

Inheritance and variation in eggshell patterning in the great tit *Parus major*

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The inheritance of patterns on avian eggshells is central to understanding the evolution of traits such as egg mimicry (e.g. in cuckoos). Yet little is known about the inheritance, or indeed function, of eggshell patterns. It has long been believed that the evolution of eggshell pattern mimicry required that patterns be determined by genes situated on the female-specific W chromosome. However, it has never been demonstrated for any bird that egg pattern traits (rather than ground colour) are female sex linked, or indeed that they are inherited. We studied the inheritance of three measures of egg-pigment patterns in a wild great tit population. Egg patterns were female specific but unrelated to female attributes such as age or condition and showed only weak environmental effects. Eggs of daughters resembled those of both their mothers and maternal grandmothers, but not of their paternal grandmothers. We conclude that this is the first demonstration of female sex-linked inheritance of avian eggshell patterning, so raising the probability that such a system operates in egg mimics and their hosts.

Keywords: egg; pigment patterns; great tit; inheritance

1. INTRODUCTION

Birds are unique among amniotes in their evolution of a pigmented eggshell. Because it consists of a calcium carbonate matrix, the base colour of bird eggshells is white, and this is considered the primitive condition (Solomon 1991). In many species, however, the cuticle and the outer part of the calcified layer of the shell are pigmented, often with complex patterns. Understanding the function of these patterns (as distinct from the eggshell's ground colour) is promoted by determining the mechanism (genetic or otherwise) by which they are inherited. We develop this argument by briefly considering the function of pigments and superficial eggshell structures.

In most species, the shell surface is covered by a cuticle of protein and carbohydrate, the functions of which are not fully understood (Board 1974). It may repel water, control water loss (Board & Halls 1973), influence shell strength or repel microbes (Burley & Vadehra 1989), and shell pigments may play some, as yet unknown, role in one or more of these functions (Solomon 1987; Burley & Vadehra 1989). Although in some cases, such as in ground-nesting species, concentrated spotting of browns, greens and black on a green–brown ground colour clearly provide crypsis, the function of eggshell pigments is not always this obvious. In many avian taxa, evidence for a cryptic function is equivocal (e.g. Lack 1958; Montevecchi 1976; Westmorland & Kiltie 1996).

In some species, in which intra- or interspecific nest parasitism occurs, eggshell patterning may allow individual egg recognition, enabling rejection of cuckold eggs (Davies & Brooke 1989). While eggshell patterns are often broadly species specific, they typically vary little within, compared with between, females' clutches (Westmorland & Kiltie 1996; illustrations in Hoehner (1974) and Gosler (1993)). Thus, an eggshell pattern may be a fingerprint-

like marker, specific to the host species or indeed to the individual host female. For obligate brood parasites like the common cuckoo *Cuculus canorus*, the species specificity of host eggs has selected for increasingly accurate egg-pattern mimicry by the cuckoo (Davies & Brooke 1991).

Eggshell patterns could vary between females because of genetic, environmental or maternal effects. Understanding the source of this variation is central to understanding the functions of eggshell patterning because this must limit the suitability of pigmentation for certain functions. For example, a large environmental component to phenotypic pattern variation in a host species might increase intraspecific variation, hampering the ability of a brood parasite to mimic that host's eggs. In the common cuckoo, which parasitizes several species, interspecific variation in host egg patterns has selected for a series of host-specific lines of female cuckoo or *gentes*, whose eggs mimic those of that *gens'* host species (Wylie 1981). This suggests that gene loci for egg pattern lie on the female-specific W chromosome, with little or no contribution from the male line (Punnett 1933; Jensen 1966; Collias 1993; Gibbs *et al.* 2000).

It is important to distinguish between eggshell patterning, the subject of this paper, and the ground colour pigmentation of the egg. It is well known, at least for the domestic fowl *Gallus domesticus*, that ground colour is generally under polygenic control inherited via autosomes, giving F₁ egg ground colours intermediate between parental egg phenotypes (Hutt 1949). Thus the female sex-linked system of Punnett and others (cited above), postulated to explain the inheritance of pattern traits, differs markedly from that already described for egg ground colour, and such a system has never been demonstrated in birds.

