Bird Study

Long-term patterns in egg mortality during incubation and chick mortality during rearing in three species of tits in an English woodland

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Looking out for birds

Long-term patterns in egg mortality during incubation and chick mortality during rearing in three species of tits in an English woodland

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Capsule Mortality from egg-laying to fledging is species-dependent with Great Tits exhibiting greater losses of chicks, Coal Tits greater losses of eggs and Blue Tits exhibiting comparable rates of mortality of eggs and chicks.

Aims To determine whether reproductive losses during incubation and chick-rearing were different and to ascertain whether there were different effects in three closely related songbirds.

Methods Breeding success of Great Tits *Parus major*, Blue Tits *Cyanistes caeruleus* and Coal Tits *Periparus ater* at Treswell Wood, Nottinghamshire, England was examined, selecting only those nests which fledged at least one chick. Mortality during incubation (i.e. loss of eggs) or rearing (i.e. loss of chicks) was recorded per nest and annual means were calculated and used in the analysis, which examined relationships between year, first-egg date and species. Key factor analysis was used to investigate the relative effects of egg or chick losses on the total breeding mortality.

Results Timing of reproduction showed a long-term trend to earlier nesting, but there was considerable variation from year to year in first-egg date. In this location there has been a long-term decline in clutch size in all three species. Previously unseen differences between these three species of tit are shown for mortality at different stages of the reproductive process. Coal Tits suffer the greatest losses through unhatched eggs, whereas Great Tit failures are greater during chick-rearing. Blue Tits exhibited problems in achieving success in both incubation and rearing.

Conclusion Closely related tit species living in close proximity exhibit different patterns of reproductive mortality during breeding.

Studies of the reproductive performance of wild birds typically report success rates in terms of fledging rates, i.e. the number of young birds that leave the nest. This statistic, however, reports the success rate of two quite distinct processes: incubation and rearing, which have different behavioural requirements of the parents. Success rates of incubation, i.e. hatchability of eggs in the nest, seem to be of less interest in reproductive studies despite their direct reflection of the ability of parent birds to convert eggs into neonates. Deeming (2003) reviewed the hatchability data reported for wild nests in 231 species from the Western Palearctic and showed an average hatchability of 72% with a range of 25–100%. However, these data were based on reports of total numbers of eggs hatched from number of eggs laid. Studies that examined hatchability of nests for any particular species over a series of breeding seasons were not reported and so it was difficult to assess how much variation existed for hatchability from one season to the next.

Incubation requires parental attendance at the nest for a sufficient period of time to ensure normal embryonic development. This typically involves birds sitting on eggs laid into nests constructed in particular locations and at particular times of the year. Successful incubation depends on how well this 'bird–nest incubation unit' (Deeming 2002), which includes the various behaviours of the adults during the incubation period, functions in maintaining an appropriate environment for development throughout the incubation period. Short-term changes in the climate or the food supply for the incubating birds may have significant impacts on the ability to

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maintain and complete incubation behaviours through to hatching. Hence, mortality of eggs may vary from year to year depending on, perhaps, prevailing weather conditions.

The second aspect of avian reproductive productivity is the period of chick-rearing, which requires a different repertoire of behaviours to ensure maximal success. Here the parents are required to provision their offspring with sufficient food to allow for maximal growth and fledging at the earliest time. Environmental factors will have significant effects on the survival of birds, through the need for adults to divide their time between brooding (females), self-maintenance, and feeding the chicks and on food availability in any year. Hence, chick survival will also vary from year to year.

The differing components of the process of converting eggs into fledglings have not often been studied in such a way that it is possible to distinguish between the effects of environmental variation on incubation and rearing behaviours. Data for nests of Carrion Crows *Corvus corone* in Scotland showed that failure to hatch accounted for almost 75% of the total losses from the start of incubation to fledging (Yom-Tov 1974). By contrast, hatchability of Mountain White-crowned Sparrows *Zonotrichia leucophrys oriantha* averaged 90% but chick mortality was 55% – here loss during incubation was only 15–21% of total losses (Morton *et al.* 1972). Analysis of nest box records for Great Tits *Parus major* and Blue Tits *Cyanistes caeruleus* for a 27-year period up to 2005 showed that incubation success in Treswell Wood, Nottinghamshire, UK varied from year to year. On average, for both species ∼9% of eggs laid failed to hatch, but the analysis did not consider losses during rearing (Deeming & du Feu 2005).

The study described here extended the preliminary analysis of Deeming & du Feu (2005) by examining the relative effects of incubation and rearing on reproductive losses from laying to fledging. Data were available from Treswell Wood not only for a longer time period of 30 years but also for Blue Tits, Great Tits and Coal Tits *Periparus ater*. Marsh Tits *Poecile palustris* also nested in the wood, but only in small numbers and on an irregular basis and thus were excluded from the study.

This study investigated how reproductive losses during reproduction from egg-laying to fledging were split between incubation and rearing. Given that these three species all nest in boxes in similar habitats in the wood, it was anticipated that mortality during these two periods would not differ significantly between the species. The data also allowed investigation of the effects of calendar year on reproductive performance. It has been shown that climate change has impacted on nesting activity in British Passerines (Crick *et al.* 1997, Crick 1999) and the 30-year time span of the data set allowed us to determine any long-term effects of year on reproductive timing, performance, or productivity. Analysis, therefore, concentrated on determining the effect of species and year on reproductive losses at this particular site.

METHODS

This study used data collected from nestbox records collected every year for a 30-year period (1979–2008) in Treswell Wood, near Retford, Nottinghamshire, UK (53°18′N, 00°51′W). The wood is a Nottinghamshire Wildlife Trust reserve of 47 ha of mixed woodland dominated by Ash *Fraxinus excelsior* with Hazel *Corylus avellana* understorey. Data were analysed for Blue Tit, Great Tit and Coal Tit nests.

