest record cards	0	1	5	9	4	1	0	0	20	5.0
Nat. Hist. Mus. data	1	0	1	6	6	5	1	0	20	5.8
Combined data	1	1	6	15	10	6	1	0	40	5.4
GREAT SPOTTED WOODPECKER										
Nest record cards	0	2	4	10	4	4	0	1	25	5.3
Nat. Hist. Mus. data	0	0	2	5	9	1	0	0	17	5.5
Combined data	0	2	6	15	13	5	0	1	42	5.4
LESSER SPOTTED WOODPECKER										
Nest record cards	1	0	2	3	3	2	0	0	11	5.2
Nat. Hist. Mus. data	0	1	4	8	2	1	0	0	16	4.9
Combined data	1	1	6	11	5	3	0	0	27	5.0

more through the fledging period (i.e. some 13 days or more old), and the brood was accurately counted in the nest chamber, or where the young were seen to fledge and to be with parents near the nest. All three species may rear up to seven young, Green and Great Spotted usually rearing 2-5 and Lesser Spotted 3-6 (table 9).

Table 9. Brood sizes of Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain, from BTO nest record cards

	BROOD SIZE							Total	Mean
	1	2	3	4	5	6	7		
Green Woodpecker	2	9	10	15	8	6	3	53	3.9
Great Spotted Woodpecker	10	19	45	29	29	7	5	144	3.6
Lesser Spotted Woodpecker	1	2	9	7	6	6	1	32	4.2

Incubation and fledging periods

The cards showed that, for all three species, eggs were laid at 24-hour intervals, rarely longer. Incubation proper started with the penultimate egg, less often with the final egg. Assuming the former, accurate incubation periods were calculated as follows: Green (five cases), 14, 17, 18 (two) and 19 days, mean 17.2; Great Spotted (five cases), 13, 15, 16 (two) and 17 days, mean 15.4; and Lesser Spotted (three cases), 13, 14 and 15 days, mean 14.0.

The fledging period was taken as the time between hatching of the first egg and fledging of the first young of the surviving brood. Periods were calculated as: Green (seven cases), 18, 21 (two), 22, 23 (two) and 24 days, mean 21.7; Great Spotted (15 cases), 18, 19, 20 (four), 21, 22 (three), 23 (four) and 25 days, mean 21.4; and Lesser Spotted (four cases), 17, 18, 19 and 23 days, mean 19.2. The actual fledging process usually took place in the early or mid morning. It was usually accomplished within the day, often quickly, one brood of five young Lesser Spotted Woodpeckers leaving over the course of 1 hour 23 minutes. It was not uncommon for broods to include one or, less often, two runts, and these may linger for a further day. In one extreme case, a poorly developed young Great Spotted Woodpecker stayed for a further 7-8 days before flying successfully.

Breeding success

Of the 252 Green Woodpecker nests studied, 48% were successful in rearing at least one young to fledging; the outcome was unknown at 47.6%, while 4.4% failed completely. Great Spotted had a success rate from 732 nests of 45.1%, just 4.2% being unsuccessful and the outcome unknown at 50.7%. Of 129 Lesser Spotted nests, 48.1% succeeded, the outcome of 42.6% was unknown and 9.3% failed. These rates may, however, be misleading. First, few nests had the contents checked on a regular basis owing to the frequent difficulty of access to the chamber, while there are problems with counting contents accurately. Secondly, many nests were found at an advanced stage (often when the young were noisy and being regularly fed), so the success rates given are likely to be higher than the true values.

A more accurate assessment of breeding success considers failures in relation to the numbers of days over which observations were made at each nest during laying, incubation and nestling periods (Mayfield 1961, 1975). This method calculates nest-failure rates, and standard errors can be calculated using Johnson (1979).

For the combined laying and incubation periods, assuming the mean lengths for each species given above, the relative success of nests (i.e. at least one egg hatching) was 86.8% for Green, 85.0% for Great Spotted and 91.8% for Lesser Spotted. For the nestling period, again taking the mean values given above, success in rearing at least one young through to fledging was 95.3% for Green, 95.3% for Great Spotted and 93.9% for Lesser Spotted. The total nest survival prospects for the combined incubation and fledging periods were thus 85.3% for Green Woodpecker, 83.5% for Great Spotted and 83.0% for Lesser Spotted over the full time period (partial losses of nest contents not taken into account). These results give further evidence of a high measure of success for these hole-nesting birds, nest failures for each species being marginally higher during egg-laying and incubation than during nestling periods.

