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## Breeding biology of the Woodcock *Scolopax rusticola* in Britain

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A total of 449 nest record cards collected by the British Trust for Ornithology during 1945–89 was used to examine timing of nesting and brood production of the Woodcock. Daily chick mortality rates were estimated from recaptures of 26 Woodcock broods during an intensive study in 1988–92. Clutches were initiated between March and July, with a mode at the end of March. On average, egg laying commenced earlier in England (median first-egg date 8 April) than in Scotland (20 April) and there were negative relationships between first-egg dates and mean March air temperatures, both between years and regionally within years. Nest survival during egg laying and incubation was  $41 \pm 1\%$  and the mean number of clutches hatched per female alive in March was 0.89 (95% CL 0.47–1.58). Chick survival until fledging was estimated as  $56 \pm 8\%$ , resulting in a mean annual production of  $1.80 \pm 0.72$  fledged young per female alive at the start of the breeding season. A small second peak in the distribution of first-egg dates in mid-May indicates that in some years females may attempt to rear second broods.

The Woodcock has a widespread breeding distribution within Britain, with appreciable absences only from southwest England, the south and west coasts of Wales and from Shetland, Orkney and the Western Isles.<sup>1</sup> Nevertheless, it generally occurs at relatively low densities. This, combined with its secretive nature, has meant that until recently little was known of its mating system, site fidelity and average breeding success. There is now good evidence from radiotracking studies for successive polygyny in the Woodcock, whereby older males may mate with several females and only remain with each female for three or four days after mating.<sup>2,3</sup> Analysis of ring recoveries has revealed that both philopatry and fidelity to a breeding site by adult birds are high in the Woodcock.<sup>4</sup> Alexander gave data on clutch and brood size,<sup>5</sup> but basic information on the productivity of Woodcock is still lacking and there is currently concern that the size of the

British breeding Woodcock population has recently declined, particularly in southern England.<sup>1,6</sup>

The nest record cards from the British Trust for Ornithology (BTO) scheme provide a valuable source of information for species such as the Woodcock, which breed at low densities and whose nests are difficult to find. Morgan & Shorten<sup>7</sup> examined the Woodcock nest cards for the period 1945–71 ( $n = 215$ ), but calculated only the proportion of nests that were successful (those from which at least one chick hatched). Crude proportions of successful nests, however, have been shown to be misleading because clutches found when partly incubated have a shorter time to survive to hatch and hence a higher probability of success.<sup>8,9</sup>

This paper gives estimates of Woodcock nest success, based on the number of days of observation according to the Mayfield method,<sup>8,9</sup> using the BTO nest record data for 1945–89. The timing of nesting is documented and the likelihood of some females raising two broods in a

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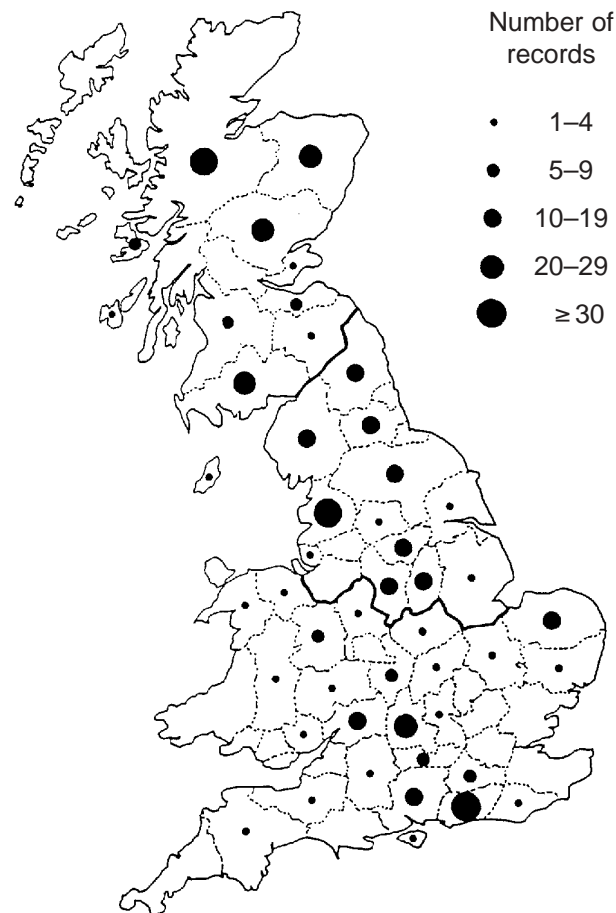
season is examined. A mean chick survival rate is estimated from data collected during repeated searches for broods in an intensive study in Derbyshire during 1988–92.

