

The implications of nest site competition from starlings *Sturnus vulgaris* and the effect of spring temperatures on the timing and breeding performance of great spotted woodpeckers *Dendrocopos major* in southern England

Ken W. Smith

Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK (e-mail: ken.smith.research@rspb.org.uk)

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A long-term study of the breeding success of an increasing population of great spotted woodpeckers in southern England has shown that nest survival has increased dramatically and the nesting season advanced over the last 20 years. Nest site interference by starlings was frequently observed in the early years of the study and was thought to be the main cause of the low nest survival and delayed nesting. Starling numbers have now declined to such an extent that they no longer nest in the study woods and nest site interference does not now occur. Great spotted woodpeckers are increasing in Britain and the reduction in nest site competition from starlings may be one of the factors contributing to this increase.

Introduction

Competition for nest sites can be important for many species of cavity nesting bird and there are many examples of competitive interactions between different species leading to suppressed breeding densities of one or the other (for references see Newton 1998). In general, woodpeckers excavate their own nest cavities and are the providers of cavities subsequently used by other species. The concept of nest webs has been proposed to describe the complex interactions between primary cavity excavators and secondary users (Martin *et al.* 2004). Starlings *Sturnus vulgaris* are secondary users of cavities and are known to compete aggressively for nest cavi-

ties. In woods where their numbers were high, starlings were shown to compete with great tits *Parus major* for nest holes (van Balen *et al.* 1982). In the Netherlands, nest site interference from starlings has been suggested as one of the factors limiting the use of small woodlands by breeding nuthatches *Sitta europea* (Schotman 2001). Cavity interference between great spotted woodpeckers and starlings has been reported in Europe but few studies have investigated the consequences. However, Mazgajski (2000, 2003) showed that starlings caused a reduced rate of re-use of nest cavities from one year to the next by great spotted woodpeckers, the effect being particularly marked in small woods.

In North America, where European starlings are introduced, there are many examples of nest site competition with native species (McGilvrey & Uhler 1971, Jackson & Tate 1974), in many cases leading to reductions in breeding densities of the local species. There are specific examples of competition with some species of native woodpecker (Troetschler 1976, Ingold 1989, 1994, Kerpez & Smith 1990, Wiebe 2003). Although population impacts have been reported at the local scale, a recent analysis at the national scale failed to find an impact of this competition at the population level for most of the 25 cavity nesting species studied (Koenig 2003).

In Britain, great spotted woodpecker numbers have been increasing for the last four decades. The reasons for this increase have never been established although initially, in the 1970s, it was thought to be related to the availability of dead wood as a result of the widespread death of elm trees (*Ulmus* sp.) throughout the landscape (Marchant *et al.* 1990). Since 1990 the increase has accelerated (Baillie *et al.* 2005) with maturation of forests and increased garden bird feeding the suggested causes. In the same four decades, starlings have declined to such an extent that they are now included in the 'red list' of the UK's Birds of Conservation Concern (Gregory *et al.* 2002). The decline of woodland breeding starlings has been especially severe (Robinson *et al.* 2002). The causes of the declines are thought to be related to loss of permanent pasture, the preferred feeding habitat, and the general intensification of livestock farming (Crick *et al.* 2002).

Here, I present evidence from my long-term intensive studies that nest site interference by starlings was once severe and may have affected the population dynamics of great spotted woodpeckers to such an extent that it may have been a factor limiting their numbers and distribution. The massive reduction in starling numbers has provided the opportunity to study a natural experiment.

Methods

Data collection

From 1984 to 2005, I studied great spotted woodpecker numbers and breeding success in

four large mature broadleaved woodlands in Hertfordshire, southern England (ca. 51°45'N, 0°10'W) (Smith 1997, 2000, 2005). The woods are large (96, 67, 73 and 62 hectares) and are all dominated by mature oaks *Quercus petraea* and *robor* with a variety of other species including hornbeam *Carpinus betulus*, ash *Fraxinus excelsior*, beech *Fagus sylvatica* and sweet chestnut *Castanea sativa*. They are set in a landscape typical of southern England with mixed farmland, woodland and human settlements. Each year I attempted to find all the great spotted woodpecker nests in two of the woods (Wormley and Hitch Woods). In the other woods (Sherrardspark and Hoddesdon Park Woods) low numbers of nests were located in the early years and full coverage was only resumed from 1994 onwards.

