



Long-term decline in the thickness of eggshells of thrushes, *Turdus* spp., in Britain

R. E. Green

Royal Society for the Protection of Birds, 17 Regent Terrace, Edinburgh EH7 5BN, UK

The thickness of eggshells of four species of thrush, *Turdus* spp., was estimated by an index based on the mass and linear dimensions of blown eggs in museum collections from Britain. Shell thickness was also measured directly for two species and was highly correlated with the index. Widespread declines in eggshell thickness since the nineteenth century were found in all species. There have been no previous reports of trends in eggshell thickness of this long duration and large spatial scale. The cause of the declines is unknown, but, for three of the four species, eggshell thinning began before the introduction of the organochlorine pesticide DDT, which caused eggshell thinning in predatory and fish-eating birds from 1947 onwards. The effect of acid deposition on the availability of calcium-rich prey is a plausible explanation.

Keywords: eggshell thickness; calcium; organochlorine; *Turdus*

1. INTRODUCTION

The thickness and structure of bird eggshells are known to be influenced by the availability of calcium in food and the effects of pollutants upon shell formation. Population-scale declines in mean eggshell thickness of birds of prey and fish-eating birds were widely reported after the introduction of the organochlorine pesticide DDT into agriculture and forest management (Ratcliffe 1970; Anderson & Hickey 1972; Newton 1979), but declines at the population level due to other causes have not been documented. The four species of thrushes, *Turdus* spp., in Britain each have breeding populations above 1000 pairs (Gibbons *et al.* 1993). In this paper I report a long-term decline in the thickness of eggshells of all four species and present evidence that contamination with DDT is unlikely to be the cause.

2. METHODS

(a) Eggshell thickness index (ETI)

All clutches taken within Britain in the collections at the Royal Museum of Scotland (Edinburgh), the Natural History Museum (Tring) and the Liverpool Museum were measured, provided that there were data on at least the year and county in which the clutch was taken. Collection sites were scattered widely (figure 1), but their distribution was clumped and concentrated around centres of human population, especially for the three species that occur mainly in the lowlands (blackbird, *Turdus merula*, song thrush, *T. philomelos*, and mistle thrush, *T. viscivorus*). Ring ouzels, *T. torquatus*, now breed only in the uplands (Gibbons *et al.* 1993), but some pairs formerly bred in lowland England (Holloway 1996). Eggs were excluded if they were dirty, broken, had large (diameter > 7 mm) holes in the shell (made for the extraction of egg contents) or rolled unevenly on a flat surface, indicating the presence inside of a dried pool of egg contents. Air-dry eggshells, stored under normal museum conditions, were weighed to 1 mg on an electronic balance that was checked frequently against a standard. Single

measurements to 0.01 mm of the length and breadth of the egg were made with digital callipers.

Egg volume was estimated by multiplying the product of length and the square of breadth by a coefficient determined for a congeneric North American species, *Turdus migratorius* (Hoyt 1979). The original surface area of each egg was estimated from the volume using equation (5) of Paganelli *et al.* (1974). The surface area of the piece of shell missing from the circular hole through which the contents had been extracted was estimated as the convex surface of a segment (with diameter that of the hole, measured to 0.1 mm) of a sphere with a diameter equal to the breadth of the egg. This value was then subtracted from the original surface. Eggshell mass (mg) was divided by surface area (mm²) to give an ETI value in mg mm⁻² for each egg. The mean index value was then calculated for the clutch. There were between one and seven measurable eggs per clutch, with four being the modal number for all species. An index of eggshell thickness used in previous studies (eggshell index (EI); Ratcliffe 1970) was also calculated for each egg as the ratio of eggshell mass to the product of length and breadth. Eggshell mass was first corrected to allow for the loss due to the missing piece of shell. Clutch means of ETI and EI were closely correlated in all four species (*T. merula*, $r=0.970$; *T. philomelos*, $r=0.977$; *T. viscivorus*, $r=0.955$; *T. torquatus*, $r=0.971$; $p<0.0001$ for all species). Both indices assume that eggshell thickness is closely correlated with mass per unit area of shell and that there is negligible systematic variation in mass per unit volume. This assumption is tested in a later part of the paper.