## METHODS

A total of 539 nest record cards collected by the BTO during the period 1945–89 was analysed. The nests were found by observers throughout Britain. Of the cards, 79 were excluded because they related only to hatched young, as were 11 cards where the nest contents were recorded as taken by predators or abandoned when first found. The distribution of records (Fig. 1)

broadly reflects the distribution of breeding Woodcock.<sup>1,10</sup>

The incubation period was taken as beginning on the day the last egg was laid and finishing on the day the last chick hatched. Records of clutch size were accepted only on two conditions: (1) if two visits to the nest more than 48 hours apart showed no increase in the number of eggs laid; or (2) where hatching was recorded, if the nest was visited during the 15 days prior to the hatch. First-egg dates were determined from nests found during laying by subtracting one day for each egg laid, and from nests for which the hatch date was known by subtracting 22 days plus



**Figure 1.** The distribution of records of Woodcock nests from the BTO Nest Record Scheme for 1945–89 ( $n = 449$ ) and the division of Britain into central and southern England, northern England and Scotland for the determination of regional differences in first-egg dates, chick ringing dates and nest failure rates.

one day for each egg. Records where the date of hatching could be determined to within  $\pm 5$  days were included.

The distribution of dates on which Woodcock chicks (EURING age 1) have been ringed in Britain was determined from the ringing dates contained in the data for birds that were subsequently recovered during the period 1909–90. A total of 352 dates was obtained, where the exact day of ringing was known. The distribution was assumed to be representative of the distribution of nest hatching dates. It was assumed that the majority of chicks were ringed during their first day, when still in or near the nest, but clearly some errors were introduced from chicks ringed when they were older.

Regional differences in the onset of egg laying and in chick ringing dates were studied by splitting Britain into three areas: central and southern England, northern England and Scotland (Fig. 1). The influence of spring air temperatures on Woodcock first-egg dates was examined using figures for the mean daily air temperature in March from the weather station nearest to each nest site. These figures were extracted from the Monthly Weather Report compiled by the Meteorological Office, Bracknell.

At least two visits were made to 339 nests, enabling the records for these to be used to calculate daily rates of nest loss. Rates of loss were estimated from the number of days during which nests were observed and from the number of losses occurring during that period using the Mayfield method<sup>8,9</sup> in a revised form which enabled statistical comparisons.<sup>11,12</sup> This method assumes that the daily survival probability ( $S$ ) during a given stage of nesting is constant and that the probability of a nest surviving throughout a stage lasting  $x$  days is  $S^x$ . Where the exact date of nest failure was not recorded, it was assumed to have been midway between visits. Nests visited at least twice were grouped into deciduous, mixed or coniferous woodland categories according to the information in the habitat box on the nest record card, where given. Regional and temporal variation in nest failure rates was examined by means of a logistic regression model with the days of observation for each nest as the number of binomial trials and the number of days that the nest survived as the dependent variable.

Of 309 occasions when the female was recorded as flushed from the nest or an egg count was made (and hence the female was assumed to have been flushed) and it was visited again, the nest was found to be deserted on 37 subsequent visits (12%). Nevertheless, nest failure was still taken as occurring midway between visits; if the date of nest failure had been taken as the date on which the parent bird was flushed from the nest, rates of nest failure might have been biased high. In order to test whether nest searching influenced clutch survival during incubation, separate rates of nest loss were calculated for the five days immediately after the nest was found and for days 6–22. This analysis was restricted to nests checked within ten days of finding; if nests that were checked at larger intervals were included, any nest that failed between finding and the first check would be scored as having failed after the five-day period after finding. Hence the estimated failure rate for the first five days would be biased low.

No information was available on the survival of Woodcock chicks from the nest record card data but a daily rate of chick mortality was estimated from recaptures of Woodcock broods during an intensive study at Whitwell Wood, northeast Derbyshire (53°18'N 1°13'W) in 1988–92.<sup>13</sup> In this study, 26 broods were located with trained dogs, ringed and then recaptured every 3–4 days. The mean age of chicks when ringed was  $5.0 \pm 1.1$  days. The rate of chick mortality was calculated on the basis of chick-days, with losses assumed to have occurred midway between brood captures, using the revised Mayfield method.<sup>11</sup> As the fates of the chicks within a brood were not independent, standard errors were obtained by bootstrapping.<sup>14</sup> In 15 of the broods (58%), chicks disappeared one at a time. It was assumed that all of the chicks were found each time a brood was located, but single chicks were known to have been missed on two occasions because they were recaptured on the next brood check. The calculated daily chick survival rate is therefore likely to be a minimum estimate. The period from hatching to flying was taken as 20 days.<sup>3</sup>