A total of 594 nesting attempts were monitored between 1984 and 2005 (Wormley Wood 257, Hitch Wood 110, Sherrardspark Wood 152, Hoddesdon Park Wood 75). Nests were found at all stages of the nesting cycle with the majority first discovered when the adults were feeding young. The clutch size, number of young and outcomes of nests were determined by inspection with a lamp and dentist's mirror and, more recently, using a miniature video camera (Smith 1994, Hancock *et al.* 2002). Nest inspections were planned to determine the clutch size and number of young fledged with the minimum disturbance. Clutch size data were limited to nests inspected during incubation; no clutches were inferred from the number of young, even if only recently hatched, as this is not reliable in this species. For all nests, first egg dates (FED) and the numbers of observed nest days during laying, incubation and chick rearing were established from regular nest observations, by assuming 11 day incubation and 21 day chick rearing periods (data from this study and Glue & Boswell 1994) and by noting the behaviour of the adult birds (Jackson 1976). Nests were visited every few days close to fledging in order to establish fledging date as accurately as possible. Data for FED were only used when it could be determined within five days. All nest failures were recorded, together with the cause where this was known. Daily nest survival rates during the egg stage (laying and incubation) and during chick rearing were estimated from total days exposure and

number of failures (Mayfield 1961). In 1984 and 1985 and in 1991–2003, the numbers of starlings breeding within the woods were counted by mapping all nests with visiting adults or calling young.

Analyses

As not all nests were observed from their initiation, a Mayfield (1961) daily nest survival approach was used to analyse nest success. For each nest the number of nest days during laying and incubation and chick rearing were estimated together with the nest outcome over the period — success or failure. Daily nest survival rates were analysed using binomial models with a logit link function. An events/trials approach was used with the outcome (0 for success and 1 for failure) as the numerator and the number of nest days as the denominator in the binomial model (Aebischer 1999). Daily nest survival rates during the laying and incubation and chick rearing periods were analysed with year and nesting Starling density as continuous predictive variables using a forward stepwise procedure. Overall nest survival and its 95% confidence intervals were calculated by bootstrapping the daily rates.

Trends in clutch size and the numbers of fledged young from successful nests were analysed with Generalised Linear Models with normal errors and an identity link function. The distribution of clutch size was a good approximation for normal and that for the number of young was slightly skewed to the left (skew = -0.62 , $z = 3.82$) and so was transformed by negative square root. Predictive variables were year, the difference between the FED and the median laying date for that year and wood (EGGDIFF), March and April Central England Temperature (CET) (Parker *et al.* 1992) and nesting starling density. Central England Temperature is the mean daily temperature averaged over the month calculated using data from a collection of weather stations distributed across southern England. The study sites are within the zone for which CET is calculated. To examine the overall trends in FED, the median laying date has been calculated for each year and wood and analysed using a Generalised

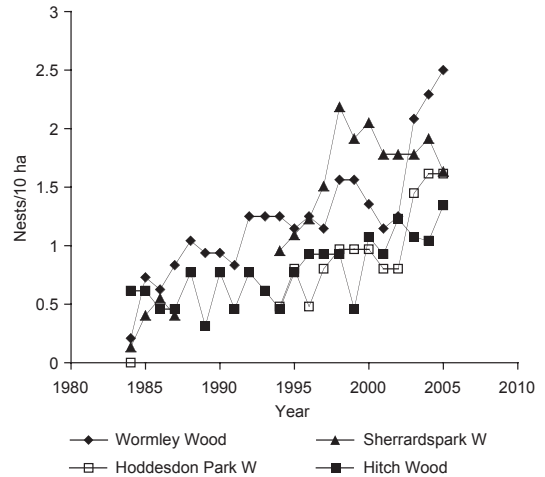


Fig. 1. Trends in the density of great spotted woodpecker nests found in the four study woods 1984–2005. No nests could be found in Hoddesdon Park Wood in 1984.