The effect of measurement error and egg asymmetry on the accuracy of ETI was estimated by weighing and measuring 20 *T. merula* eggs, each from a different clutch, on ten occasions. The complete set of measurements was obtained on all the eggs and the records put out of sight before beginning to measure the eggs again in the same order. The within-egg standard deviation (s.d.) of ETI was 0.0016 mg mm⁻², 0.7% of the mean.

(b) Eggshell thickness

Eggshell thickness was measured directly to 1 µm, using a modified digital micrometer (Digimatic Outside Micrometer:

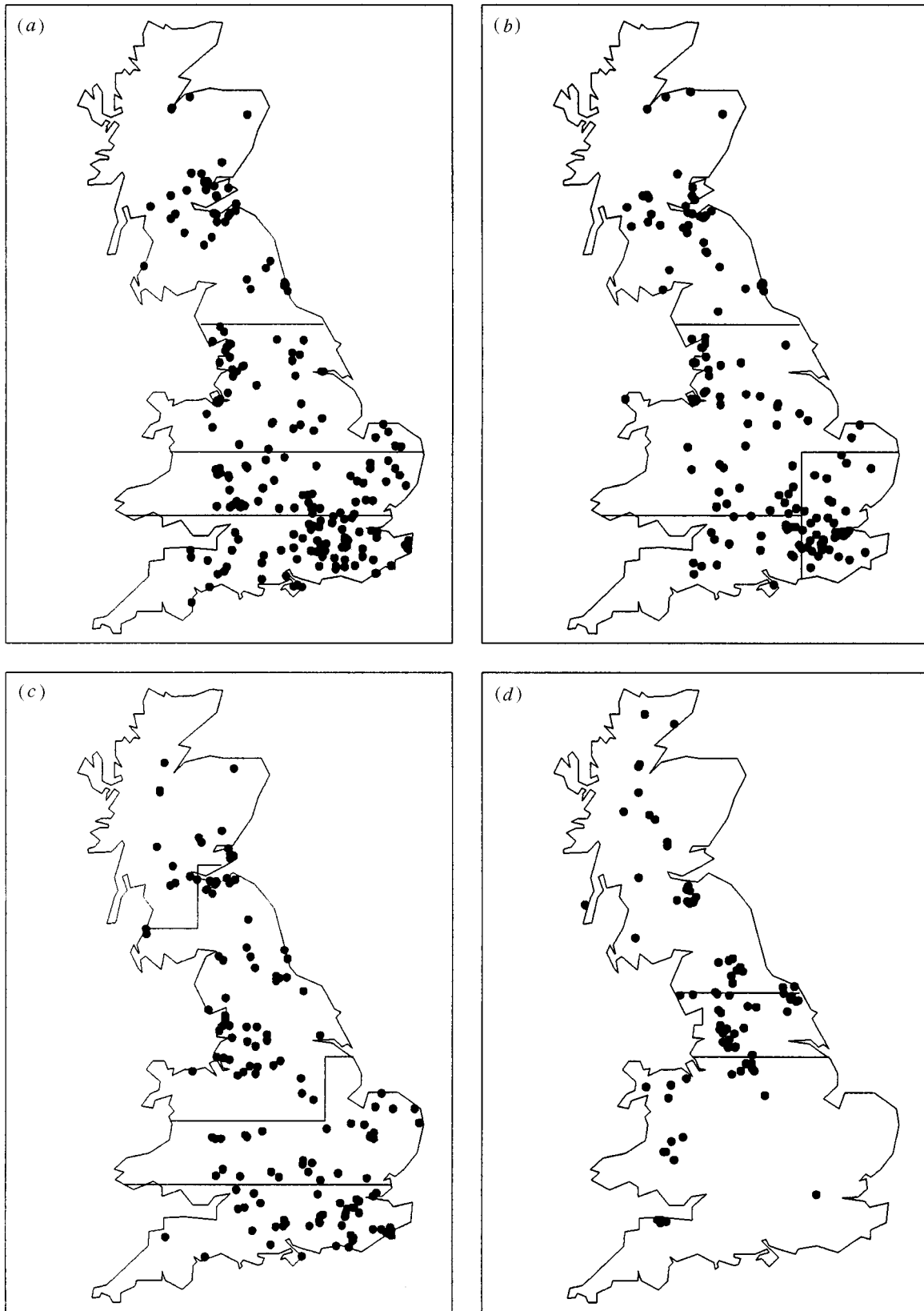


Figure 1. Collection sites within Britain of clutches of (a) *Turdus merula*, (b) *T. philomelos*, (c) *T. viscivorus* and (d) *T. torquatus*. Lines show the boundaries, based upon 100-km National Grid squares, of regions used in the analysis of within-region trends.