Mean values are given with standard errors except where stated otherwise. Confidence intervals for the proportion of females alive in March that hatched a clutch of eggs and the

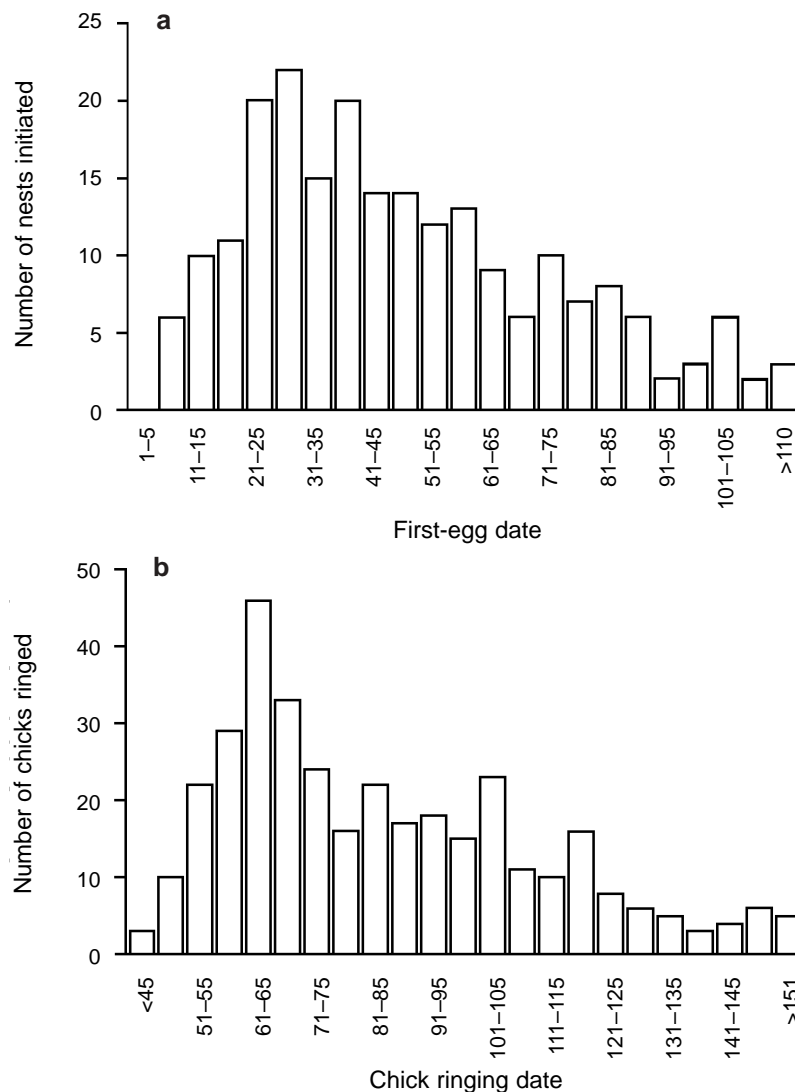
proportion of females that laid second clutches were calculated by bootstrapping, as was the standard error for the mean annual production of fledged young per female.

## RESULTS

### Laying dates, clutch size and incubation period

First-egg dates ( $n = 219$ ) ranged from 8 March

to 21 July, although occasional nests are initiated earlier as the first chick ringing date was 11 March. There was a peak in egg laying at the end of March (Fig. 2). The median first-egg date was 13 April and the distribution was significantly skewed (skewness  $g_1 = 0.773$ ,  $P < 0.001$ ). The frequency distribution of first-egg dates is likely to have been affected by a slight reduction in nest searching effort in July<sup>15</sup> and the growth of ground vegetation is likely to have reduced the detectability of nests later in



**Figure 2.** Distribution of Woodcock first-egg dates (a) from the BTO Nest Record Scheme for 1945–89 ( $n = 219$ ) and of ringing dates (b) for Woodcock chicks subsequently recovered during 1909–90 ( $n = 352$ ). Data presented as the frequency during five-day intervals after 1 March (1 March = day 0).

the season. There is a small second peak in egg laying in the second half of May (Fig. 2), which would probably be larger if detectability and searching effort were similar to early in the season. This is suggestive of second broods, as most replacement nests would be expected in late April.