Linear Model with normal errors and an identity link function with starling density and March and April CET as the predictive variables. All statistical analyses have been performed in SAS (SAS Institute 1999–2001).

Results

The numbers of great spotted woodpecker nests have increased substantially in all four woods since 1984 (Fig. 1), in all cases at a greater rate than the UK national population index which has increased by 53% over the period (Baillie *et al.* 2005).

In 1984 and 1985, there was considerable evidence of competition between great spotted woodpeckers and starlings for nest cavities. Starling numbers were high throughout the woods and, particularly in Wormley Wood, there appeared to be a shortage of nesting cavities for starlings with birds taking over woodpecker cavities as soon as they were excavated. There were a number of instances of loss of nests during egg laying. Starlings appeared to dominate in competitive disputes over nest holes. From 1986 onwards, although there were no formal counts, starling numbers declined in the woods and there was less direct evidence of competitive interactions although subtle effects cannot be ruled out.

The daily nest survival rates of the Hertfordshire great spotted woodpeckers are summarised by five year periods from 1984 to 2003 and 2004/2005 in Table 1. The causes of the nest failures (Table 2) were not always known but were dominated by interference by starlings, particularly during laying and incubation (overall 7 of 10 failures with known causes and 6 of 7 losses during laying and incubation). All the failures attributed to starlings occurred before 1986. These daily nest survival rates mean that in 1984–1988 the nest survival over the full period of laying and incubation was 0.54 (95% range 0.47–0.62) compared with 0.92 (95% range 0.89–0.95) in 2004–2005. Nest survival over the chick rearing period was higher but was still significantly different between the two periods (1984–1988, 0.93 (95% range 0.90–0.95); 2004–2005, 0.992 (95% range 0.988–0.995)).

The numbers of starling nests in the four woods are summarised in Table 3. Although data are incomplete, in 1984 the numbers were high in all woods, but extremely high in Wormley, Sherrardspark and Hoddesdon Park Woods where densities exceeded one nest per hectare. Numbers fell rapidly after 1984 so that by 1992 only low numbers remained and by 1996 none were found nesting within the interior of any of the woods.

The daily nest survival rate during egg laying and incubation decreased strongly with starling density ($\text{logit}(\text{daily failure rate}) = -5.269 + 3.570 \times \text{starling density}$, $\chi_1^2 = 16.03$, $p < 0.001$, $n = 91$ nests). There was a less strong, but significant, increase in nest survival with year ($\text{logit}(\text{daily failure rate}) = 237.4 - 0.121 \times \text{year}$, $\chi_1^2 = 5.99$, $p < 0.05$, $n = 91$ nests) but adding year to the model with starling density gave no significant

improvement to the model ($\chi_1^2 = 0.55$, n.s.). The daily nest survival during chick rearing decreased significantly with starling density ($\text{logit}(\text{daily failure rate}) = -7.558 + 5.043 \times \text{starling density}$, $\chi_1^2 = 3.86$, $p = 0.05$, $n = 495$ nests) but did not increase with year ($\chi_1^2 = 1.05$, n.s.). The relationship was far less strong than that during egg laying and incubation.

Clutch size was determined for 76 nests (mean = 5.34, SE = 0.10, range 3–7). Seven of these could not be included in the modelling because starling density was not available for all years. Clutch size was significantly related to EGGDIFF alone ($\chi_1^2 = 30.16$, $p < 0.001$, $n = 69$ nests) but the addition of starling density significantly improved the model ($\chi_1^2 = 4.80$, $p < 0.05$). Adding March and April CETs or year gave no significant improvements to the model (March CET, $\chi_1^2 = 2.80$, n.s.; April CET, $\chi_1^2 = 0.12$, n.s.; year, $\chi_1^2 = 0.04$, n.s.) The full model was: clutch size = $5.27 - 0.0897 \times \text{EGGDIFF} - 1.477 \times \text{starling density}$ ($\chi_2^2 = 34.96$, $p < 0.001$, $n = 69$ nests). The number of young fledged from successful nests was determined in 228 cases (mean = 4.18, SE = 0.07). The only significant variable in the model was EGGDIFF with no other variable making a significant contribution (starling density, $\chi_1^2 = 0.02$, n.s.; March CET, $\chi_1^2 = 0.46$, n.s.; April CET, $\chi_1^2 = 1.14$, n.s.; year, $\chi_1^2 = 0.42$, n.s.). The full model was: $\text{SQRT}(7 - \text{no fledged}) = 1.64 + 0.0199 \times \text{EGGDIFF}$ ($\chi_1^2 = 4.94$, $p < 0.05$, $n = 200$ nests). There were clear trends for birds laying relatively early to have larger clutches and to fledge more young (Figs. 2 and 3).