Mitutoyo Corporation, Tokyo). A steel needle (24 mm long, diameter 1.3 mm), tapering to a hemispherical tip (radius 0.35 mm), was cemented to the flat-end of the micrometer spindle. The tip of the needle was passed through the single hole previously made near the equator of the egg to extract the

egg contents and advanced until the shell opposite the hole was held between the needle tip and the flat anvil. A force of 5.4 N was applied to the needle by slowly turning a spring-loaded knob to advance the screw. All suitable clutches of *T. merula* and *T. philomelos* at the Royal Museum of Scotland and Natural

History Museum were measured. Some clutches could not be measured because the hole was too small to admit the needle or was too far from the equator for the needle to approach the shell normal to its internal surface. It was only possible to measure shell thickness within one small part of an intact eggshell. Therefore, the effect of measurement error and variation in eggshell thickness around the equator of eggs was investigated in 18 eggs of domesticated Japanese quail, *Coturnix japonica*. The eggs' contents were removed and the shells dried to constant mass at 30 °C. Eggshell thickness was measured with the micrometer at ten places evenly spaced around the equator after the shell had been cut open. The within-egg standard deviation of these measurements was 8.3 µm (4.2% of the mean).

(c) Curve fitting

Least-squares regression was not used to describe the relationship between ETI or thickness and year of collection because inspection of the data suggested that the residual variance varied with year. Instead, ETI and thickness were assumed to be normally distributed with the mean and standard deviation both varying as polynomial functions of year of collection. Maximum-likelihood values of the coefficients of the polynomials were obtained using the NONLIN module of SYSTAT v. 5.03. Thirty-six models were fitted for each species: one null model with no effect of year and the remaining models with first- to fifth-degree polynomials describing both the mean and standard deviation. The model with the lowest value of the Akaike Information Criterion (Akaike 1974) was selected. For ETI, the degree of the polynomials of the selected models were as follows: *T. merula* 3/2, *T. philomelos* 1/1, *T. viscivorus* 1/1 and *T. torquatus* 1/4. For eggshell thickness, the degree of the polynomials of the selected models were as follows: *T. merula* 4/3 and *T. philomelos* 3/0. The number before the slash is the degree of the polynomial describing the trend in the mean, whereas that after the slash is the degree of the polynomial for the s.d.

3. RESULTS

(a) Trend in the index of eggshell thickness

The index of eggshell thickness (ETI; see §2) declined over the years in all four species (figure 2; *T. merula*, Spearman rank correlation coefficient $r_s = -0.247$, $p < 0.001$, $n = 427$ clutches; *T. philomelos* $r_s = -0.187$, $p < 0.01$, $n = 258$; *T. viscivorus* $r_s = -0.176$, $p < 0.02$, $n = 224$; *T. torquatus* $r_s = -0.151$, $p < 0.05$, $n = 187$). Inspection of figure 2 indicates that the decline began by 1900 in *T. merula*, *T. philomelos* and *T. viscivorus*. However, the date of its onset is difficult to determine, especially for *T. torquatus*. There was some indication of a recent recovery in ETI after 1960 for *T. merula* (figure 2a).

(b) Geographical distribution of trend

The trends in ETI were not confined to one heavily sampled region and were not spurious patterns generated by geographic variation in eggshell thickness combined with changes in the geographical distribution of collection sites. Spearman rank correlation coefficients between ETI and year of collection were calculated separately for regions of Britain, defined by pooling data for adjacent 100-km National Grid squares until each region contained at least ten clutches collected in each of the periods 1850–1900 and 1901–1995. Species differences in region bound-

aries were required to meet this criterion (figure 1). ETI and year of collection were negatively correlated in all four regions for *T. merula*, *T. philomelos* and *T. viscivorus* and in two of the three regions for *T. torquatus*. Hence, there was a highly significant excess of species–region combinations with a negative trend (14 out of 15; sign test, $p < 0.0001$). Five of the region-specific negative correlations were significant at $p < 0.05$.

