

MALE SITE TENACITY REVEALS AN ENVIRONMENTAL
CONTRIBUTION TO EGG SIZE IN PIED FLYCATCHERS
FICEDULA HYPOLEUCA

LA FILOPATRÍA DE LOS MACHOS REVELA UNA CONTRIBUCIÓN
AMBIENTAL AL TAMAÑO DEL HUEVO EN EL
PAPAMOSCAS CERROJILLO *FICEDULA HYPOLEUCA*

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It is an usual assumption in bird studies, implicit in most cases, that many reproductive traits (breeding date, clutch size, egg size) are entirely 'female' traits, ones on whose determination males would have little or no genetic or environmental control (see Sheldon *et al.*, 2003 for a recent exception). However, both sexes may contribute to traits they do not express, both genetically and environmentally. For instance, although the male genotype does not influence clutch size, male great tits *Parus major* pass on genes for clutch size to their daughters (van Noordwijk *et al.*, 1981). On the contrary, quantitative genetic analyses using the grandoffspring and offspring generations have shown genetic and maternal inheritance, but no paternal genetic influence on egg size in the pied flycatcher *Ficedula hypoleuca* (Potti, 1993, 1999). However, egg and clutch sizes are also likely examples of environmentally-influenced, potentially male-mediated traits only expressed in females that, while being strongly dependent on female 'identity' and condition, may proximately also depend on the resource-holding potential of their male mates, i.e. on habitat quality, food abundance or nest-site adequacy for laying females (Nisbet, 1973).

An indirect role for males on egg size determination may be given by the quality of their

territory, which may influence the size of the eggs the females will form therein (Potti, 1993). A more direct role for males in influencing egg size may be through courtship feeding while the female is forming eggs (e.g., Nisbet, 1973), in the sense that increased food resources directly supplied by males to their pairs while forming eggs would be reflected in improved female condition and thus a larger than average egg size (Christians, 2002).

In the pied flycatcher there are strong female identity effects (including permanent genetic and long-term environmental variation, as well as maternal effects) and effects of female body condition, on the egg size that females produce in a given breeding attempt (Potti, 1993, 1999). No consistency of egg size within individual males was found in an earlier work with smaller sample sizes (four study years: Potti, 1993), leading to the preliminary conclusion that an influence of males on egg size did not exist. Here I re-examine this question with an extended data set of 16 years which allows further testing of the possible role of males in the determination of egg size. For doing this I use repeatability, a useful parameter which gives in a statistic (range 0 - 1) the 'consistency' of measurements in relation to a factor which often, as in this case, is an indi-

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vidual's identity (e.g., ring number). Any significant consistency in a trait, as egg size herein, may indicate the importance of an individual's identity for explaining variation in it. Therefore, I examine the repeatability of egg size of different females paired to the same individual male in different years. This value should be close to zero if males (or their territories) have no influence on egg size.

I studied the egg size of pied flycatchers breeding in nest boxes in an oak (*Quercus pyrenaica*) forest in La Hiruela (Madrid) during 16 years (1988 to 2006, with no egg data for the years 1996, 2002 and 2003). Repeat clutches were discarded from this study. All eggs in clutches (range 3 - 8) were measured during incubation with callipers to the nearest 0.1 mm for maximum length (L) and breadth (B) and a mean egg volume (V , in cm^3) was calculated for each clutch using Hoyt's (1979) formula ($V = 0.51 * L * B^2$). The greatest component of variation in egg volume occurs between females, while within-clutch and yearly variation are small (Potti, 1993, 1999). Egg dimensions and volume are highly consistent both within clutches and across years and do not vary across the range of female ages (Potti, 1993). Therefore, unique values of egg volumes were obtained by averaging egg volumes within a clutch. Almost all breeding males and females were captured while they were incubating or feeding nestlings, ringed and released. I measured height and width of the male forehead patch with callipers to the nearest 0.05 mm and calculated patch area as a rectangle. Residuals from the within-year regressions of female body weight recorded at incubation on tarsus length were used as indices of body condition.

For the analyses of the putative male influences on egg size I first selected those males that had repeated records of egg size in the nests they were attending. After excluding all remated pairs and secondary nests (Potti and Montalvo, 1993), repeatability analyses were conducted to look for any consistency of av-

erage egg dimensions and volume in relation to male identity. Repeatabilities were computed by means of the intra-class (within-individual) correlation (r), using variance components from one-way ANOVAs with an individual's identity as factor (Lessells and Boag, 1987). There were repeated records on the size of eggs in their nests for 261 males, whose females' eggs were measured in 2 to 6 times (years). A small, yet statistically significant contribution of male identity to egg size was apparent, as both egg breadth ($r = 0.16$, $F_{260,402} = 1.48$, $P < 0.001$) and egg volume ($r = 0.08$, $F_{260,402} = 1.22$, $P = 0.036$) were repeatable within individual males. Egg length, on the contrary, showed no consistency within males [in fact, a 'no sense' (Lessells and Boag, 1987) negative repeatability: $r = -0.03$, $F_{260,402} = 0.93$, $P = 0.75$].

Therefore, males of the pied flycatcher are consistent to some degree in the average egg size and one of its dimensions along their yearly breeding attempts, pointing to a small, apparent significant influence of males on the size of the eggs their females lay in their territories (i.e., nest sites; von Haartman, 1956). In turn, the presumed male influence could have an environmental direct or indirect origin that I will briefly discuss below. In the only previous study that, to my knowledge, has analysed the putative influence of males on their female's egg size, van Noordwijk *et al.*, (1980) found similarly low repeatabilities of egg size within great tit *Parus major* males of 8 % for egg length, 19 % for egg breadth and 12 % for egg volume, although in this case none of them reached statistical significance.