As well as causing nest failures, interference from starlings would be expected to lead to delayed nesting as woodpeckers that had lost their cavities were forced to excavate or find new

Table 1. Daily nest survival rates for the four Hertfordshire woods grouped by five year periods (1984–2003) and 2004–2005. Numbers in brackets are the number of nest days and failures in each period.

Period	Laying and incubation		Chick rearing	
	Survival	95% range	Survival	95% range
1984–1988	0.9600 (150/6)	0.9138–0.9819	0.9963 (539/2)	0.9853–0.9991
1989–1993	0.9583 (24/1)	0.7565–0.9942	1.00 (639/0)	–
1994–1998	1.00 (155/0)	–	0.9994 (1543/1)	0.9954–1.00
1999–2003	0.9944 (355/2)	0.9778–0.9986	0.9996 (2262/1)	0.9969–1.00
2004–2005	0.9935 (306/2)	0.9743–0.9984	0.9992 (1278/1)	0.9941–1.00

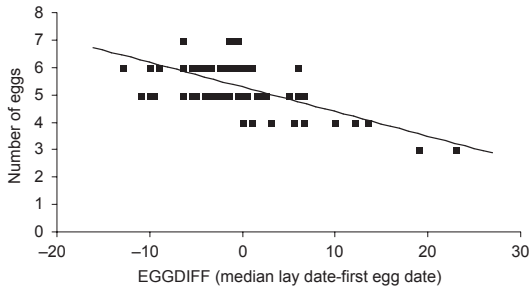


Fig. 2. The clutch size against EGGDIFF for all nests ($n = 76$). Trend line is plotted for starling density = 0 using the relationship given in the text.

ones. In both Wormley and Hitch Woods there was a significant trend to earlier nesting over the 22 year study (Fig. 4), although the trend was by no means linear with most of the change occurring before 1990. Both starling nest density and April CET were significant predictors of the median laying date for both woods with March CET making no additional contribution to the model (median laying date = $72.00 + 13.30 \times$ starling density $- 4.65 \times$ April CET, $F_{3,12} = 21.1$, $p < 0.001$).

Discussion

Although I have used the term 'nest site competition' in this paper, the interaction is more correctly a case of 'cavity kleptoparasitism' (Kappes 1997, Mazgajski 2003) in that the starlings benefit at the cost of the woodpeckers. Mazgajski (2000, 2003) showed that starling interference

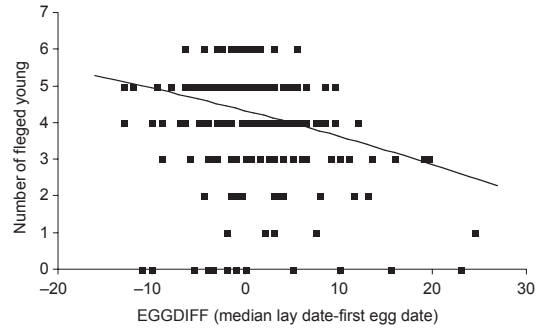


Fig. 3. The numbers of fledged young plotted against EGGDIFF for all nests ($n = 228$). Trend line is plotted using the relationship given in the text fitted only to data for successful nests.

reduced the rate of reuse by great spotted woodpecker of their cavities from one year to the next. In my studies I have shown an impact of starlings on the dynamics of cavity creation and occupation by great spotted woodpeckers in early spring. Such interactions are difficult

Table 2. Causes of great spotted woodpecker nest failures in four Hertfordshire woods, 1984–2005.