To study this further, it is necessary to compare the eggs of related individuals of a species with patterned eggs. Most domesticated species lay unspotted eggs. However, small hole-nesting passerines of many families (e.g. Hirundinidae, Troglodytidae, Paridae, Aegithalidae, Certhiidae, Sittidae, Muscipidae and Sylviidae), lay

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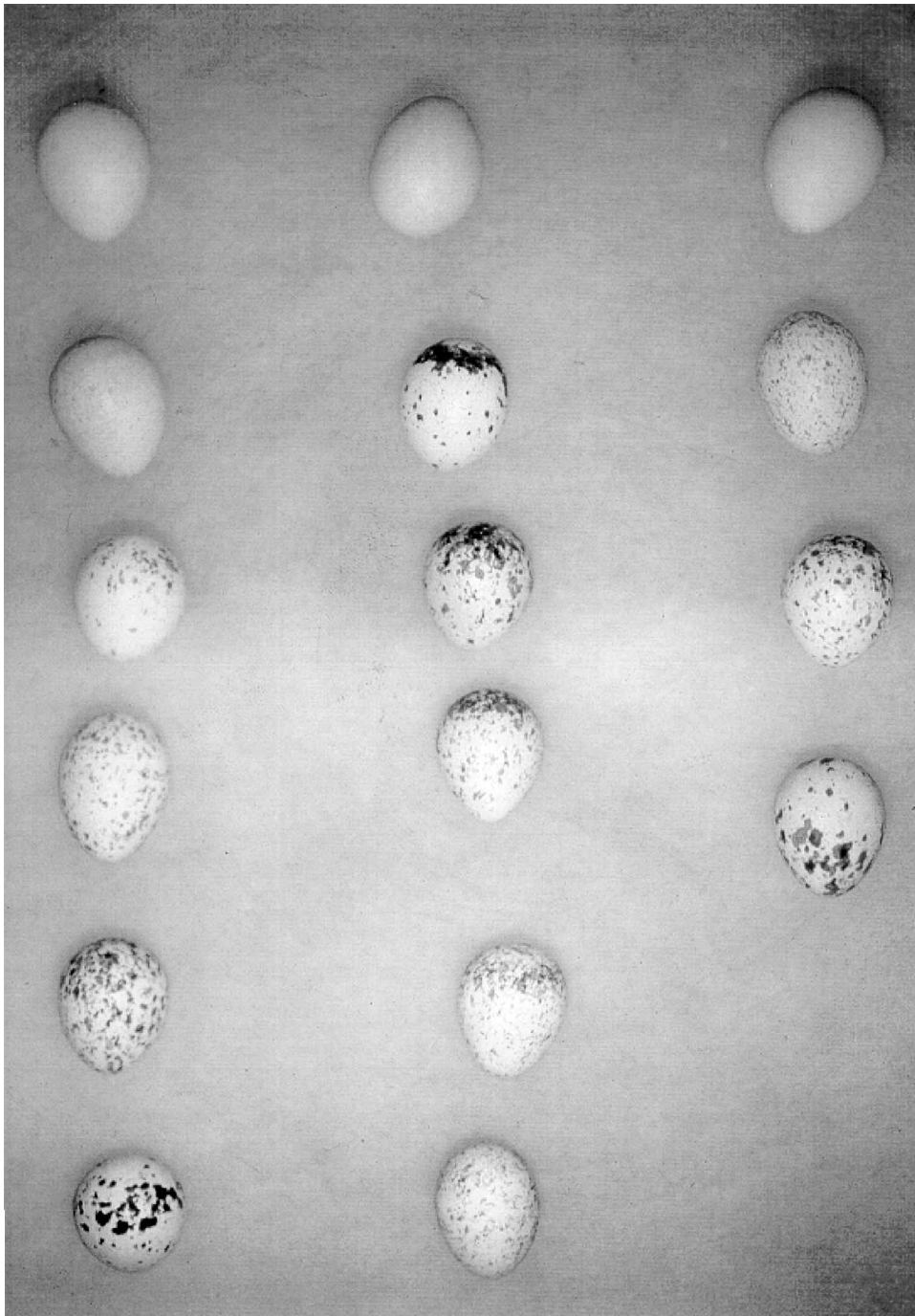