Nestboxes were monitored once a week during each breeding season through to fledging to record progress in nest-building, presence of eggs, the incubating adult and hatched chicks. During laying and the first week of incubation eggs were counted if the female was not on the nest. During the second week of incubation, most sitting Blue and Coal Tits were lifted to count the eggs; we have no evidence of desertion caused by such lifting. Great Tits, which we know to be at risk of desertion if handled in this way, were not lifted. Clutch size for those was calculated as number of hatchlings plus number of unhatched eggs. After the breeding season all nests were carefully searched for unhatched eggs or small dead chicks. The number of chicks hatched was assumed to be the clutch size minus any unhatched eggs.

In all years there was an excess of available nestboxes in the wood, suggesting that nest site availability did not limit breeding. For each year data for all species were recorded on the basis of nests that contained eggs and split into their fate: deserted, predated or successful. From this large data set a subset of those eggs that hatched at least one chick was selected, thereby excluding those that had been deserted or predated before incubation. These fates were seen as catastrophic failures of reproduction that did not reflect upon the incubation behaviour of the parents. From this data subset those nests where all hatched chicks were predated or deserted were then also removed. Again these instances were considered catastrophic failures that did not necessarily reflect upon the rearing ability behaviour of the
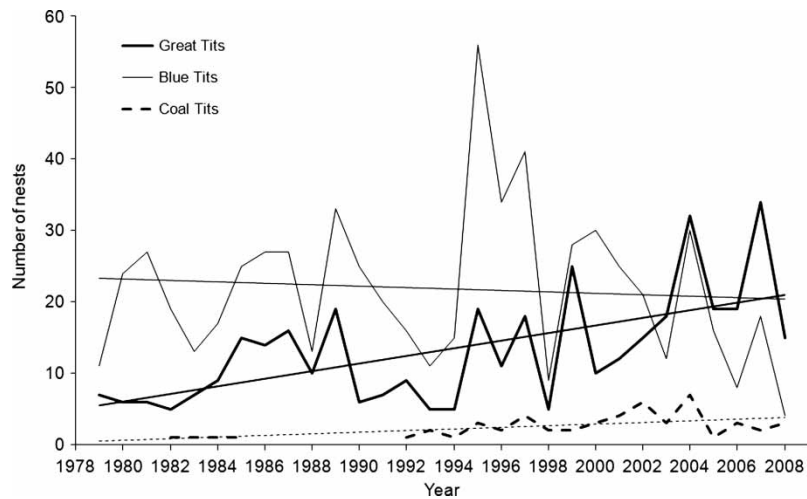
Figure 1. Numbers of nests per year used in the study for the three species of tit at Treswell Wood from 1979 to 2008. Lines indicate regression estimates shown in Table 2.

parents. It is accepted that some chick desertion could have been attributed to poor abilities of the parents, but it was impossible to distinguish these cases from other instances of desertion, due to adverse weather conditions or predation of one or both parents. Therefore, the data set for each year consisted of nests that fledged at least one chick.

The number of nests per species was recorded for each year (see Fig. 1 and Table 1 for average numbers per year). The first-egg date (FED) was recorded and the date of the start of incubation was calculated for each year by adding the number of eggs (the birds almost

Table 1. Mean values (means $\pm$ se) for nest count, laying, and start of incubation dates, together with clutch sizes and numbers of chicks hatched and fledged for three species of tit recorded at Treswell Wood averaged over 30 years for Great and Blue Tits and for 21 out of 30 years for Coal Tits. Within each row, values with different superscripts indicate significant differences between means at least $P < 0.05$.

	Blue Tit	Great Tit	Coal Tit
Number of years recorded	30	30	21
Annual number of nests	21.8[a] $\pm$ 2.0	13.3[b] $\pm$ 1.4	2.5[c] $\pm$ 0.4
First-egg date	116.9[a] $\pm$ 1.2	122.1[b] $\pm$ 1.3	107.6[c] $\pm$ 1.8
Start incubation date	125.5[a] $\pm$ 1.2	130.3[b] $\pm$ 1.3	117.3[c] $\pm$ 1.8
Annual clutch size	9.3[a] $\pm$ 0.2	8.3[b] $\pm$ 0.2	9.7[a,c] $\pm$ 0.2
Annual number of chicks hatched	8.4[a] $\pm$ 0.2	7.7[a,b] $\pm$ 0.2	8.9[a,c] $\pm$ 0.3
Annual number of chicks fledged	7.2[a] $\pm$ 0.3	6.6[a] $\pm$ 0.3	8.6[b] $\pm$ 0.4

Values sharing superscripts were not significantly different from each other.

invariably lay one egg per day) to the FED. In a very few cases, birds suspended egg-laying for some days, generally because of very bad weather. In these cases the start of incubation date was calculated as FED plus number of eggs plus length of suspension of laying. In some nestboxes there was a pause between clutch completion and the start of incubation, but these were difficult to identify in the records. Given that such events were relatively rare in this large data set of over 1100 nests and analysis was based on mean values per year, it was assumed in this study that the start of incubation coincided with clutch completion in all cases. These dates were then expressed as the ordinal date (1 April = day 91 or day 92 in a leap year). The numbers of eggs laid and hatched together with the numbers of chicks fledged were recorded. It should be noted that failure of an egg to hatch might be due to infertility or embryonic mortality, but the eggs were not examined so it was not possible to distinguish between these separate causes. Hereafter, egg mortality refers to those eggs that fail to hatch for whatever reason. Similarly, the cause of chick mortality in the nest was not recorded and in the analysis it is the numbers that fail to fledge that were of interest, rather than the cause of mortality.

The extent of egg mortality during incubation, or chick mortality during rearing, was determined in a variety of ways: (1) for all nests the number of eggs that failed to hatch, or chicks that died, were recorded and also expressed as a percentage of the initial clutch size or the number of chicks hatched in the nest; (2) the number of nests that did not have 100% hatchability or fledging was expressed as a percentage of the total

nests that year; (3) unhatched eggs expressed as an average number, and as a percentage of the initial clutch, were described for only those nests that did not achieve 100% hatchability; (4) chicks that died during rearing, expressed as an average number and as a percentage of the initial clutch, were described for only those nests that did not achieve 100% fledging. This approach was adopted because in any year there were a significant number of nests that experienced 100% hatchability and so distribution of the data for egg mortality was not normal. The extent to which this skewed the mean results varied between years. Given that the number of nests varied between years and species, expressing mortality in terms of the nests experiencing mortality as a percentage of the total number of nests each year allowed for easier comparison between years and species. Averaging mortality figures for those nests that experienced a loss gave an indication of the levels of mortality of eggs or chicks when mortality occurred.