Mean first-egg dates for each year were weakly but significantly negatively related to mean March air temperatures ( $r = 0.34$ ,  $df = 39$ ,  $P < 0.05$ ), although some of the values were probably for repeat or second clutches and were not strictly independent. When nests initiated after 20 April (those likely to be repeat or second clutches) were excluded, there was still a negative trend but it was no longer significant ( $r = 0.27$ ,  $df = 39$ ,  $P = 0.088$ ). Analysis of covariance, with temperature as the covariate and year as a grouping variable, was performed to see whether within-year variation in first-egg dates was related to regional variation in temperature. With the complete data set, slopes between years were not quite homogeneous but were sufficiently similar for this not to be a major concern ( $F = 1.52$ ,  $df = 33, 143$ ,  $P = 0.049$ ). There was no significant difference between the intercepts (year  $F = 0.99$ ,  $df = 33, 176$ , ns) and the slopes differed significantly from zero (March temperature  $F = 9.05$ ,  $df = 1, 176$ ,  $P < 0.01$ ), indicating that within-year variation in first-egg dates was indeed related to regional variation in temperature. Excluding data for nests initiated after 20 April, the slopes between years were homogeneous ( $F = 0.85$ ,  $df = 27, 63$ , ns) and the intercepts were similar (year  $F = 0.94$ ,  $df = 27, 90$ , ns), but the slopes did not differ significantly from zero (March temperature  $F = 2.83$ ,  $df = 1, 90$ ,  $P = 0.096$ ).

The median first-egg dates were 8 April ( $n = 87$ ) in central and southern England, 10 April ( $n = 67$ ) in northern England and 20 April ( $n = 65$ ) in Scotland. There was no significant difference in the timing of nesting between central and southern England and northern England (Mann–Whitney  $U = 2632.5$ ,  $n = 87, 67$ , ns), but a clear difference between England (median first-egg date 8 April) and Scotland (Mann–Whitney  $U = 3882.5$ ,  $n = 154, 65$ ,  $P < 0.01$ ). There was no significant difference in the frequency distribution of first-egg dates between England and Scotland when the difference in the medians was subtracted from the Scottish records (Kolmogorov–Smirnov

$D = 0.09$ ,  $n = 154, 65$ , ns). Ringing dates of Woodcock chicks ( $n = 352$ ) ranged from 11 March to 15 August, with a peak in early May and a median of 18 May (Fig. 2). The distribution of ringing dates follows a similar pattern to that for the first-egg dates and is also significantly skewed (skewness  $g_1 = 0.726$ ,  $P < 0.001$ ). The median ringing dates were 14 May in central and southern England ( $n = 18$ ), 12 May in northern England ( $n = 76$ ) and 21 May in Scotland ( $n = 258$ ). There was no significant difference in the median ringing dates between central and southern England and northern England (Mann–Whitney  $U = 638.0$ ,  $n = 18, 76$ , ns), but England (median ringing date 13 May) and Scotland differed significantly (Mann–Whitney  $U = 9766.5$ ,  $n = 94, 258$ ,  $P < 0.01$ ). The distributions of ringing dates in England and Scotland, with the difference in medians subtracted, were similar (Kolmogorov–Smirnov  $D = 0.09$ ,  $n = 94, 258$ , ns).

The clutch size ranged from two to five eggs, but 88.8% of nests contained four eggs and 9.0% contained three eggs. The mean clutch size was 3.89 eggs ( $n = 277$  nests). Eggs were usually laid on consecutive days or, less frequently, on alternate days. The mean laying interval for 12 nests observed for at least part of the laying period was 1.25 days, giving an average laying period of 3.8 days for a clutch of four eggs. There were 15 accurate records of the incubation period: one of 17 days, one of 19 days, three of 21 days, three of 22 days, five of 23 days and two of 24 days, giving a mean of 21.9 days.

#### Daily rate of nest loss

The daily rates of nest loss during egg laying and during incubation were  $0.030 \pm 0.017$  ( $n = 100$  nest-days) and  $0.034 \pm 0.003$  ( $n = 3070$  nest-days) respectively. These rates are not significantly different ( $z = 0.20$ , ns) and the rate for egg laying and incubation combined is  $0.033 \pm 0.003$  ( $n = 3170$  nest-days). The daily rate of nest loss due to desertion, during egg laying and incubation combined, is not significantly different from that caused by predation:  $0.014 \pm 0.002$  ( $n = 3170$  nest-days) and  $0.020 \pm 0.002$  ( $n = 3170$  nest-days) respectively ( $z = 1.76$ , ns). The rate of nest desertion was significantly higher immediately after nests were found,



whereas the rate of other loss was similar during days 1–5 and 6–22 (Table 1).

The daily rate of loss during egg laying suggests that a clutch of four eggs taking four days to complete has a probability of  $0.89 \pm 0.06$  of surviving the laying period. Egg loss at this stage may be relatively unimportant, however, because although not demonstrated in the Woodcock, females of other waders will continue laying in another scrape if an incomplete clutch is taken during laying. During the 22-day incubation period, the daily rate of nest loss from the nest record cards suggests that  $0.47 \pm 0.03$  nests survive to hatch. The probability of an average clutch surviving from the day the first egg is laid until hatching is therefore  $0.41 \pm 0.01$ . The fates of 933 eggs from 277 nests where the clutch size was determined accurately were recorded. In all, 74% of the eggs survived incubation and of these 7.2% were added or damaged by the parent bird.