(c) Trend in eggshell thickness

The decline in eggshell thickness, measured directly with a micrometer for *T. merula* and *T. philomelos*, was as marked as that for ETI in both species (figure 2b, $r_s = -0.318$, $p < 0.001$, $n = 238$; figure 2c, $r_s = -0.188$, $p < 0.02$, $n = 184$, respectively). There were highly significant correlations between mean eggshell thickness and mean ETI for clutches of *T. merula* and *T. philomelos* ($r = 0.867$, $p < 0.001$, $n = 238$, and $r = 0.840$, $p < 0.001$, $n = 178$, respectively). There was some indication for both species of a recovery in eggshell thickness after 1960.

(d) Magnitude of the decline

The magnitude of the decline in eggshell thickness since the mid-nineteenth century was assessed by comparing the mean ETI and thickness values for 1960, estimated from fitted polynomial functions (see figure 2 and §2), with the mean for clutches collected between 1850 and 1890. The decline in ETI was 7.4% of the 1850–1890 value for *T. merula*, 3.6% for *T. philomelos*, 2.2% for *T. viscivorus* and 3.5% for *T. torquatus*. The equivalent declines in eggshell thickness were 10.7% for *T. merula* and 4.3% for *T. philomelos*.

(e) Time invariance of the relationship between eggshell thickness and the index of eggshell thickness

Linear least-squares regressions of eggshell thickness on ETI were compared among four periods (1850–1900, 1901–1920, 1921–1940, 1941–1995) chosen to contain a minimum of 30 clutches for *T. merula* and *T. philomelos*. Eggshell thickness was selected as the dependent variable because measurements were less precise than those for ETI (see §2). There was no significant variation in the regression parameters among periods for either *T. merula* ($F_{6,230} = 1.01$, $p > 0.30$) or *T. philomelos* ($F_{6,170} = 1.41$, $p > 0.20$).

(f) Influence of egg volume on ETI

If eggshell thickness is correlated with egg volume, then the decline in ETI could be a consequence of a change in egg volume. Egg volume, estimated from length and breadth, showed a significant trend over time only in *T. merula* ($r_s = -0.101$, $p < 0.05$), for which there was no significant correlation between ETI and volume index ($r_s = 0.058$, $p > 0.20$). The other species showed no significant trend over time (*T. philomelos*, $r_s = 0.002$, $p > 0.90$; *T. viscivorus*, $r_s = -0.010$, $p > 0.90$; *T. torquatus*, $r_s = -0.047$, $p > 0.50$). ETI showed a significant positive correlation with volume index for *T. viscivorus* ($r_s = 0.134$, $p < 0.05$) and *T. torquatus* ($r_s = 0.217$, $p < 0.01$), but not *T. philomelos* ($r_s = -0.075$, $p > 0.020$). Hence, the combination of a significant correlation between ETI and egg volume with a significant correlation between volume and year was not observed for any species.