Figure 1. Egg colour variation and recording in the great tit. Columns represent, left to right, intensity (I , scored 0–5), distribution (D , 0–5) and spot size (S , 0–3). Rows represent increasing values from top to bottom. Intermediate values (e.g. 1.5, 2.5) were also interpolated, giving 11 classes for I and D , and six for S . Standard photographs of a series of clutches were used to maintain consistency over years. Principal classes: 0, unspotted; I : 1, feint, 2, pale, 3, medium, 4, some intense spots, 5, intense; D (approximate percentage spotting in one-half, typically the blunt end): 1, > 81%, 2, 71–80%, 3, 61–70%, 4, 51–60%, 5, 50%; S : 1, small, 2, medium, 3, large.

(usually) glossy white eggs more or less spotted with small reddish to brown or black spots deposited prior to laying (Flanagan & Morris 1975, p. 59). The function of these spots is unknown. Eggs of the great tit *Parus major*, which vary greatly in spotting pattern between, but not within, clutches (Mänd 1988; Gosler 1993), are typical. The Edward Grey Institute's population study of the great tit in Wytham Woods near Oxford allowed us to study inheritance of eggshell patterning by examining

many clutches laid by identified females and lineages over several years. Here, we report findings that strongly support the hypothesis that egg pigmentation is under genetic control, inherited specifically via the female line.

2. METHODS

General methods of this long-term study have been published many times (e.g. Lack 1966; Perrins 1979; Gosler 1993). Brief

Table 1. *Repeatability of egg colour scores*

(Repeatability (intraclass correlation) of egg pigment intensity (I), distribution (D) and spot size (S). Observer repeatability is based on 100 clutches scored twice within three weeks by the same observer. All other repeatabilities are between years. 'Box' is repeatability of different pairs in the same nest-box. 'Male' is repeatability of different females with the same male. Three estimates of female repeatability are shown: DM, females with different males; ALL, across all females; CY, birds laying in consecutive years. Where possible, repeatabilities were calculated both including (+pw) and excluding (-pw) pure white clutches.)

	<i>n</i> groups (<i>n</i> clutches)	<i>I</i>	<i>D</i>	<i>S</i>
observer (+pw)	100 (200)	0.806	0.597	0.733
observer (-pw)	96 (192)	0.768	0.869	0.759
box	119 (312)	-0.042	0.000	-0.084
male	65 (142)	0.096	-0.048	0.069
female DM (+pw)	156 (365)	0.661	0.515	0.510
female DM (-pw)	155 (362)	0.662	0.488	0.517
female ALL (+pw)	220 (560)	0.686	0.466	0.554
female ALL (-pw)	217 (551)	0.666	0.462	0.544
female CY (+pw)	85 (170)	0.820	0.525	0.652
female CY (-pw)	81 (162)	0.749	0.580	0.571

details follow. The Wytham great tit population nests almost exclusively in nest-boxes, which are more or less predator-proof (Perrins 1979). The present study was undertaken in the nest-box rounds called 'extra' (134 boxes), 'great wood' (105 boxes) and 'common piece' (48 boxes), covering some 100 ha (Minot & Perrins 1984). Nest-boxes were visited weekly from early April to record the progress of nest-building, egg-laying, incubation and hatching. Prior to incubation, the mean mass of at least three eggs in each clutch is recorded.

Since 1988, eggshell spot-patterns have been recorded by one observer (A.G.G.) for every clutch in the study area using three series of simple scores describing spot pigment intensity (I), distribution of spotting over the surface (D), and average spot size (S). Because of the consistency in appearance of eggs within a clutch (e.g. Gosler 1993, p. 71), single I , D - and S -values were recorded for each clutch. The criteria used for each score are illustrated in figure 1. Note that in each case '0' is a pure white egg. This means that a zero score is only truly continuous with the rest of its scale for pigment intensity (indicating no pigment), since a pure white egg cannot be scored for spot distribution or size. Therefore, unless otherwise stated, pure white clutches (score [I, D, S] = 0,0,0) were excluded from the analysis. In 35 clutches (3.2%), up to three eggs differed by more than a score unit from the majority (which resembled each other), and in 11 of these, the dissimilar eggs were pure white. In these cases, which may indicate intraspecific nest parasitism, the score value of the majority egg-type was used for analysis. Data collected between 1988 and 1996 are used in this paper.