Losses due to desertion were largely attributable to man, either through accidental flushing of sitting birds ( $n = 31$ ) or disturbance caused by forestry activities ( $n = 4$ ). Three nests were deserted owing to adverse weather. The cause of desertion was not known for six nests but it is likely that most of these losses were due to the female being killed while feeding away from the nest. Other nest losses were mainly caused by predation, although the identity of the predator was rarely recorded. Fifty-six nests contained the remains of eggshells or were empty. In two cases, both eggshells and an adult carcass were found and in four cases the adult was known to have been predated away from the nest. Of the predators that were reported, Jays *Garrulus glandarius* ( $n = 3$ ), a Carrion Crow *Corvus corone*, a Woodmouse

*Apodemus sylvaticus* and a Hedgehog *Erinaceus europaeus* were responsible for egg predation, a Fox *Vulpes vulpes* was reported as taking both a parent bird and eggs, and a Tawny Owl *Strix aluco* as killing a female.

These causes of nest failure and rates of loss may be unrepresentative of losses in an undisturbed situation, because the act of visiting a nest may increase desertion and predation rates. Nevertheless, if the unknown causes of nest desertion are assumed to have been predation of the female away from the nest, the percentage of failed nesting attempts during which the female is killed can be estimated as approximately 11.3% (12 females killed, 106 failed nests).

The proportion of nests recorded in deciduous woods decreased and the proportion in coniferous woodland increased from central and southern England to Scotland ( $\chi^2 = 14.49$ ,  $df = 4$ ,  $P < 0.01$ ). However, the daily rates of nest loss, during egg laying and incubation combined, were similar in central and southern England, northern England and Scotland (Table 2). The logistic regression model revealed that there was no relationship between daily rate of nest loss and region ( $\chi^2 = 0.29$ ,  $df = 2$ , ns) or the interaction of region and time period ( $\chi^2 = 2.67$ ,  $df = 4$ , ns). The daily rate of nest loss was appreciably lower during 1980–89 than during 1945–69 or 1970–79 and although the relationship was close to significance ( $\chi^2 = 5.66$ ,  $df = 2$ , ns), the linear component of the deviance was not significant ( $\chi^2 = 3.80$ ,  $df = 1$ , ns), indicating that time period did not have a consistent influence on the daily rate of nest loss. The median first-egg dates for the three time periods were similar (Kruskal–Wallis  $\chi^2 = 1.77$ ,  $df = 2$ , ns).

**Table 1.** Daily rates of Woodcock nest loss ( $\pm$  se) in relation to days after finding.

	Rate of nest loss after		Significance*
	1–5 days ( $n = 953$ nest-days)	6–22 days ( $n = 832$ nest-days)	
Rate of desertion	$0.022 \pm 0.005$	$0.012 \pm 0.004$	$z = 1.65$ $P < 0.05$
Rate of other loss	$0.024 \pm 0.005$	$0.023 \pm 0.005$	$z = 0.18$ ns
Total rate of loss	$0.046 \pm 0.007$	$0.035 \pm 0.006$	$z = 1.22$ ns

Analysis restricted to nests found during incubation and re-visited within ten days.

\*One-tailed test because nest finding is only likely to increase the risk of loss.

### Annual rate of brood production

Woodcock will generally re-nest after the loss of a clutch,<sup>3</sup> but radiotagged females have never been observed to lay more than one replacement clutch. The same was true in radiotracking studies of American Woodcock *Scolopax minor*<sup>16</sup> and Snipe *Gallinago gallinago*.<sup>17</sup> Assuming that losses during egg laying are unimportant, but that in most seasons females only have time for one replacement of partly incubated nests, it is possible to estimate the proportion of females alive in March that hatch a clutch of eggs. It was assumed that the distribution of first-egg dates of first nests was symmetrical with a mean equal to the mode of the distribution of first-egg dates of all nests. Hence the number of first nests is twice the number of nests with first-egg dates below the modal date plus the number with the modal date. This gives 116 (53%) of the 219 nests in Fig. 2 as first nests. The mean number of clutches laid per female alive at the beginning of the breeding season is therefore  $219/116 = 1.888$  and the mean number of clutches that hatch per female can be obtained by multiplying this by the Mayfield estimate of clutch survival, giving  $1.888 \times 0.472 = 0.89$  (bootstrap 95% CL 0.47–1.58). However, any tendency to detect a smaller proportion of late than early nests will have a large effect on this calculation.