Human interference and nest-robbing were causes of failure common to all three woodpeckers (one, 12 and two instances, respectively, for Green, Great Spotted and Lesser Spotted), while Green and Great Spotted also failed through displacement by Common Starlings *Sturnus vulgaris* (one and six cases, respectively) and possibly predation by grey squirrels *Sciurus carolinensis* (two and one). Cold, damp weather caused the failure of three Great Spotted Woodpecker nests and one Lesser Spotted, and the latter species was usurped by Tree Sparrows *Passer montanus* (once) and possibly by Great Spotted Woodpeckers (three times). In addition, one Great Spotted nest was destroyed during egg-laying when the tree snapped where the excavation had rendered the walls very thin; another pair lost a brood when the tree blew down in a gale.

Discussion

The nesting habitats occupied by the three British woodpeckers are broadly the same as those used in central Europe (Glutz & Bauer 1980), the former Soviet Union (Dementiev & Gladkov 1951) and Finland (Pynnonen 1939; Haapanen 1965), although the proportion of coniferous trees (notably spruces

Picea) used is greater in ancient and primeval woodlands on the Continent (e.g. the Białowieża Forest of Poland: Wesolowski & Tomiaśojc 1986). In Britain, all three woodpeckers may co-exist and foraging ranges overlap in deciduous woodlands and a few other habitats. For example, in 1970, nests of each with young were located within 175 m in one section of ancient and ornamental woodland in the New Forest (Glue 1972).

Morphologically, the woodpeckers possess features such as bill size, tongue length, and structure of feet and tail that enable them to forage by excavating in wood (Jenni 1981). In winter, they are ideally adapted to exploit food sources on and in the tree trunk, a relatively little-used microhabitat (Hogstad 1978; Conner 1979). In summer, all three species feed almost exclusively on arthropods when rearing young. Classical theories of community ecology (e.g. MacArthur & Levins 1967; MacArthur 1968; Lack 1971) predict that mechanisms may exist to reduce niche overlap, so enabling birds to avoid interspecific competition. How may woodpeckers share resources?

The present study has shown that egg-laying tends to peak at much the same time for each species (late April-May), the nestling periods also overlapping considerably, but differences in the spans of the respective breeding seasons reflect variations in diet. The Lesser Spotted Woodpecker feeds its young very largely on Lepidoptera larvae and aphids (Aphididae) gleaned from the tree canopy, taking fewer spiders (Araneidae), adult dipterans, Lepidoptera pupae and other items (Witherby *et al.* 1938; Török 1990). The Great Spotted also takes large quantities of Lepidoptera larvae, more Phalangidae, Hymenoptera, and adult Diptera (Witherby *et al.* 1938; Török 1990), gleaning and probing the foliage and branches and feeding more often on the trunk than the smaller woodpecker. It has a more varied diet, with parents observed bringing in small molluscs, dead nestling Tree Sparrows and Blue Tits *Parus caeruleus*, and others foraging for supplementary items such as bread and poultry foods in gardens (Glue 1982).

Both of the 'spotted' woodpeckers, however, rely heavily on Lepidoptera larvae, and it has been argued that such temporarily abundant foods can relax the pressures of competition and allow greater overlap among sympatric species (Rabernold 1978). In contrast, the Green Woodpecker takes far fewer arthropods captured from the tree trunk and branches, the young being fed largely on an insect diet of ants and their pupae; this food source is regularly available to the Green Woodpecker with its sophisticated feeding apparatus (Cramp 1985), and is not subject to pronounced peaks in availability outside the winter months.

The present study also shows subtle differences in the tree species and in the degree of decay in trees selected by the three woodpeckers. The two larger species especially are capable of excavating a nest chamber in externally sound timber, but all British woodpeckers are drawn overwhelmingly to trees already partly or substantially decaying and hence of limited commercial value. Modern commercial forests have benefited woodpeckers to some extent during the twentieth century, but woods managed on a strict commercial basis involve periodic brashing, or thinning, before premature felling. Such woods offer limited food and shelter for woodpeckers, whereas those that include a

scattering of over-mature standards, tree stumps and rotten boughs—reflecting natural succession—are ideal.