Analyses were performed on the annual mean values calculated for each variable for each species and year. Sample size was 30 for both Blue Tits and Great Tits but only 21 for Coal Tits because of their failure to nest in nestboxes in Treswell Wood during the 1980s. Central limit theorem suggested that these mean values would be normally distributed and this was confirmed using Kolmogorov–Smirnov tests. Data were analysed with SPSS ver. 17. One-way analysis of variance was used to determine the effect of species on the variables. Pearson product moment correlation analysis examined the effect of year on reproductive parameters and the relationships between species for egg or chick losses over the study period. In some instances it was deemed more appropriate to use Spearman's signed-rank correlation analysis.

To determine whether overall losses in reproductive productivity were better correlated with mortality during incubation or during rearing, we used Key Factor analysis (Järvinen 1987, Stilling 2002). Total breeding mortality K was calculated on an Excel spreadsheet for each year between 1979 and 2008:

$$K = k_1 + k_2$$

where $k_1 = LN\ N_t - LN\ N_{t+1}$; $k_2 = LN\ N_{t+1} - LN\ N_{t+2}$; N_t = mean clutch size; N_{t+1} = mean number of hatchlings; and N_{t+2} = mean number of fledglings. Spearman correlation analysis was used to investigate the relationships between K, k_1 and k_2 – significant correlations indicated the factor(s) that were having the greatest impact upon overall mortality.

RESULTS

Effects of breeding season on reproduction

Summary statistics for the nests for the three species are shown in Table 1. Numbers of nests for the three species were not constant over the 30-year time period (Fig. 1), although records were available for Coal Tit nests for only 21 years because this species bred in relatively low numbers in Treswell Wood. The number of Blue Tit nests varied from year to year, being most numerous up to 2002, but thereafter the number of nests declined as Great Tit nests became the most numerous. The increase in Blue Tit nests recorded in 1996 was in part associated with provision of nestboxes for a dormouse re-introduction into Treswell Wood in 1995 (Bright & Morris 2002). Over the time period there was a no significant correlation in Blue Tit nest numbers with breeding season (Table 2). By contrast, over the study period the numbers of both Great and Coal Tit nests significantly increased with time (Table 2), although the number of nests of the latter species was relatively low (Fig. 1). Species had a significant effect on the mean number of nests in the analysis, i.e. those that produced at least one fledged chick each year (one-way ANOVA: $F_{2,78} = 34.6$, $P < 0.001$; Table 1).

First-egg date (FED) and the start of incubation (StI_p) varied between successive years for all species, although over the study period both FED (Fig. 2) and StI_p (not shown) exhibited significant ($P < 0.05$ for all species) negative correlations with year (Table 2). Hence, for Blue Tits and Great Tits both FED and StI_p were around 10 days earlier, and for Coal Tits around 15 days earlier, in 2008 than was the case in 1979. Over the study as a whole, species differences were observed for means of mean FED and StI_p ($F_{2,78} = 25.5$, $P < 0.001$ and $F_{2,78} = 20.3$, $P < 0.001$, respectively; Table 1) with Coal Tits starting clutches and incubation earlier than Blue Tits, which in turn, were earlier than Great Tits. There were significant negative correlations with FED and the total number of nests in Treswell Wood in any year for Great Tits ($r = -0.501$, df = 28, $P = 0.005$) but not for Blue Tits ($r = -0.249$, df = 28, $P = 0.184$) or for Coal Tits ($r = -0.297$, df = 19, $P = 0.191$).

Mean annual clutch size varied from year to year (Fig. 3) and showed a significant effect of species ($F_{2,78} = 13.3$, $P < 0.001$) with Blue Tits and Coal Tits laying the most eggs and Great Tits the fewest (Table 1). For Blue Tits and Great Tits mean clutch size showed significant negative correlations with year but there was non-significant negative correlation for Coal Tits (Table 2). For Blue Tits mean clutch size decreased by about two

Table 2. Regression estimates ($\pm$ se for slopes) for the relationships between reproductive parameters and year shown in Figs. 1–5. F-values from the ANOVA for regression model and Pearson product moment correlations (*r*) are also shown together with the *P*-value.

	Blue Tit	Great Tit	Coal Tit
Number of nests (*n*)	$n = 221.9 - 0.100^{\pm0.232}Y$	$n = -1049.3 + 0.533^{\pm0.131}Y$	$n = 222.0 + 0.112^{\pm0.040}Y$
	$F_{1,28} = 0.19, r = -0.081$	$F_{1,28} = 16.45, r = 0.608$	$F_{1,19} = 8.00, r = 0.544$
	$P = 0.669$	$P < 0.001$	$P = 0.011$
Mean first egg date (FED)	$FED = 775.0 - 0.330^{\pm0.124}Y$	$FED = 799.4 - 0.340^{\pm0.133}Y$	$FED = 1225.6 - 0.560^{\pm0.201}Y$
	$F_{1,28} = 7.07, r = -0.449$	$F_{1,28} = 6.57, r = -0.436$	$F_{1,19} = 7.76, r = -0.538$
	$P = 0.013$	$P = 0.016$	$P = 0.012$
Mean start of incubation (S_tI_p)	$S_tI_p = 799.1 - 0.338^{\pm0.121}Y$	$S_tI_p = 1023.6 - 0.448^{\pm0.128}Y$	$S_tI_p = 1286.4 - 0.585^{\pm0.199}Y$
	$F_{1,28} = 7.86, r = -0.468$	$F_{1,28} = 12.35, r = -0.553$	$F_{1,19} = 8.63, r = -0.559$
	$P = 0.009$	$P = 0.002$	$P = 0.008$
Mean annual clutch size (C)	$C = 126.9 - 0.059^{\pm0.014}Y$	$C = 225.5 - 0.109^{\pm0.016}Y$	$C = 61.06 - 0.026^{\pm0.029}Y$
	$F_{1,28} = 17.07, r = -0.615$	$F_{1,28} = 46.22, r = -0.789$	$F_{1,19} = 0.81, r = -0.203$
	$P < 0.001$	$P < 0.001$	$P = 0.378$
Mean number of eggs hatched (H)	$H = 170.9 - 0.082^{\pm0.017}Y$	$H = 1225.5 - 0.109^{\pm0.017}Y$	$H = 151.4 - 0.071^{\pm0.041}Y$
	$F_{1,28} = 24.30, r = -0.682$	$F_{1,28} = 43.40, r = -0.780$	$F_{1,19} = 3.07, r = -0.373$
	$P < 0.001$	$P < 0.001$	$P = 0.096$
Mean number of chicks fledged (F)	$F = 250.4 - 0.122^{\pm0.022}Y$	$F = 261.9 - 0.128^{\pm0.019}Y$	$F = 184.6 - 0.088^{\pm0.040}Y$
	$F_{1,28} = 30.36, r = -0.721$	$F_{1,28} = 45.49, r = -0.787$	$F_{1,19} = 4.77, r = -0.448$
	$P < 0.001$	$P < 0.001$	$P = 0.042$