Cause	Failure during laying and incubation	Failure during chick rearing
Interference from starling	6	1
Human interference	0	1
Flooding	1	0
Nest tree fallen	0	1
Unknown cause	4	2
Total	11	5

Table 3. Counts of starling nests in the four Hertfordshire study woods ('–' indicates no count in the particular year). Since 1996 there have been no Starlings nesting in the woods. Note the missing years from 1986 to 1990 where there were no counts.

Year	Wormley Wood (96 ha)	Sherrardspark Wood (73 ha)	Hoddesdon Park Wood (62 ha)	Hitch Wood (67 ha)
1984	132	194	105	36
1985	60	–	–	18
1986–1990	–	–	–	–
1991	4	–	–	–
1992	3	–	–	0
1993	0	–	0	0
1994	0	2	0	0
1995	0	1	0	0
1996	0	0	0	0

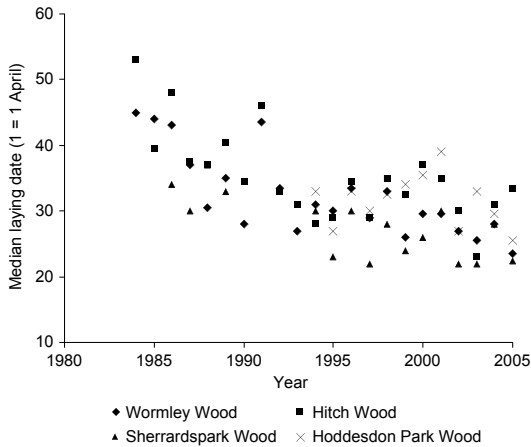


Fig. 4. Median first egg date against year for the four study woods.

to observe and quantify given that woodpeckers may select and lose a number of potential nest sites before they get to laying. My observations of the impacts on timing and success once eggs are laid are therefore likely to underestimate the severity of the impact.

The high densities of nesting starlings in the study woods in the 1980s impacted the woodpeckers in a number of ways but the daily nest failure rates during egg laying and incubation were particularly affected. As well as the direct impact on nest survival, egg laying was delayed by up to 10–15 days. The models indicate that this would reduce the number of young fledged from successful nests from 4.23 to 3.83. Thus, overall, the great spotted woodpeckers were producing an estimated 1.91 young per pair in 1984–1988 compared with 3.88 in 2004–2005. Excavation of a new cavity and relaying could ameliorate the impact to some extent but within the observed egg laying period (around 30 days) the opportunities for this will be limited.

Without data on the other demographic rates, their density dependence and the re-nesting dynamics, it is not possible to calculate the population consequences of these nest survival and productivity figures. However, the differences are substantial and given that great spotted woodpeckers are essentially single brooded, an impact is quite likely. In three out of four of the study woods, the numbers of great spotted wood-

peckers were clearly depressed in 1984 and 1985 and rose rapidly thereafter as starling numbers collapsed. In Hitch Wood, starling density was not as high as the other two woods and the main effect was a delayed nesting season, with no evidence of a big increase in numbers once the starlings had gone. So the evidence from the four Hertfordshire woods is that, where starling numbers were particularly high, there was an impact on the woodpecker populations and in all woods there was some impact on either the breeding success or nesting season of the woodpeckers.

Although the most obvious mechanism for the delayed nesting in woodpeckers is loss of cavities and the excavation of new ones, it is also possible that late nesting may have evolved as a consequence of the conflict with starlings (Wiebe 2003). Given that starling competition has been an issue for great spotted woodpeckers for many decades (Tracy 1933) it would be surprising if such an adaptation had not occurred. However the pressure to nest at the optimum time for invertebrate food supplies for chick rearing probably limits the ability of the woodpeckers to do this (Wiebe 2003). This is likely to be particularly the case in temperate broadleaved woodlands where the spring flush of defoliating invertebrates on which most bird nestlings are fed is very short lived.