The small second peak in the distribution of

first-egg dates in mid-May (Fig. 2) suggests that a proportion of female Woodcock may be double-brooded. On average 53% of first nests would have failed and 11% of the females from these failed nests would have been predated, so 54 nests are likely to have been replaced. The total number of first nests and replacement clutches was therefore 170, leaving 49 nests which could have been second nesting attempts by females which had already hatched a brood. The proportion of all females that laid a second clutch is therefore  $49/116 = 42.2\%$ , although this could include some females re-nesting after the loss of young chicks.<sup>3</sup> However, the bootstrap 95% CL range from 0 to 100% and it is safe to conclude only that second nests might have been possible in some years.

### Chick survival and production of fledged young

Data for 595 chick-days from 26 Woodcock broods monitored at Whitwell Wood gave a daily rate of chick mortality of  $0.029 \pm 0.007$ . This rate of mortality gives  $0.56 \pm 0.08$  chick survival during the 20-day period until fledging. The mean annual production of fledged young per breeding female alive at the start of the season is mean clutch size (3.89) multiplied by egg fertility (0.928) by clutches hatched per female (0.891) and by chick

**Table 2.** Regional and temporal variation in daily rates of Woodcock nest loss ( $\pm$  se) during egg laying and incubation combined.

Time period	Region			Overall
	Central & S England	N England	Scotland	
1945–69	$0.044 \pm 0.011$ (321)	$0.034 \pm 0.010$ (355)	$0.037 \pm 0.009$ (434)	$0.038 \pm 0.006$ (1110)
1970–79	$0.034 \pm 0.009$ (435)	$0.045 \pm 0.011$ (331)	$0.044 \pm 0.014$ (203)	$0.040 \pm 0.006$ (969)
1980–89	$0.022 \pm 0.006$ (677)	$0.032 \pm 0.011$ (251)	$0.012 \pm 0.009$ (163)	$0.023 \pm 0.005$ (1091)
Overall	$0.031 \pm 0.005$ (1433)	$0.037 \pm 0.006$ (937)	$0.034 \pm 0.006$ (800)	

Nest-days given in parentheses.



survival (0.560), which gives a value of  $1.80 \pm 0.72$ .

## DISCUSSION

The Woodcock is an early nesting species compared with many other waders and it is not surprising that March air temperatures appear to affect the onset of nesting. Lack<sup>18</sup> proposed that breeding in birds is timed so that the young hatch when food is most abundant and temperature has since been shown to be a proximate cue determining the precise time of laying in a range of species.<sup>19–22</sup> It is conceivable that in some years, particularly in Scotland and northern England, the ground may remain frozen for long enough temporarily to prevent females laying down sufficient fat reserves for incubation. Using data for 262 first-egg dates in Denmark, Clausager<sup>23</sup> found that in years when the mean March temperature was at least 0.5°C above normal, 43% of Woodcock nests were initiated before 7 April, but in years when the temperature was 0.5°C or more below normal, only 13% of nests were initiated before this date. Thompson *et al.*<sup>24</sup> found that Greenshank *Tringa nebularia* clutches in Sutherland were completed earlier in May in years when April soil temperatures were relatively high.

The nest record card data indicate that adult Woodcock may be predated by Foxes and Tawny Owls during the breeding season. At Whitwell Wood, a radiotagged Woodcock was taken off the nest by a Tawny Owl;<sup>13</sup> Woodcock remains have been reported as constituting up to 3.3% of the bird component in Tawny Owl pellets in Holland.<sup>25</sup> Incubating female Woodcock are most likely to be killed by mammalian predators, particularly Foxes, but also occasionally by Stoats *Mustela erminea*.<sup>13</sup> When off the nest foraging, Woodcock are susceptible to Sparrowhawks *Accipiter nisus*,<sup>13</sup> although in southern Scotland they constituted only 0.7% of the prey items in the diet of Sparrowhawks, equivalent to 3.5% by weight.<sup>26</sup> Interestingly, Woodcock nest failure rate was lowest during 1980–89, when the numbers and distribution of Sparrowhawks and Goshawks *Accipiter gentilis* were increasing.<sup>1</sup>

In most cases, nest desertion cannot be distinguished from predation of the female away from the nest. Nevertheless, apparent desertion seems to be an important cause of

nest failure in the Woodcock, accounting for more than a third of all nest losses. Other authors have commented that Woodcock nests appear to be particularly prone to desertion.<sup>27–29</sup> In the Pheasant *Phasianus colchicus*, another ground-nesting bird which frequents similar woodland habitats to Woodcock early in the breeding season, the daily rate of nest loss due to desertion is also high, being approximately equal to the rate of loss to predation and other factors.<sup>30</sup> Pheasants are more prone to desertion on the day when the nest is first found,<sup>30</sup> and this also seems to be the case in the Woodcock.