eggs from 1979 (around 10 eggs) to 2008 (around eight eggs). The difference for Great Tits was around three eggs over the same period (from just under 10 eggs in 1979 to just under seven eggs in 2008). Clutch size in Coal Tits remained around 10 eggs over the study period.

Given that both FED and mean clutch size varied between the years and species, it was possible that in years when FED was relatively late the clutch size may have been relatively small (and vice versa). The relative effect of changes in FED on mean clutch size was investigated by determining linear regression estimates for each variable against year. Residuals for FED were then correlated with the residuals for mean clutch size regressed against year. For Blue Tits there was a significant negative correlation between these residuals (*rho* $= -0.482$, df $= 28$, $P < 0.01$) indicating that relative changes in FED had an impact on the mean clutch size. By contrast, for Great Tits and Coal Tits, there was no significant correlation between the residuals (*rho* $= -0.302$, df $= 28$, $P < 0.05$ and *rho* $= 0.220$, df $= 19$, $P < 0.05$, respectively). Over the study period there were no significant correlations between clutch size and the total number of nests in Treswell Wood ($P > 0.05$ in all species).
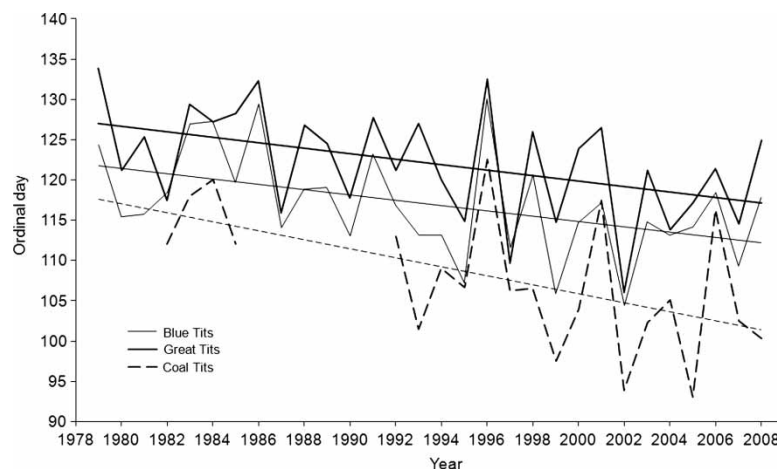
Figure 2. First-egg date per year for the three species of tit at Treswell Wood from 1979 to 2008. Lines indicate regression estimates shown in Table 2.
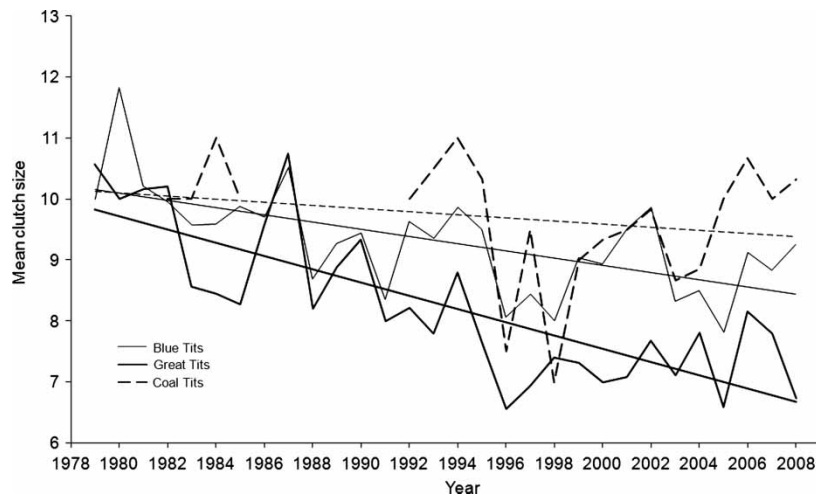
Figure 3. Mean annual clutch size for the three species of tit at Treswell Wood from 1979 to 2008. Lines indicate regression estimates shown in Table 2.

The mean numbers of chicks hatched over the study period were significantly affected by species ($F_{2,78} = 5.8$, $P < 0.01$), with Coal Tits hatching significantly more chicks than Great Tits (Table 1), but see below for relative egg losses. All three species exhibited significant negative correlations between numbers of eggs hatched and year (Table 2).

Similarly, species affected the average numbers of chicks fledged on an annual basis ($F_{2,78} = 10.9$, $P < 0.001$; Fig. 4) with Coal Tits fledging on average more chicks than either of the other two species (Table 1), but see below for relative egg losses. Significant negative correlations between numbers of

chicks fledged and year were recorded for all three species (Table 2).