At least a week after the eggs hatch, the parents are trapped at the nest and identified by a uniquely numbered British Trust for Ornithology leg ring. Thus their identity is not known when egg characters are recorded. The parents are aged (as first-year in the year after hatch, or older) and sexed from plumage (Svensson 1984). Wing and tarsus lengths are measured to 0.5 mm and the birds are weighed to 0.1 g on a 'Pesola' spring balance. Fat reserves (fat score) and muscle volume (muscle

score) are also recorded as measures of parental body condition (Gosler 1991, 1996). Nestlings are ringed and weighed on day 15 (hatch day = 1).

We shall show (see §3) that the three pattern scores are inter-correlated. Hence, as a summary measure of egg pattern, we have also used a single score consisting of the first principal component (PC1, explaining 56.7% of the total variance, where $PC1 = 0.634I - 0.560D + 0.533S$) of the correlation matrix of the original I , D - and S -values.

Shapiro-Wilks' tests showed that no pattern-score frequency distribution departed sufficiently from normality to invalidate the use of parametric statistics. Nevertheless, further validation from non-parametric correlation was used for the critical analysis of sex linkage. MINITAB 13 statistical software was used throughout, statistical treatments following Sokal & Rohlf (1995).

Repeatability represents the proportion of phenotypic variance due to genetic (V_G) plus general environmental (V_{Eg}) variance (Falconer 1981), and sets a ceiling for heritability. Repeatability of egg-colour traits (with and without pure white clutches) was calculated by intraclass correlation (Lessells & Boag 1987) of 560 clutches laid by 220 females, and repeated for the subset of females breeding with different males. These necessarily represent female repeatability among years. To reduce the time over which the repeatability was estimated, the calculations were repeated on 85 females that laid eggs twice in consecutive years. Following Van Noordwijk *et al.* (1981) and Van Noordwijk (1987), two potential general environmental effects were also assessed: a nest-box effect (repeatability of 119 boxes with 312 different pairs) representing an effect of variance between territories, and a male effect (repeatability of 142 different females with 65 males), which may be important because much of the female's food during egg development comes from the male (Royama 1966). Data rank deficiency and collinearity prevented simultaneous calculation of female, male and nest-box contributions. Observer error was estimated in the same way by scoring 100 clutches twice over a three-week period.

To determine whether egg-spot patterns were related to female age, size or condition, we constructed general linear models with I , D , S or PC1 as the dependent variable and a series of female attributes, together with year, as predictors. Year, mother identity and age were entered as factors; wing length, tarsus length, female mass, fat and muscle scores as covariates.

Clutch size and egg mass both vary greatly through the laying season (in the Wytham great tit population) in relation to changes in food availability and quality (Perrins 1979). We therefore used ANCOVA to examine whether patterning traits varied with date (where 1 April = 1) through the season or with clutch size. Year, and the year \times date interaction were also fitted.

We determined the lines of inheritance from the correlation between daughter and mother, and daughter and (maternal and paternal) grandmother trait values. Correlations with grandmothers were calculated to test for a contribution through the male line, because although the father cannot influence these traits directly, genes from the paternal grandmother could. Formal estimation of narrow-sense heritability (Falconer 1981) was also carried out by regression across daughter-mother dyads, although this might underestimate heritability slightly due to the bounding effects of using score variables.

