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From mating to laying: genetic and environmental variation in mating dates and prelaying periods of female pied flycatchers *Ficedula hypoleuca*

Jaime Potti

Potti, J., Departamento de Biología Animal, Universidad de Alcalá, E-28871 Alcalá de Henares, Madrid, Spain

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The duration of the period comprised between mating and the onset of laying and its correlates and consequences for aspects of female breeding performance are investigated in a population of pied flycatchers studied for 5 years. That duration may represent a compromise between the selective pressure on females to breed as early as possible and the need for females attempting to breed to be in prime nutritional condition. It is shown that the duration of the prelaying period is shorter for late breeders, but is apparently unrelated to subsequent condition of the female and indices of breeding performance. A low, significant between-year repeatability ($R = 0.16$) in the duration of female prelaying period was detected. However, there was a large component of environmental, as opossed to genetic, variation which may reflect stochasticity affecting timing of breeding and age factors. Overall, the evidence supports models of strategic adjustment of breeding date to offspring prospects, rather than those based on condition-constrained breeding date.

1. Introduction

Among spring migrant passerine birds, an early arrival to the breeding areas enhances male and female reproductive success (Alatalo *et al*. 1981, Slagsvold 1986, Slagsvold & Lifjeld 1988, Andersson 1994, Møller 1994, Aebischer *et al*. 1996, Potti 1998a). While some of the fitness components contributing to increased success of the earlier-arrived males have been repeatedly documented (e.g., choice of better territories and increased mating opportunities) the main identified advantage of an early settlement from spring migration for female passerines is an early breeding onset, an obvious correlate of an early arrival (e.g., Alatalo *et al*. 1984, Potti & Montalvo 1991a, Lundberg & Alatalo 1992). Proximate routes for the fitness advantages accrued to females from an early arrival have been less investigated. Selection may have shaped the behaviour of females to time both their arrival to the breeding area and their onset of breeding so that the difference between both dates is optimal, assuring enough time and resources to be ready to commence breeding. The duration of the period between mating and laying, the *prelaying period* hereafter, may thus represent a compromise between the selective pressure to breed as early as possible (e.g., Winkler & Allen 1996, Verboven & Visser 1998) and a postulated need for females attempting to breed to be in prime condition (Price *et al.* 1988, Rowe *et al.* 1994).

Rowe *et al.* (1994) elaborated a model for adaptive seasonal decline in clutch size on the basis of a postulated conflict between the advantages of breeding early (greater offspring value) and those derived from delaying breeding (greater accumulated condition and hence clutch size; Drent & Daan 1980). Their model is based on the idea that clutch size and timing of breeding are probably constrained by parental condition, i.e. in any one season individuals in prime condition would typically produce larger and earlier clutches. As Rowe *et al.* (1994: 709) stated "... birds may arrive at breeding sites at different times but all in similar depleted condition. Those arriving early start to gain condition sooner than those arriving later, and they should therefore produce earlier and larger clutches. The interval between arriving at the breeding site and production of the clutch (...) will be correlated". Positive relationships between the duration of the prelaying period and indices of female breeding performance, namely a higher mass or better condition during the incubation, and/or a larger clutch size and increased recruitment rate are therefore predicted by this model. On the basis of evidence on prelaying periods and laying dates by Lundberg & Alatalo (1992: p. 64), the case of Scandinavian pied flycatchers (*Ficedula hypoleuca*) was presented by Rowe *et al.* (1994) as supporting evidence for their model on condition-dependent breeding time.

Here, I document variation in the duration of the prelaying period of female pied flycatchers in a southern European population studied for five years. I test predictions derived from Rowe *et al.*'s (1994) model regarding relationships of the prelaying period with date of the season, breeding performance and nutritional condition. I also focus on variation in the prelaying period from the point of view of its consistency or stability within females, in an attempt to estimate its degree of genetic and environmental variation by means of repeatability and heritability estimates based on familial resemblance.

2. Material and methods

I studied a population of pied flycatchers breeding in nest boxes in a mature deciduous (*Quercus pyrenaica*) forest in La Hiruela, central Spain, during the breeding seasons of 1989–1991 and 1993–1994. After the first males arrived from spring migration, nest boxes were checked daily to examine their contents. Females arrive about one week later than males and old females before young ones (Potti & Montalvo 1991a, Lundberg & Alatalo 1992). Only females paired with monogamous males (Potti & Montalvo 1993) were entered into the computations. I assigned the *mating date* of a female as the first day there were clear signs of nest building (Slagsvold & Lifjeld 1988, Potti & Montalvo 1991a, Lundberg & Alatalo 1992). Mating dates are used as indices of female phenology. The prelaying period was computed as the time (in days) elapsed between mating and laying dates (defined as the day the first egg in the clutch was laid). I recorded clutch size, and numbers of hatched young and local recruits. From 1989 to 1991, I also scored the onset of incubation which may vary between starting to incubate on days –3 to 0, day 0 being that of clutch completion (Potti 1998b).