Egg mortality

Egg mortality during incubation varied from year to year irrespective of the method used to measure losses (Fig. 5). For all nests the number of unhatched eggs was not significantly affected by species ($F_{2,78} = 2.3$, $P > 0.05$; Table 3) and only Coal Tits showed a significant positive correlation with year ($rho = 0.452$, $P = 0.04$). Unhatched eggs, expressed as a percentage of eggs in the clutch for all nests, were not significantly affected by
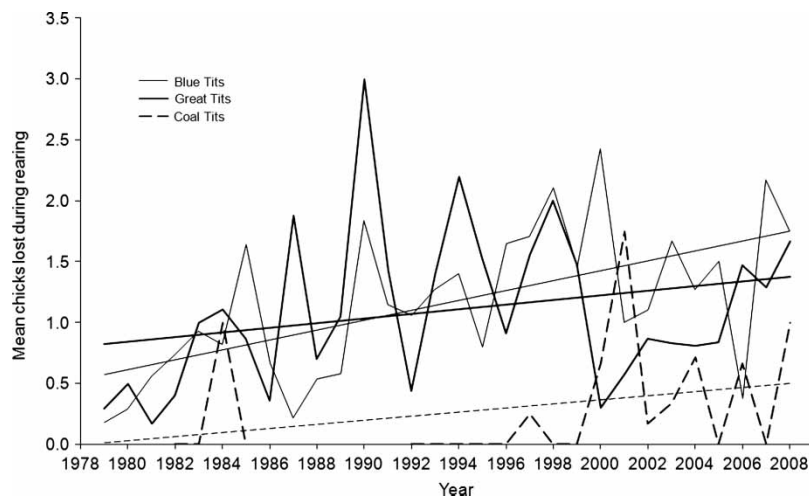

Figure 4. Mean annual losses of chicks during rearing (i.e. chicks that fail to fledge) for the three species of tit at Treswell Wood from 1979 to 2008. Lines indicate regression estimates shown in Table 2.
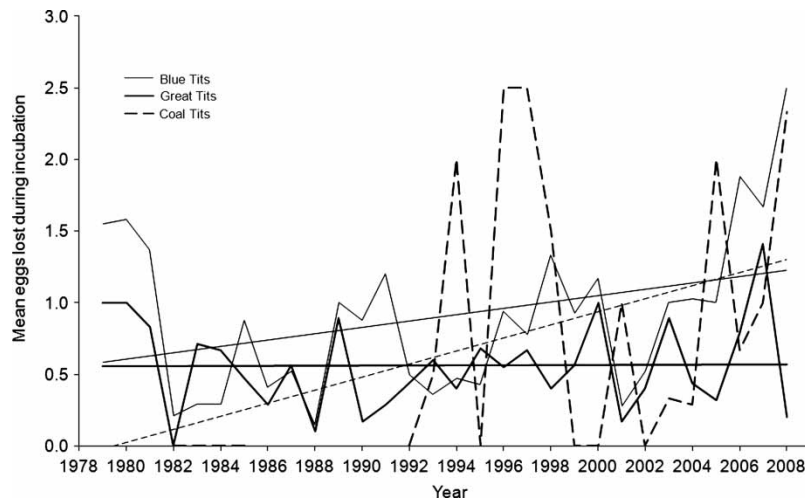
Figure 5. Mean annual losses of eggs during incubation (i.e. eggs that fail to hatch) for the three species of tit at Treswell Wood from 1979 to 2008. Lines indicate regression estimates shown in Table 2.

species ($F_{2,78} = 1.4$, $P > 0.05$; Table 3), but significantly increased as the years progressed for Blue Tits ($rho = 0.435$, df $= 28$, $P = 0.016$) and Coal Tits ($rho = 0.444$, df $= 19$, $P = 0.044$) but not Great Tits ($rho = 0.142$, df $= 28$, $P > 0.05$). The percentage of nests exhibiting some unhatched eggs was not affected by species ($F_{2,78} = 1.7$, $P > 0.05$), but there was a positive correlation ($rho = 0.415$, df $= 28$, $P = 0.022$) between percentages of nests with unhatched eggs and year for Blue Tits; a similar relationship for Coal Tits only approached significance ($rho = 0.417$, df $= 19$, $P = 0.06$).

Table 3. Summary statistics (means $\pm$ se) for various measures of egg losses for three species of tit recorded at Treswell Wood averaged over 30 years for Great and Blue Tits and for 21 out of 30 years for Coal Tits. Values are means ($\pm$ se). Within each row, values with different superscripts indicate significant differences between means at least $P < 0.05$. Values sharing superscripts were not significantly different from each other.

	Blue Tit	Great Tit	Coal Tit
Egg mortality in all nests	$0.9^a \pm 0.1$	$0.6^a \pm 0.1$	$0.8^a \pm 0.2$
Egg mortality in all nests as % of clutch size	$10.1^a \pm 1.2$	$7.0^a \pm 0.8$	$8.7^a \pm 2.4$
% of nests experiencing egg mortality	$43.8^a \pm 4.4$	$32.7^a \pm 2.9$	$33.2^a \pm 8.1$
Egg mortality for nests experiencing egg mortality	$2.0^a \pm 0.1$	$1.7^{a,b} \pm 0.1$	$1.3^b \pm 0.3$
Egg mortality for nests experiencing egg mortality as % of initial clutch	$22.0^a \pm 1.2$	$20.7^a \pm 1.4$	$15.0^a \pm 3.7$

When numbers of unhatched eggs were considered in the subset of nests where egg mortality occurred, the average number of unhatched eggs was significantly affected by species ($F_{2,78} = 3.2$, $P < 0.05$; Table 3) with egg mortality being numerically lowest for Coal Tits. There were no correlations with year for egg mortality in nests of Blue Tits or Great Tits but for Coal Tits the number of unhatched eggs in this subset showed a significant positive correlation with year ($rho = 0.537$, df $= 19$, $P < 0.05$). When expressed as a percentage of the clutch in those nests not experiencing 100% hatchability there was no effect of species ($F_{2,78} = 3.01$, $P > 0.05$; Table 3) but again, for Coal Tits, there was a positive correlation with year ($rho = 0.492$, df $= 19$, $P < 0.05$).

In summary, species differences for egg mortality were small, irrespective of the method used to assess egg losses. Significant positive correlations for mortality with year were only observed for some of the measures in Blue Tits and Coal Tits.