Starling interference has not been an issue in my study woods since the late 1980s and there are now no starlings whatsoever nesting within the woods. It is not known why starling numbers were so high in the 1980s, nor why they have subsequently declined so markedly, but this is almost certainly related to changes in the management of the surrounding agricultural land (Crick *et al.* 2002), rather than factors within the woodlands themselves. It appears to be quite exceptional for starlings to nest throughout such large woodland blocks. Elsewhere in Europe starling interference at great spotted woodpecker cavities was more prevalent in smaller woodland plots (Mazgajski 2000, 2003) although these ‘small’ plots were similar in area to my study woods. In the fragmented landscape of Britain interference would always be expected to be high.

Although it cannot be ruled out that the increase in great spotted woodpeckers has been

a factor in the decline of the starling, this is considered most unlikely. All my observations and those of other workers show that it is the woodpeckers that suffer in encounters between the species. The decline of the starling in Britain started at a time when great spotted woodpeckers had been stable in numbers for some time and the major increase in the woodpeckers took place after the starlings had already declined. A recent analysis of national data on the declining starling has found no evidence of reduced breeding success which would be expected if nesting interaction with woodpeckers were an issue. In fact, starling breeding performance has, if anything, increased (Freeman *et al.* 2002).

Even though starling competition is no longer an issue, woodpecker populations have continued to increase at a high rate. It is possible that this is simply the long-term effect of increased breeding success but other factors are now likely to be involved, including maturation of woodlands and the consequent increase in dead wood resources and the increased provision of artificial food at garden feeders in Britain. There is some evidence from my studies to support the increased dead wood hypothesis. Wormley Wood, which has shown the most spectacular increase in woodpecker numbers, has been managed by non-intervention for more than 50 years with increasing volumes of dead wood present (K. Smith pers. comm.). On the other hand, Hitch Wood, where the woodpeckers were showing little upward trend until the last five years, is managed for timber production and firewood and so has lower levels of dead wood.

The impact of higher spring temperatures on the breeding seasons of birds has been widely reported with many bird species in UK nesting around seven days earlier in the last decades (Crick & Sparks 1999). The FEDs of my woodpeckers have advanced far more than this but the analysis shows that this is related to two factors; higher spring temperatures as indicated by the significant relationship with April CET and also the reduction in the nest site interference from starlings. There was no evidence from my study that spring temperature had any impact on clutch size, nesting success of the number of young fledged from successful nests.

Early nests tend to have larger clutches and to fledge more young than later ones. This is similar to the trends found for both great and lesser spotted woodpeckers (van Manen 1993, Wiklander *et al.* 1994, 2001, Mazgajski 2002, Rossmann 2005) where two factors were thought to be operating. Experienced pairs were shown to nest earlier, lay larger clutches and fledge more young. In addition, as the season progressed, feeding conditions tended to deteriorate and chick provisioning became more difficult for the adults. It is probable that similar factors are operating for my great spotted woodpeckers.

Smith (2005) has analysed the national nesting data for the great spotted woodpecker held by the Nest Record Scheme (NRS) of the British Trust for Ornithology (BTO) and compared this with the Hertfordshire results. He found similar trends in the daily nest survival rates and laying dates suggesting that nest site competition from starlings was not just a Hertfordshire phenomenon but occurred more widely. He suggested that the reduction in competition since the 1980s may have been one of the factors leading to the increase in great spotted woodpeckers.

In an earlier analysis, Glue and Boswell (1994) examined the BTO NRS data for the great spotted woodpecker from 1939 to 1989. They did not report any trends in nest survival for the period they covered, but their reported clutch size (5.40, SE = 0.18, $n = 42$) was similar to my Hertfordshire figures (5.34, SE = 0.10, $n = 76$; $t = 0.30$, $p = 0.76$, n.s.). However, the numbers of fledged young from successful nests was significantly lower (3.62, SE = 0.12, $n = 144$; Hertfordshire, 4.18, SE = 0.07, $n = 228$; $t = 4.05$, $p < 0.001$). Why this should be so is not clear although it may reflect the later nesting in the pre 1990 period or be due to other factors entirely.

Although many generalist bird species are known to occupy both farmland and woodland habitats (Fuller 1982), this is the first case where a specialist farmland species, the starling, has been shown to compete directly with a specialist woodland species. What is more, it is possible that the decline of the starling on farmland has facilitated the spread of the great spotted woodpecker into small farm woodlands and hedgerow trees.

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