For further confirmatory analysis, I selected only those pairs where both the male and the female had repeated and independent (i.e., all rematings excluded) records of the egg size in their nests and subjected the data to variance component analyses using Satterthwaite's method for computing degrees of freedom (see Sheldon *et al.* (2003) for the same approach to address the hypothesis of a male

contribution to breeding dates in the collared flycatcher, *Ficedula albicollis*). The repeated egg size of 258 females and 144 males returned non-significant components of variance for males ($P > 0.10$ in all cases), while yielding highly significant components of variance for females. These were 60.4 % for egg breadth ($F_{285,168.4} = 3.44$, $P < 0.001$), 74.4 % for egg length ($F_{285,167.5} = 5.64$, $P < 0.001$) and 64.9 % for egg volume ($F_{285,167.7} = 3.95$, $P < 0.001$).

Given that both males and females show strong site tenacity in my study population (Montalvo and Potti, 1992), significant repeatabilities in the egg sizes of different females mated to a male may be interpreted in terms of constancy of male and/or habitat quality (Potti, 1993). As the median distance moved by males across successive breeding seasons is about 110 m (Montalvo and Potti, 1992), it is likely that different females breeding with a particular male share very similar environmental conditions. These conditions, e.g. foraging substrates and niches, prey abundance, availability of suitable perches, etc., could be reflected in the daily intake of prelaying and laying females. In turn, this should affect to a certain degree the size of eggs they lay. This, of course, assumes that prey abundances are predictable (i.e., repeatable) across years, which is not known. Under this view, repeatabilities of egg size within males would be reflecting constancy of environmental/territory factors experienced by their female mates while forming the eggs. In support of this hypothesis, repeatabilities of egg dimensions (by different females and males) within the same individual nestboxes yielded very similar values (egg breadth: $r = 0.11$, $F_{203,510} = 1.43$, $P < 0.001$; egg volume: $r = 0.08$, $F_{203,510} = 1.22$, $P = 0.036$; egg length: $r = 0.01$, $F_{260,402} = 1.05$, $P = 0.34$) to those reported within males irrespective of their nestbox. Further, as seen above, the apparent influence of males on egg size vanished in the variance component analysis with repeated

male and female measurements of egg size, giving hold to attributing a certain role in egg size determination in this population to constancy of environmental conditions, rather than to male identity itself. Thus, habitat characteristics, rather than males, probably are a source of variation in the egg size of pied flycatchers, which does seem indeed to be a 'female' trait, as indirectly tested here.

There is at least one alternative explanation to the consistency of egg dimensions within males in that their courtship feeding performance in the prelaying stage could have an influence on egg size while their females are forming eggs. Courtship feeding, or rather 'incubation feeding', may have a positive impact on a female's energetic schedule (e.g., Lifjeld and Slagsvold, 1986) although to my knowledge its role in the prelaying stage (Nisbet, 1973), the relevant one for egg size, has not been assessed in the pied flycatcher. Though I lack data on the frequency or importance of this behaviour in my population, for courtship feeding to be reflected in the eggs of different females would need that the male trait, i.e. their courtship feeding behaviour, would be consistently repeated across years. There is no information on the consistency of this behaviour, although it is known that other parental behaviours in birds may have a genetic component, as indicated by repeatability (Freeman-Gallant and Rothstein, 1999; Potti *et al.*, 1999) and heritability (MacColl and Hatchwell, 2003) analyses. However, if male parental behaviour were both consistent and responsible for an influence on their females' egg size we would also expect that different females paired with one particular, individual male were also repeatable in their body condition during incubation. This was not the case ($r = -0.04$, $F_{294,325} = 0.93$, $P = 0.74$), falsifying this hypothesis. Still another hypothesis would posit that males, by showing to females exaggerated sexual selected traits, may provoke differential investment of females in egg size (the differential

allocation hypothesis; Burley, 1986). However, size of the white forehead patch, the main sex trait candidate for signalling male attractiveness in this population (Potti and Montalvo, 1991) is unrelated to egg volume (Ancova with female condition and forehead patch size as covariates and study year as a random factor; year effect: $F_{11,512} = 3.61$, $P < 0.001$; effect of female condition: $F_{1,512} = 34.23$, < 0.001 ; effect of forehead patch size: $F_{1,512} = 0.09$, $P = 0.76$). In conclusion, the chances are high that a direct 'male performance' contribution to egg size in the pied flycatcher is very small or absent. In site-tenacious populations, as that from this study (Montalvo and Potti, 1992), male and territory (nest site) factors may heavily interact, resulting in potentially confusing patterns as seen here for a within-male repeatability of egg size that was most likely caused by constancy of habitat quality.

RESUMEN.—*En este estudio se encuentran consistencias (repetibilidades) bajas, pero estadísticamente significativas en el tamaño del huevo (16 % para la anchura, 8 % para el volumen) en los nidos de 261 machos de papamoscas cerrojillos que se reprodujeron con diferentes hembras entre dos a seis años. Otros análisis indican, sin embargo, una contribución directa del territorio (nido) y que la contribución de los machos al tamaño del huevo es descartable. La consistencia encontrada parece deberse a la acusada filopatria de los machos, que origina que hembras diferentes críen en territorios de calidad similar. Se confirma así una contribución ambiental al tamaño del huevo enmascarada bajo una aparente contribución masculina a este carácter.*

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