Chick mortality

Irrespective of the method used to measure losses, chick mortality prior to fledging also varied on an annual basis (Fig. 4). For all measures of mortality there was a significant effect of species that was solely due to the low values exhibited for all measures of chick mortality in Coal Tit nests (Table 4). Values for Blue Tits and Great Tits were comparable (Table 4). For all nests the number of dead chicks was significantly affected by species ($F_{2,78} =$

Table 4. Summary statistics (means ± se) for various measures of chick losses for three species of tit recorded at Treswell Wood averaged over 30 years for Great and Blue Tits and for 21 out of 30 years for Coal Tits. Values are means (± se). Within each row, values with different superscripts indicate significant differences between means at least $P < 0.05$. Values sharing superscripts were not significantly different from each other.

	Blue Tit	Great Tit	Coal Tit
Chick mortality in all nests	$1.2^a \pm 0.1$	$1.1^a \pm 0.1$	$0.3^b \pm 0.1$
Chick mortality in all nests as % of hatched	$14.3^a \pm 1.5$	$14.4^a \pm 1.5$	$3.5^b \pm 1.2$
% of nests experiencing chick mortality	$46.1^a \pm 3.2$	$46.2^a \pm 3.7$	$20.8^b \pm 7.0$
Chick mortality for nests experiencing chick mortality	$2.3^a \pm 0.2$	$2.3^a \pm 0.2$	$0.7^b \pm 0.2$
Chick mortality for nests experiencing chick mortality as % of hatched	$30.2^a \pm 2.0$	$30.2^a \pm 1.9$	$7.6^b \pm 2.3$

14.5, $P < 0.001$; Table 4) but only Blue Tits showed a significant positive correlation with year ($rho = 0.586$, df = 28, $P < 0.001$). Data for Coal Tits only approached significance ($rho = 0.426$, df = 19, $P = 0.06$). The number of dead chicks, expressed as a percentage of hatchlings in the clutch, for all nests was significantly affected by species ($F_{2,78} = 16.6$, $P < 0.001$; Table 4), and there were significant positive correlations with years for all species (Blue Tits: $rho = 0.642$, df = 28, $P < 0.001$; Great Tits: $rho = 0.456$, df = 28, $P < 0.05$; Coal Tits $rho = 0.440$, df = 19, $P = 0.046$). The percentage of nests exhibiting some dead chicks was affected by species ($F_{2,78} = 9.4$, $P < 0.001$) and Blue Tits and Great Tits exhibited significant positive correlations with year ($rho = 0.491$, df = 28, $P < 0.01$; $rho = 0.373$, df = 28, $P < 0.05$, respectively). The positive correlation with year for Coal Tit nests exhibiting some chick mortality only approached significance ($rho = 0.384$, df = 19, $P = 0.086$).

When numbers of dead chicks were considered in the subset of nests where fledging was less than 100%, then there was a significant affect of species ($F_{2,78} = 27.3$, $P < 0.001$; Table 4). As for egg mortality, the only significant correlation with year and numbers of dead chicks was for Coal Tits ($rho = 0.548$, $P < 0.01$). When expressed as a percentage of the clutch in those nests not experiencing 100% fledging, there was a significant effect of species ($F_{2,78} = 36.0$, $P < 0.001$; Table 4) and all three species exhibited significant positive correlations with year (Blue Tits: $rho = 0.404$, $P <$

0.05; Great Tits: $rho = 0.407$, $P < 0.05$; Coal Tits: $rho = 0.573$, $P < 0.01$).

In summary, species differences were seen for all methods of measuring chick mortality. Significant positive correlations for mortality with year were common in all three species with chick mortality increasing with progressive years.

Comparison of losses during incubation or rearing

For none of the species was there a significant correlation between the numbers of unhatched eggs and the numbers of chicks dying per year over the 30-year period. Similar non-significant patterns were observed when egg and chick losses were expressed as percentages of the total clutch. Inter-species comparison showed a significant positive correlation between annual values for egg loss in Blue Tits and Great Tits ($rho = 0.442$, $P = 0.014$), but the correlation between numbers of chicks lost during rearing by these two species only approached significance ($rho = 0.352$, $P = 0.056$). There were no significant inter-specific correlations with data for Coal Tits.

For all of the years in the study the average proportions of the egg losses due to hatching failure did not differ significantly between species ($F_{2,78} = 0.696$, $P > 0.05$): 0.430 ± 0.037, 0.357 ± 0.038, and 0.441 ± 0.097 for Blue, Great and Coal Tits, respectively. However, key factor analysis showed that the influence of incubation and rearing on overall mortality varied between species. For Blue Tits, factors describing mortality during both incubation (k_1 – egg mortality) and rearing (k_2 – chick mortality) showed significant correlations with the total breeding mortality (Table 5). By contrast, for Great Tits, the only significant correlation with the total breeding mortality was with the mortality during rearing (Table 5). For Coal Tits the opposite was

Table 5. Correlation coefficients (rho) from Spearman's rank analysis comparing total breeding mortality (K) with breeding mortality during incubation (k_1) or rearing (k_2), and the correlation between these two fractional mortalities over a 30-year period for three species of British tit.

Correlation	Blue Tit ($n = 30$ years)	Great Tit ($n = 30$ years)	Coal Tit ($n = 21/27$ years)
K & k_1	0.700 (<0.001)	0.286 (0.126)	0.915 (<0.001)
K & k_2	0.841 (<0.001)	0.936 (<0.001)	0.422 (0.057)
k_1 & k_2	0.351 (0.057)	−0.018 (0.925)	0.098 (0.673)

true: the only significant correlation with the total breeding mortality was with mortality during incubation (Table 5). Correlations between k_1 and k_2 were not significant although for Blue Tits the value did approach significance (Table 5).

DISCUSSION

Although long-term studies of breeding are relatively common (e.g. Visser *et al.* 2003), this study is the first to specifically examine the effects of differential mortality of eggs and chicks for these species and over such a long period of time. Data confirmed that timing of reproduction has shown a long-term trend to earlier nesting, but there is considerable variation from year to year in first-egg date (FED). In this location there has been a long-term decline in clutch size in all three species. It highlighted previously unseen differences between these three species of tits at different stages of the reproductive process. Coal Tits suffer the greatest losses due to unhatched eggs, whereas Great Tits suffer greater losses during chick-rearing. Blue Tits exhibited similar degrees of problems in achieving success during both incubation and rearing.