To avoid pseudoreplication in daughter-mother comparisons, whenever clutches laid by more than one descendent from a parental clutch were measured in a subsequent season, the mean of their values was used. Similarly, in daughter-grandmother comparisons, both the mother's brood means, and the

Table 2. *Inheritance of egg colour scores*

(Correlation coefficients (rank correlation in brackets) between daughters and their mothers, maternal and paternal grandmothers in independent great tit lineages for spot intensity (*I*), distribution (*D*) and size (*S*) and their first principal component (PC1) (see text).)

relatives	<i>I</i>	<i>D</i>	<i>S</i>	PC1
daughter–mother (<i>n</i> = 167)	0.307 <i>p</i> < 0.0001 (0.308 <i>p</i> < 0.0001)	0.226 <i>p</i> < 0.01 (0.218 <i>p</i> < 0.01)	0.196 <i>p</i> < 0.05 (0.198 <i>p</i> < 0.05)	0.344 <i>p</i> < 0.0001
daughter–maternal grandmother (<i>n</i> = 84)	0.219 <i>p</i> < 0.05 (0.336 <i>p</i> < 0.01)	0.175 n.s. (0.218 <i>p</i> < 0.05)	0.218 <i>p</i> < 0.05 (0.250 <i>p</i> < 0.01)	0.323 <i>p</i> < 0.01
daughter–paternal grandmother (<i>n</i> = 77)	−0.036 n.s. −0.060 n.s.	0.159 n.s. 0.177 n.s.	−0.020 n.s. −0.024 n.s.	0.011 n.s. —

grandmother's brood means were calculated. While this reduces sample size, it produces a series of unreplicated lineages of one or two generations. Data were pooled across years in repeatability and heritability analyses because year effects were trivial or absent compared with female effects.

3. RESULTS

In total, 1104 great tit clutches were scored for pattern between 1988 and 1996. Females (*n* = 654) were identified for 994 of these. These clutches produced 7357 fledged young from 820 broods (863 clutches) where the mother was identified. This represents the potential pool of offspring for heritability analysis.

Across the 654 identified females, taking the first clutch for each when more than one was recorded, the three score series were significantly intercorrelated (*I* and *D*, $r_{646} = -0.403$; *I* and *S*, $r_{646} = 0.434$; *D* and *S*, $r_{646} = -0.231$; $p < 0.001$ for all); further ANCOVA showed that these correlations were consistent in all years. So when spots were scored as more evenly distributed, they tended to be scored as smaller and paler. These correlations could reflect an optical interference between spot intensity, distribution and size. For example, a greater concentration of spots might give the impression that they are darker when they are not. However, this would not undermine the analyses of repeatability and heritability, which follow, and are taken into account explicitly in our use of PC1. Across 574 weighed first clutches, *I*, *D* and *S* scores showed no correlation with mean egg mass ($r_{572} < 0.1$, all n.s.), including or excluding pure white eggs.

Repeatability estimates are given in table 1. Observer repeatability (excluding four pure white clutches) was highly significant at around 80% (all $p < 0.0001$). Nest-boxes showed no discernible repeatability. Male repeatability was negligible (and none significant statistically), although a repeatability of 9.6% for pigment intensity, not reflected in the repeatability of females that changed male partners, may indicate a weak effect of diet, delivered by the male, on this trait. Across all clutches and years, female repeatability was *ca.* 45–70%, but increased to 50–80% when only clutches laid in consecutive years were considered. Because observer repeatability must constrain observed female repeatability (and female identity is unknown when eggs are scored), this demonstrates that females are remarkably consistent in their egg patterns between years.

Most of the variance among clutches was attributable to the mother (88.8% of the variance in *I*, $F_{485,205} = 4.68$; 80.8% of *D*, $F_{485,205} = 2.23$; 86.2% of *S*, $F_{485,205} = 3.24$; and 87.9% of PC1, $F_{485,205} = 3.86$; all $p < 0.0001$). Year effects were very weak, accounting for 0.7% of the variance in *I* ($F_{7,205} = 2.41$; $p = 0.021$), 1.1% of *D* ($F_{7,205} = 2.08$; $p = 0.047$), 1.5% of *S* ($F_{7,205} = 3.78$; $p = 0.001$) and non-significant for PC1. No other female attributes were significant predictors of egg-pattern variation.