The total daily rate of nest loss in the Pheasant is significantly higher during egg laying than during incubation, probably because of the long laying period (16 days for an average clutch of 11.4 eggs) during which the eggs are relatively exposed. The short egg laying period in the Woodcock probably accounts for the similar daily rates of nest loss during egg laying and incubation. Clutch survival appears to be considerably higher in the Woodcock (0.413) than the Pheasant (0.071 from BTO nest record cards and 0.214 from records from keepered sporting estates<sup>30</sup>), although Pheasants may make three nesting attempts.

The figure of 0.56 for the mean chick survival rate should be treated with caution, because it is likely that chick mortality is higher during the first 3–4 days until the chicks are able to thermoregulate. If so, this violates the assumption of a constant mortality rate during the period from hatching to fledging required for the calculation of chick mortality rate by the Mayfield method.<sup>8,9</sup> There are no published quantitative estimates of the survival rates of Eurasian Woodcock chicks. Of the broods located during the Woodcock Inquiry of 1934–35,<sup>5</sup> 89% consisted of at least three chicks, but because their ages are not given this information is of little value. Using the Inquiry data, McCabe & Brackbill<sup>31</sup> calculated the survival rate in the first month after hatching as 78%, but gave no indication of how this figure was obtained. Estimates of chick survival rates to fledging for American Woodcock range from 58% to 84%.<sup>32–35</sup> Clearly, chick survival rates will vary annually and there is evidence that mortality may be higher in years with low June rainfall, possibly reflecting reduced availability of earthworms.<sup>3,36</sup> The error associated with the

figure of 1.80 fledged young per breeding female alive at the start of the season is too great to enable any firm conclusion to be drawn about whether recruitment is sufficient to compensate for annual adult mortality.

The small second peak in the distribution of Woodcock first-egg dates is suggestive of double-brooding by some females, but a far larger data set is required to determine with any precision the proportion of females that lay second nests. At present the only direct evidence for second broods in the Woodcock comes from two descriptions of incubating birds surrounded by a brood of chicks.<sup>37,38</sup> Alexander reported six cases of Woodcock laying into the same nest and two cases of displaying or mating following the fledging of a brood,<sup>5</sup> but in these instances there was no proof that only one female was involved. In Denmark, 90% of Eurasian Woodcock nests were found over a period of 15 weeks,<sup>23</sup> whereas the same proportion of American Woodcock nests is generally found in only 5–6 weeks.<sup>28</sup> Kalchreuter believed that this was suggestive of double-brooding in the Eurasian Woodcock and concluded that the number of broods per year probably fluctuates regionally and annually.<sup>28</sup> The monitoring of a large sample of radiotagged females is the only means of resolving this question.

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#### REFERENCES

- Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993) *The New Atlas of Breeding Birds in Britain and Ireland 1988–91*. Poyser, London.
- Hirons, G. (1980) The significance of roding by Woodcock *Scolopax rusticola*: an alternative explanation based on observations of marked birds. *Ibis*, **122**, 350–354.
- Hirons, G. (1983) A five-year study of the breeding behaviour and biology of the Woodcock in England – a first report. In *Proc. 2nd European Woodcock and Snipe Workshop, 1982* (ed. H. Kalchreuter), pp. 51–67. IWRB, Slimbridge.
- Hoodless, A.N. & Coulson, J.C. (1994) Survival rates and movements of British and Continental Woodcock *Scolopax rusticola* in the British Isles. *Bird Study*, **41**, 48–60.
- Alexander, W.B. (1946) The Woodcock in the British Isles. *Ibis*, **88**, 1–24.
- Marchant, J.H., Hudson, R., Carter, S.P. & Whittington, P.A. (1990) *Population Trends in British Breeding Birds*. BTO, Tring.
- Morgan, R. & Shorten, M. (1974) Breeding of the Woodcock in Britain. *Bird Study*, **21**, 193–199.
- Mayfield, H.F. (1961) Nesting success calculated from exposure. *Wilson Bull.*, **73**, 255–261.
- Mayfield, H.F. (1975) Suggestions for calculating nest success. *Wilson Bull.*, **87**, 456–466.
- Sharrock, J.T.R. (1976) *The Atlas of Breeding Birds in Britain and Ireland*. Poyser, Berkhamsted.
- Hensler, G.L. & Nichols, J. (1981) The Mayfield method of estimating nest success: a model, estimators and simulation results. *Wilson Bull.*, **93**, 42–53.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*, 2nd edn. W.H. Freeman & Co., New York.
- Hoodless, A.N. (1994) *Aspects of the Ecology of the European Woodcock Scolopax rusticola L.* PhD thesis, University of Durham.
- Efron, B. & Tibshirani, R. (1986) Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Stat. Sci.*, **1**, 54–77.
- Crick, H.Q.P. & Baillie, S.R. (1996) *A Review of the BTO's Nest Record Scheme. Its Value to the Joint Nature Conservation Committee and Country Agencies, and Its Methodology*. BTO Research Report No. 159. BTO, Thetford.
- McAuley, D.G., Longcore, J.R. & Sepik, G.F. (1990) Renesting by American Woodcocks (*Scolopax minor*) in Maine. *Auk*, **107**, 407–410.
- Green, R.E. (1988) Effects of environmental factors on the timing and success of breeding common snipe *Gallinago gallinago* (Aves: Scolopacidae). *J. Appl. Ecol.*, **25**, 79–93.
- Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Oxford University Press, Oxford.
- O'Connor, R.J. & Morgan, R.A. (1982) Some effects of weather conditions on the breeding of the spotted flycatcher (*Muscicapa striata*) in Britain. *Bird Study*, **29**, 41–48.
- Turner, A.K. (1982) Timing of laying by swallows