First-egg date

The timing of breeding in some British passerines has been starting progressively earlier in the year since the early 1970s (Crick *et al.* 1997) and has been demonstrated for Blue Tits in Treswell Wood (between 1979 and 1998, Visser *et al.* 2003) and elsewhere in the UK for Great Tits and Blue Tits nesting in Wytham Woods (McCleery & Perrins 1998, Visser *et al.* 2003). The current set of data confirms these results, demonstrating a significant effect of year on FED for Great Tits at Treswell Wood and adding information about how time is affecting breeding of Coal Tits in the same way. All this information adds to the growing evidence that nesting is starting earlier for birds across Europe (Visser *et al.* 1998, 2003, Crick & Sparks 1999, Sanz 2002, Both *et al.* 2006, Dunn & Winkler 1999, 2010). This has the potential for trophic mismatch between the temperature-dependent emergence of caterpillar prey, which is associated with the timing of bud-breaking in trees, and nesting events (Perrins 1979, McCleery & Perrins 1998).

However, it is interesting to note that there is considerable variation in the timing of breeding between years, which has been reported previously (e.g. Visser

et al. 1998 for Great Tits). The reason for this is not clear, but probably in part reflects the variation between years for prevailing weather. Factors such as air temperature, which influences the mass of Blue Tit nests (Britt & Deeming 2011), are likely to be important (Visser *et al.* 2006). However, rainfall, numbers of broods per year, food abundance, breeding density (a negative correlation between nest numbers and FED was shown in this study for Blue and Great Tits), photoperiod and hormones may also be significantly influencing the timing of nest-building and FED (Dawson 2008, Dunn & Winkler 2010). It is unclear whether the factors affecting timing of breeding for one species are comparable in other closely related species. Further research should seek to better explain how localized weather conditions, or more generalized climate change, are affecting timing of nesting on an annual basis.

In general, clutch size changes with FED and is a function of the number of breeding attempts a year (Crick *et al.* 1993). Although British Tits are typically single-brooded, it is interesting to note that a delay in FED did reduce mean clutch size relative to the average in Blue Tits studied here. This species was single brooded in Treswell Wood and any delay in nesting seemed to prevent the birds from producing a maximal clutch size. A similar effect of reduced clutch size with later laying date was reported in Blue Tits by van Balen (1984) and so the relationship between FED and clutch size (Crick *et al.* 1993) is not restricted to multi-brooded species. That this effect was absent in Coal Tits may reflect their generally earlier FED. In Great Tits the delay in FED has a small impact on clutch size because there is apparently still sufficient time to produce a near normal clutch. Extended laying dates have been shown to reduce clutch size in Great Tits, but the initial clutch size was much higher (usually over 10 eggs) than reported here (van Balen 1984, Barba *et al.* 1995).

Changes in clutch size

Clutch size shows a natural variation from year to year, e.g. as seen in Great Tits (Boyce & Perrins 1987) but the factors that affect optimization of clutch size are not well understood. Experiments with manipulation of clutch size in Great Tits suggest that there is selection for greater clutch size (Tinbergen & Sanz 2004). Over a period of 25 years clutch size increased in a colony of Mute Swans *Cygnus olor*, a process influenced by additive genetic and permanent environmental effects

associated with relaxation of food constraints and predation pressure (Charmantier *et al.* 2006). Gibbs (1988) concluded that variation in clutch size in Darwin's Medium Ground Finches *Geospiza fortis* reflects proximate environmental factors which vary from year to year, but have yet to be identified.

Over the 30-year period of this study clutch size decreased significantly in all three species studied. This seemed to be in part due to changes in FED on a per-year basis, with late dates being associated with smaller clutches in Blue Tits, but the long-term trend was for earlier FEDs. There was no relationship between clutch size and total numbers of breeding events in nest-boxes within Treswell Wood, which perhaps implies that there was no density-dependent effect operating in this situation. However, the data set used here did not represent all of the nests started in boxes by the tits in the wood each year and so it is possible that density-dependent effects were being masked by the selection criteria used in this study. A different analysis of a slightly smaller set of these data indicated that, for Blue Tits and Great Tits between 1979 and 2005, when all nests started in Treswell Wood are taken into account, there are significant density dependent effects on clutch size (Deeming & du Feu 2005) and these are comparable to previous reports (Perrins 1965, Both 2000, Both *et al.* 2000). Other than reduction in territory size or quality (van Balen 1984) it is unclear from our study what other factors might be involved in this reduction in clutch size.

Egg and chick mortality

Recorded mortalities from laying to fledging for these three species were comparable to previous reports, which exhibit considerable variation between location and year (see Perrins 1993). Egg mortality recorded here was comparable to that reported for Marsh Tits *Parus palustris* but lower than that reported for Sombre Tits *Parus lugubris* and Siberian Tits *Parus cinctus* (see Perrins 1993).

Key factor analysis of annual patterns of mortality in bird populations has shown that losses of offspring during the breeding season do not have a major effect on the population size. In populations of Pied Flycatchers *Ficedula hypoleuca* and Redstarts *Phoenicurus phoenicurus* in Finland and Sparrowhawks *Accipiter nisus* in Scotland, it was mortality outside of the breeding period that was the only significant key factor explaining patterns of mortality (Järvinen 1987, Newton 1988).

Neither of these studies investigated patterns of mortality during the breeding period alone and so neither were directly comparable. However, data reported by Newton (1988) allow an equivalent key factor analysis to be carried out for Sparrowhawks, and, like Blue Tits, both mortality of eggs and chicks showed significant correlations with the total breeding mortality (Deeming, unpubl. analysis). Our study was always intended to compare the losses during incubation and rearing and so it is interesting that the three tit species exhibited different patterns when mortality was considered in key factor analysis. Applying this kind of analysis to particular phases of the life cycle of birds may reveal some interesting patterns and is worthy of further application.