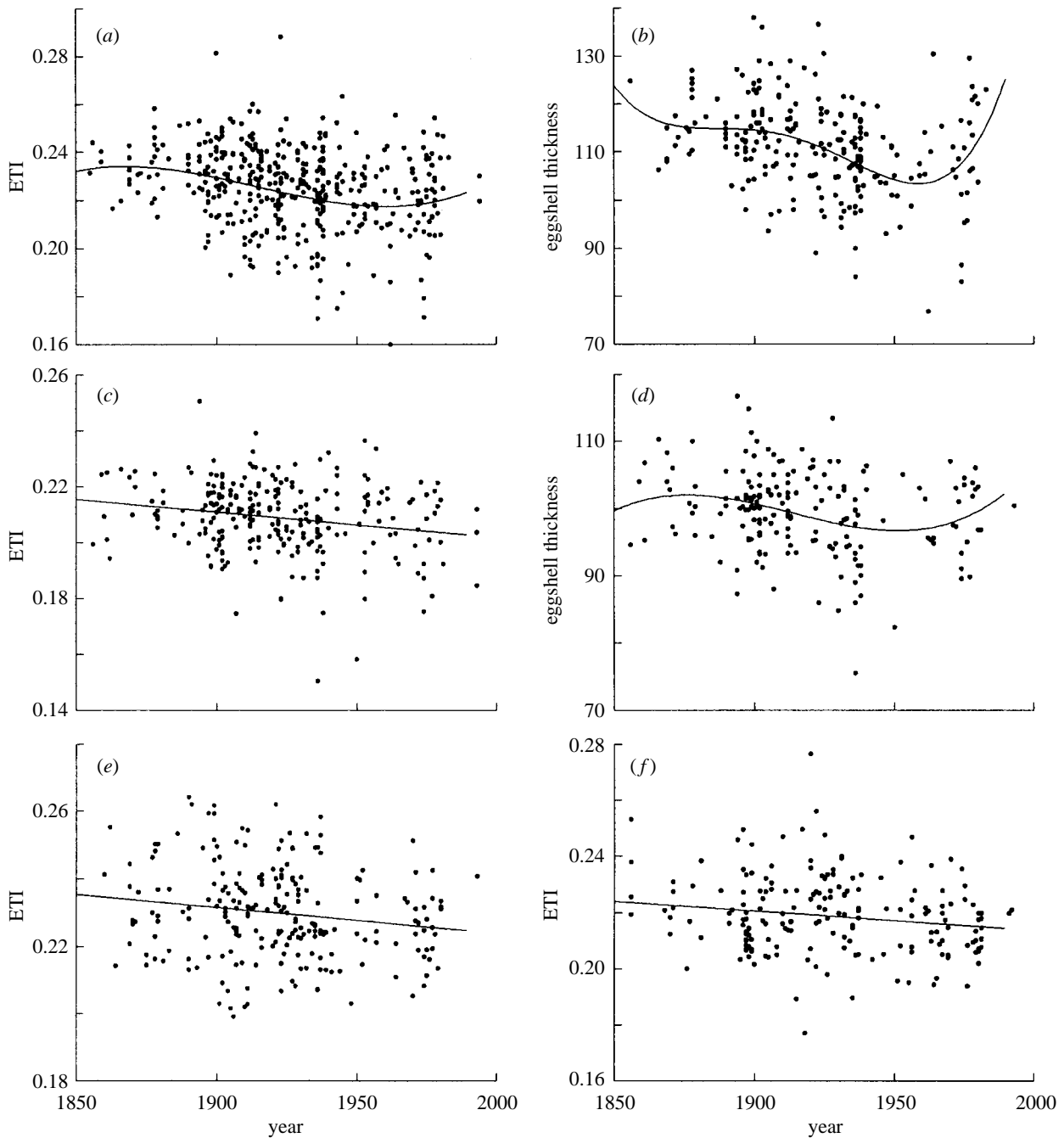


Figure 2. Relationships between eggshell thickness index (mg mm^{-2}) and year of collection for (a) *Turdus merula*, (c) *T. philomelos*, (e) *T. viscivorus* and (f) *T. torquatus*. Relationships between eggshell thickness (μm) and year are also shown for (b) *T. merula* and (d) *T. philomelos*. Each point represents the mean for a clutch. Curves are polynomials fitted by a maximum-likelihood method.

(g) Trends in ETI and eggshell thickness prior to the introduction of DDT

To exclude a possible effect of the organochlorine pesticide DDT, the correlation analysis was repeated after excluding clutches collected after 1946. Significant declines in ETI were still found for *T. merula* ($r_s = -0.223$, $p < 0.002$, $n = 322$), *T. philomelos* ($r_s = -0.202$, $p < 0.01$, $n = 208$) and *T. viscivorus* ($r_s = -0.151$, $p < 0.05$, $n = 183$), but not for *T. torquatus* ($r_s = 0.021$, $p > 0.80$, $n = 131$). When clutches collected after 1946 were excluded, the sign of the correlation between ETI and year was still negative in all four regions for *T. merula* and *T. philomelos*, and was negative for three of four regions for *T. viscivorus* and for two of three regions for *T. torquatus*. The excess of negative

species–region coefficients was significant (13 out of 15; sign test, $p < 0.008$). Three of the region-specific negative correlations were significant at $p < 0.05$. Significant declines in eggshell thickness, measured directly with a micrometer, were still found after excluding clutches collected after 1946 (*T. merula*, $r_s = -0.326$, $p < 0.001$, $n = 196$; *T. philomelos*, $r_s = -0.242$, $p < 0.01$, $n = 155$).