Across all clutches, we found no significant effect of clutch size on any trait, but all varied significantly with lay date (*I*, $F_{1,753} = 17.39$; $p < 0.0001$; *D*, $F_{1,753} = 19.06$; $p < 0.0001$; *S*, $F_{1,753} = 3.98$; $p = 0.046$; and PC1, $F_{1,753} = 21.75$; $p < 0.0001$). Inclusion of white eggs did not alter these results. *I*, *S* and PC1 tended to decline (spots paler and smaller) through the season, while *D* tended to increase (more evenly distributed). Despite their significance, the date effects on *I*, *D*, *S* and PC1 were weak, explaining only 2.2, 2.4, 0.5 and 2.7% of the variance of each, respectively. In addition, *D*-scores showed significant, but weak (explaining 2.3% variance), year effects ($F_{8,753} = 2.27$; $p = 0.021$). No interactions were significant.

Table 2 shows correlations between egg characteristics of daughters and their mothers, their maternal and paternal grandmothers. Significant resemblance is shown between the eggs of relatives on the female line across two generations, but not the male, *i.e.* daughters' eggs resembled those of their mothers and maternal grandmothers, but not those of their paternal grandmothers. Mother–daughter and mother–maternal grandmother correlations of PC1 did not differ significantly (z -test, $\chi^2_1 = 0.029$; n.s.), but maternal and paternal grandmother correlations with daughters did differ significantly (z -test, $\chi^2_1 = 4.06$; $p < 0.05$). Assuming inheritance entirely from the maternal line (*i.e.* $h^2 = b$; Falconer 1981), regressions of daughter on mother suggest heritabilities of 0.32 ± 0.077 (s.e.) for *I*, 0.23 ± 0.076 for *D*, 0.19 ± 0.073 for *S*, and 0.35 ± 0.073 for PC1.

4. DISCUSSION

The function of eggshell patterning in the great tit is unknown. If egg-spotting were merely a by-product of excretion, we might expect it to be essentially random, and therefore to show little repeatability within females. However, great tit spot patterns showed the high

repeatabilities of other egg characteristics (e.g. volume; Van Noordwijk 1987).

Avian egg pigments are actively transported across the epithelial cells of the shell gland and deposited during calcification of the eggshell in the outer part of the calcified layer and the cuticle of the egg (Solomon 1987). Little is known about the mechanism of pigment deposition that results in the faithful reproduction of pigment patterns in eggs laid in successive years. However, we do know that as the egg calcifies, it spirals within the shell gland and specific epithelial cells within the shell gland wall deposit precise amounts of pigment.

The mechanics of pigment deposition suggest that while environmental factors, such as food, might influence the biosynthesis of egg-spotting pigments, we might expect the sites of their deposition to be less plastic because they depend on the physical distribution of the pigmenting epithelial cells concerned. Thus, while nutrition might affect pigment intensity, we might expect the size and distribution of spots to be largely fixed within and between clutches of a given female. Consistent with this, we found no territory (nest-box) effect on any trait and a mere suggestion (non-significant) of a male effect on spot intensity.

The lack of consistent environmental effects implies that resemblance among relatives reflects genetic similarity. We found significant egg-pattern resemblance across two generations of the maternal line of great tits, but no discernible resemblance across the paternal line.

Our aim in this paper has been to demonstrate the likely involvement of female sex-linked genes in the determination of eggshell patterning in birds, rather than to shed light on the function of those patterns. The ultimate reasons why pigment spots are reproduced so faithfully between eggs in a non-mimic, non-host species, and indeed why pigmentation is under genetic control, remain obscure. Indeed, because a large environmental component to phenotypic variance of host egg patterns should hamper the ability of a brood parasite to mimic eggs, one might even expect selection to favour a loss of genetic control in parasitized species. Even so, it may be that the sporadic occurrence of inter- and intraspecific nest parasitism through avian evolution has resulted in the inheritance of eggshell patterning being conserved.

Nevertheless, we conclude that genetic inheritance is by far the most parsimonious explanation of eggshell patterning in the great tit, in which case the relevant genes lie on the female sex-specific W chromosome. Although we cannot prove that the inheritance of egg patterns in egg-mimic species (e.g. cuckoos) is female sex linked, as suggested by Punnett (1933), we have demonstrated for the first time, to our knowledge, that such a system exists.

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