The differences in mortality associated with both incubation and rearing have not been fully considered in birds, although comparable data are available. A brief examination of the literature shows that the proportion of all losses happening during incubation shows great variation between species. It is very high in some species, such as Blue Tits (100%, van Balen 1984), Macaroni penguins *Eudyptes chrysolophus* (91% of A eggs although only 65% for B eggs; Williams 1980) and Rockhopper penguins *Eudyptes chrysocome* (82%; Williams 1980), Great Tits (83%; van Balen 1984), Yellow-head Blackbirds *Xanthocephalus xanthocephalus* (79%; Howard 1963) and Carrion Crows (72%; Yom-Tov 1974). The proportion of losses is about two-thirds of the total in other species, such as Red-winged Blackbirds *Agelaius phoeniceus* (66%; Howard 1963). In Roseate Spoonbills *Ajaja ajaja* losses during incubation (45%) are more like those losses during rearing (White *et al.* 1982). Values of 43–44% were recorded for Blue and Coal Tits in the present study. In White-fronted Bee-eaters *Merops bullockoides* 40% of all losses between laying and fledging were during incubation (Wrege & Emlen 1991) with a value of 36% reported for Great Tits (present study) and 32% reported for Crested Caracaras *Caracara plancus* (Morrison 1999). Relatively low values of 15–20% are observed in Mountain White-crowned Sparrows (Morton *et al.* 1972) and Long-billed Curlews *Numenius americanus* (9%; Redmond & Jenni 1986).

These examples are not an exhaustive survey of the literature but do illustrate the variation in the degree to which the proportions of total losses attributed to incubation can vary between species. The examples given above do not represent a systematic search of the literature and so it is difficult to ascertain from the examples given what factors are important in

determining whether losses during incubation are going to be relatively high or low. It has to be noted that the studies may not be directly comparable to the values presented for the species of tit described in this study because of the constraints imposed on the data analysed. In the present study losses of eggs due to desertion or predation were excluded and so failure of an egg to hatch may be down to physical damage, infertility, a developmental problem, or the inability of the adults to incubate efficiently. However, the range of values from published reports does suggest that the chances of an egg hatching are not equal between species.

In the three species here, egg losses may reflect on the ability of the adult to incubate efficiently. The large clutches of Coal Tits and Blue Tits have a total mass that is over 100% of the female body mass compared with the clutch of Great Tits eggs equating to 80% of the female body mass (data from Perrins 1993). Nur (1986) suggested that differences in clutch size in Blue Tits may reflect differences in the ability of the female to lay and/or incubate the clutch. That egg mortality is a key part of total losses in these smaller species may reflect the inability of the female to incubate all of the eggs, but whether this is generally applicable requires further investigation. There would be considerable merit in a more systematic survey of the literature in order to determine if there are patterns in hatchability related to, for instance, female body mass, clutch size, breeding location, nest location or type. Annual losses during incubation correlated for Blue Tits and Great Tits, implying that there may be general environmental effects that impact on the general reproductive success of a range of species.

Explanation of the variation in chick survival may be more straightforward. The ability of the parents to provision the offspring with sufficient food from hatching through to fledging may reflect the ability of individual pairs of parents or the quality of the available foraging territory. Pryzbylo *et al.* (2001) demonstrated that territory quality was more important than parentage in a study of Blue Tit breeding success in Sweden. Both & Visser (2003) demonstrate density-dependence between population size (pairs per ha) of Great Tits and fledging success, although because of the nature of the data set this was not investigated in the present study. Moreover, in a German study, mate retention in Blue Tits and Great Tits had no significant advantage in breeding success (Pampus *et al.* 2005). These reports suggest that the habitat of Treswell Wood perhaps somehow limited the ability of the tit species to find sufficient food for their chicks. The trends for

lower clutch sizes, and higher chick mortality, through time at Treswell Wood suggest that the habitat became increasingly less able to support these populations of breeding tits. It is interesting to note that, despite the larger numbers of chicks to feed, Coal Tits were less affected by chick mortality than the other two species, which may indicate that there is spatial separation of foraging habitats between the three species (e.g. see Fuller 1995) or that Coal Tits are exploiting a particular foraging niche that is not used by the other two tit species. It would be interesting to determine whether these differences exist in other populations or habitats.

Other factors may be important in chick mortality. For example, Richner *et al.* (1993) showed that Blue Tit nests infested with the haematophagus hen flea *Ceratophyllus gallinae* fledged lower proportions of the clutch than nests without these ectoparasites. Nest weight or materials may be important in insulating chicks as they develop (Tomás *et al.* 2006, Britt & Deeming 2011). Overall female health or level of nutrition may be important (Tomás *et al.* 2006). In relation to long-term climate change the phenologies of breeding and caterpillar biomass may also be critical for rearing success (Visser *et al.* 2006), although one population of Great Tits at least appears to have been able to maintain the synchrony between hatching and food supply (Cresswell & McCleery 2003). It is likely that environmental variation, e.g. fluctuations in temperature, will impact upon all species in a location and affect their ability to rear their offspring – although not quite significant this appeared to be the case for Blue and Great Tits in this study. Some or all of these factors may be involved in determining rearing success, but what is clear is that the factors that could impact upon rearing behaviour are much more numerous and complex than those that probably impact upon success during the incubation phase.

CONCLUSION

The ability of Great Tits to raise their offspring from egg to fledging was more affected by the losses during raising the hatched chicks and contrasted with Coal Tits, which have more problems hatching all of their eggs. The patterns of losses for Blue Tits are similar during incubation and rearing. These differences between closely related tit species have not been reported before, although data are available for granivorous species on farmland (Siriwardena *et al.* 2001), and their biological cause, or effect, is as yet unclear. What is not known from this study is

whether losses of eggs are caused by infertility or embryonic mortality at particular stages of development. It is unclear whether the results shown for tits at Treswell are typical of other populations at different locations or habitats. Further research should ascertain whether these different failure rates at the two nesting stages can be replicated in other places or habitats. There is also considerable scope for further analysis of the reasons why different species have different nest mortality patterns. It is hoped, now the differences in mortality between these two reproductive stages has been demonstrated, that research will start to tease apart those factors that are affecting overall reproductive success in these species.

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