- (*Hirudo rustica*) and sand martins (*Riparia riparia*). *J. Anim. Ecol.*, **51**, 29–46.
21. Fredga, S. & Dow, H. (1983) Annual variation in the reproductive performance of goldeneyes. *Wildfowl*, **34**, 120–126.
  22. Newton, I. & Marquiss, M. (1984) Seasonal trend in the breeding performance of sparrowhawks. *J. Anim. Ecol.*, **53**, 809–830.
  23. Clausager, I. (1973) Skovsneppens *Scolopax rusticola* yngletid i Danmark. *Dansk. Ornithol. Foren. Tidsskr.*, **67**, 129–137.
  24. Thompson, D.B.A., Thompson, P.S. & Nethersole-Thompson, D. (1986) Timing of breeding and breeding performance in a population of Green-shanks (*Tringa nebularia*). *J. Anim. Ecol.*, **55**, 181–199.
  25. Zomerdijs, P. (1983) De houtsnip (*Scolopax rusticola*), deel II. *De Graspieper*, October 1983. pp.107–121.
  26. Newton, I. (1986) *The Sparrowhawk*. Poyser, Calton.
  27. Shorten, M. (1974) *The European Woodcock (Scolopax rusticola). A Search of the Literature since 1940*. The Game Conservancy Trust, Fordingbridge.
  28. Kalchreuter, H. (1983) *The Woodcock*. Verlag Dieter Hoffmann, Mainz.
  29. Nethersole-Thompson, D. & Nethersole-Thompson, M. (1986) *Waders: Their Breeding, Haunts and Watchers*. Poyser, Calton.
  30. Robertson, P.A. (1991) Estimating the nest success and productivity of British Pheasants *Phasianus colchicus* from nest-record schemes. *Bird Study*, **38**, 73–79.
  31. McCabe, R.A. & Brackbill, M. (1973) Problems in determining sex and age of European Woodcock. In *Proc. 10th Congress Int. Union Game Biol.*, 1971, pp. 619–637. Office National de la Chasse, Paris.
  32. Sheldon, W.G. (1971) *The Book of the American Woodcock*. University of Massachusetts Press, Amherst.
  33. Dwyer, T.J., Derleth, E.L. & McAuley, D.M. (1982) Woodcock brood ecology in Maine. In *Woodcock Ecology and Management*. Wildlife Research Report No. 14 (ed. T.J. Dwyer & G.L. Storm), pp. 63–70. U.S. Fish & Wildlife Service.
  34. Gregg, L. (1984) *Population Ecology of Woodcock in Wisconsin*. Technical Bulletin No. 114. Department of Natural Resources, Wisconsin.
  35. Wiley II, E.N. & Causey, M.K. (1987) Survival of American Woodcock chicks in Alabama. *J. Wildl. Manage.*, **51**, 583–586.
  36. Hirons, G. (1988) Some factors affecting age ratios among Woodcock wings collected from hunters in Britain. In *Proc. 3rd European Woodcock and Snipe Workshop*, 1986 (ed. P. Havet & G. Hirons), pp. 92–95. IWRB, Slimbridge.
  37. von Zedlitz, O. (1927) Contributions a l'étude biologique de la bécasse. *Rev. Fr. Ornithol.*, **11**, 74–81.
  38. Pay, L.M. (1937) *Die Waldschneepfe*. München.

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