Individual trees may be used for nesting over a decade, although a fresh nest chamber is invariably excavated each year (Sielmann 1959; Dougharty & Hughes 1990; see also Nest site, above). Fresh borings are frequent, and may be security against predators that may remember holes from year to year (von Haartman 1957; Soncrud 1985). The borings of woodpeckers provide, mainly in subsequent years, niches for a wide range of other woodland animals, notably cavity-nesting birds such as tits (Paridae), Pied Flycatcher *Ficedula hypoleuca*, Common Starling and Eurasian Jackdaw *Corvus monedula* (Campbell & Ferguson-Lees 1972), some vespertilionid bats and arboreal mammals. There is great scope for ornithologists to (a) quantify the importance of the role of woodpeckers in providing niches for other animals, (b) advise forest-managers and landowners of the existence of long-term nest trees, and (c) experiment in suitable nestbox designs as substitute woodpecker nest sites.

Acknowledgments

This paper was made possible through the dedicated efforts of contributors to the British Trust for Ornithology's nest record scheme over 50 years. The Forestry Commission kindly allowed access to certain woodlands. The Natural History Museum, Tring, readily made available data on clutch size and related matters. We thank especially Dr S. J. Baillie, Dr H. Q. P. Quick, Dr J. J. D. Greenwood, Dr R. J. O'Connor and Dr K. Smith for making valuable comments on an earlier draft, and Mrs C. Dudley and Mrs E. Murray for, respectively, collating records and producing artwork. Mrs S. Waghorn and Miss L. Aylward typed from the manuscript. Dr H. Q. P. Quick kindly helped with statistical analyses. The BTO's nest record scheme operates through financial support from the Joint Nature Conservation Committee on behalf of English Nature, the Countryside Council for Wales and Scottish Natural Heritage, and under a contract from the Department of the Environment for Northern Ireland.

Summary

The nesting habits of Green *Picus viridis*, Great Spotted *Dendrocopos major* and Lesser Spotted Woodpeckers *D. minor* in Britain are examined, drawing largely on nest record cards submitted to the BTO during 1939-89, and supported by observations made by the authors in Hampshire and Hertfordshire during 1970-89. For each species, three-quarters or more of nests were at altitudes below 150 m (highest sites: Green, 400 m; Great Spotted, 320 m; Lesser Spotted, 274 m), and broadleaved and mixed woodland were the main habitats (only occasionally pure conifer forest), but each species was found in a wide spectrum of habitats. Nest chambers were excavated in a wide range of trees: Green chiefly in oak *Quercus*, ash *Fraxinus excelsior*, birch *Betula* and elm *Ulmus*; Great Spotted mainly in birch and oak; and Lesser Spotted often in birch, alder *Alnus glutinosa*, willow *Salix* and fruit trees *Prunus*. Nest height varied: Green usually 2-6 m, Great Spotted 3-7 m, Lesser Spotted 2-8 m. Differences were also detected in the thickness of the trunk or branch selected for the nest, with mean widths of 39.4 cm for Green, 28.6 cm for Great Spotted and 19.9 cm for Lesser Spotted. Green nested most often in the trunk, the other two more frequently in branches, with stumps used regularly by all three species. Green and Great Spotted excavated most often in sound, mature timber, with Lesser Spotted heavily reliant upon dead or decaying wood, and nest-chamber size increased in proportion to the size of the woodpecker.

Laying seasons overlapped considerably. For all species, most clutches were started in May, although the season length varied: mid March to the end of June for Green, late March to early June for Great Spotted, and mid April to late May for Lesser Spotted. Eggs are normally laid at daily intervals. Individual clutch sizes varied widely: for Green usually 5-6 eggs (extremes 2-8), for Great Spotted 5-6 (3-9) and for Lesser Spotted 5 (2-7). Incubation was shared by the sexes, with periods of 14-19 days (mean 17 days) for Green, 13-17 (15) for Great Spotted, and 13-15 (14) for Lesser Spotted. All three species may rear 1-7 young: both Green and Great Spotted usually 2-5, and Lesser Spotted normally 3-6.

Nest survival, using the Mayfield (1961, 1975) analysis, showed high measures over the combined incubation and fledging periods: 85.3% of Green Woodpecker nests, 83.5% of Great Spotted and 83.0% of Lesser Spotted nests reared at least one young to fledging. The major reasons given for failure were interference or nest-robbing by man, competition with Common Starlings *Sturnus vulgaris* and grey squirrels *Sciurus carolinensis*, and cold and damp weather.

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