4. DISCUSSION

It is necessary to consider the possibility that the trends in eggshell thickness index were artefacts of the methods used to prepare and store eggs. Such an explanation seemed unlikely because trends in eggshell

thickness prior to the introduction of DDT have not been detected in previous studies of other bird species using the similar eggshell index (EI, see §2; Ratcliffe 1970; Newton 1979). However, possible changes in the quantity of egg contents left within the shell after washing, and/or contamination of the shell pores with fine dust or preservatives applied to suppress the growth of mould, might be significant for the small eggs of thrushes. Both of the postulated effects would alter eggshell mass, and hence ETI. However, this can be excluded as the cause of the observed trends using direct micrometer measurements of eggshell thickness available for a sub-sample of clutches of *T. merula* and *T. philomelos*. Measured eggshell thickness would not be increased by residual egg contents because they tended to accumulate on the side of the egg in which the hole was made, and away from the site of measurement, when the washed egg was drained with this side downwards. Trials with pieces of domestic Japanese quail eggshell, coated on the inside with dried egg contents, showed that the micrometer displaced the residues anyway. Contamination of the eggshell pores with dust or preservatives would not be expected to affect the micrometer measurement of eggshell thickness. If contamination was the cause of the trends in ETI, then it would be expected that no trend in eggshell thickness would be observed and that there would be changes over time in the relationship between the ETI and eggshell thickness. Contrary to this expectation, there were well-marked declines in eggshell thickness and no evidence that the relationship between thickness and ETI varied among time-periods. Hence, for the two species in which thickness was measured directly, there was no support for the hypothesis that ETI declined because of changes in methods of eggshell preparation or storage.

The organochlorine pesticide DDT had a large effect upon the eggshell thickness of birds of prey and fish-eating birds (Ratcliffe 1970; Anderson & Hickey 1972; Newton 1979). The EI of sparrowhawk, *Accipiter nisus*, in Britain declined by 17% in a step-like manner in 1947 when DDT began to be used widely in agriculture (Ratcliffe 1970) and has increased since the 1970s when the use of DDT was restricted (Newton 1986). By contrast, ETI and eggshell thickness of thrushes began to decline gradually well before 1947, and these variables do not show an obvious step-like decline in 1947. The indications of recent increases in *T. merula* (ETI and thickness), and perhaps *T. philomelos* (thickness only), are the only points of detailed resemblance between the trends for sparrowhawk and those for the thrushes. This suggests that some factor other than DDT has predominated in causing changes in the thickness of thrush eggshells.

Variation in the incidence of shell defects or eggshell thickness in forest and freshwater passerine birds is related to the calcium content of leaf litter (Graveland *et al.* 1994) and the pH of stream-water (Ormerod *et al.* 1988), respectively. In both cases, the mechanism involves the effect of soil or water chemistry on the availability of those invertebrates (or their shells) that are an important source of calcium during eggshell formation. Acid deposition, caused by anthropogenic emissions of sulphur dioxide, nitrogen oxides and ammonia, is thought to have caused declines in the calcium content of woodland leaf

litter and the abundance of snails on poorly buffered soils in the Netherlands and Sweden (Graveland & Van der Wal 1996; Wärebörn 1992). A high and increased proportion of defective eggshells of great tits, *Parus major*, was found in an area with an acidified podzolic soil, where a long-term decline in the abundance of small snails, an important component of the birds' diet during eggshell formation, was also observed (Drent & Woldendorp 1989; Graveland *et al.* 1994; Graveland & Van der Wal 1996). The incidence of thin, malformed shells was much reduced, and breeding success improved by supplementary feeding with calcium-rich food (Graveland & Drent 1997). Snails are likely to be an important source of dietary calcium for thrushes in Britain, but trends in their abundance and that of other calcium-rich terrestrial invertebrate prey have not been studied in relation to acidification and soil type. Declines since the nineteenth century in the pH of undisturbed soil, detected in archived soil samples from southern England, are consistent with the expected effects of acid deposition (Goulding & Blake 1993). Further studies are required to correlate differences among regions in trends in eggshell thickness with geographical differences in the reconstructed history of the pH and calcium content of leaf litter and soil and of other factors, such as agricultural practice, which might also have caused changes in the availability of prey. If a causal connection between eggshell thinning and soil acidification is established, then measurements of the large numbers of eggs held in museum collections may provide a means to reconstruct historical changes in the calcium content of soils.

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