Females were captured around the 6th or 7th day of incubation, aged as either first year birds or older, individually colour-ringed, measured and released. Immigrant birds aged as "older" at first capture were assigned a minimum age of two years (Potti and Montalvo 1991b). Females were measured for tarsus length (Potti & Merino, 1994a) and weighed with a spring balance to the nearest 0.1 g. Body condition during the incubation was assessed as the within-year residual of significant regressions of mass (corrected for significant variation with daily time of capture; Potti & Merino 1995) on tarsus length. Except in 1993, all eggs (range 3–8) were measured for maximum length (L) and breadth (B) and an average egg volume (V, in cm^3) was calculated for each clutch using Hoyt's (1979) formula ($V = 0.51 \times L \times B^2$).

Previous breeding experience was scored as the number of years (0, 1, 2 or > 2) a female had bred in my study area before a given year. A few females skipped one year and were scored as breeding in that year because they probably bred in natural holes (J. Potti, unpubl.). Survival was approximated by local recaptures or resightings in later years. Capture and identification efforts of adults were intensive and constant throughout years and, furthermore, this population has one of the highest return rates ever reported in the literature on the species (Lundberg & Alatalo 1992, Mon-

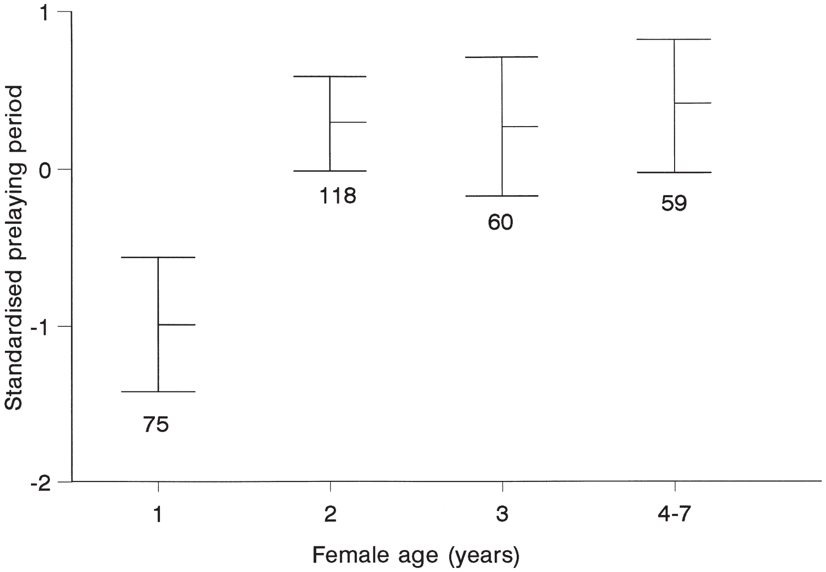

Fig. 1. Variation in the prelaying period (in days, standardised for yearly variation) with age in female pied flycatchers. Shown are means ± S.E. Figures below bars are sample sizes.

talvo & Potti 1992) making reliable the use of return rates to ascertain survival.

To assess the stability or consistency of the prelaying period within females as they age, I performed repeatability analyses (Falconer 1986, Boag & van Noordwijk 1987). Repeatability is estimated by making repeated (annual, in this case) records in a sample of females and then calculating the ratio of the among-females variance to the sum of both the among-females and within-female variances (R, the intraclass correlation coefficient; Sokal & Rohlf 1981, Lessells & Boag 1987, Boake 1989). Components of variance are estimated by one-way ANOVA. The standard error of the repeatability was calculated following Becker (1984). A high repeatability indicates that variation within females is much smaller than among different females. Repeatability is low if measurements within females are very different.

The heritability was computed as twice the slope of the linear regression of standardised data of female offspring on those of dams (Roff 1997). The standard error of the regression coefficient was also doubled. Data were averaged when there was more than one datum (from different years) from a particular individual. Values for sibships were also averaged in some cases with more than one female offspring per family.

Statistical tests (Zar 1996) are two-tailed. Sample sizes may differ due to missing data, most often due to predation by weasels (*Mustela nivalis*) and great spotted woodpeckers (*Dendrocopos major*). However, nests that were predated after the clutch was complete were included in the analyses, except for those were we used the number of young and recruits. Adult survival rates were unaffected by nest predation (Potti & Merino 1994b), hence all females were included in the tests. Known replacement clutches were excluded from computations. Means are given ± one standard deviation (S.D.) except where indicated.

3. Results

3.1. Correlates of variation in the prelaying period

The prelaying period ranged from 2 to 26 days (mean = 9.0 ± 4.5, $n = 312$) and varied significantly among years ($F_{4,311} = 52.81$, $p < 0.0001$). 1993 was the year where laying took more time to begin since mating (mean 13.2 ± 5.8 days), with some females starting to lay up to 10 days above the range for the rest of the study years. On the contrary, 1994 had the shortest prelaying periods (mean 4.3 ± 1.3 days). Therefore, the years when breeding started in a more advanced calendar date, as seen by average laying dates, were also those where mean prelaying periods were shorter ($r = -0.91$, $n = 5$, $p = 0.03$). Yearly variation in prelaying periods was accounted for in subsequent analyses by using the residuals from the above ANOVA.

Duration of the prelaying period was longer for older females ($F_{1,311} = 8.38$, $p = 0.004$; Fig. 1), although all pairwise significant differences involved yearling vs older females, there being no significant variation among females aged ≥ 2 years (Tukey *a posteriori* tests). Old females start laying earlier than one-year old females, however, and their longer prelaying periods are therefore due to their earlier arrival from spring migration when compared to yearling females (Lundberg &

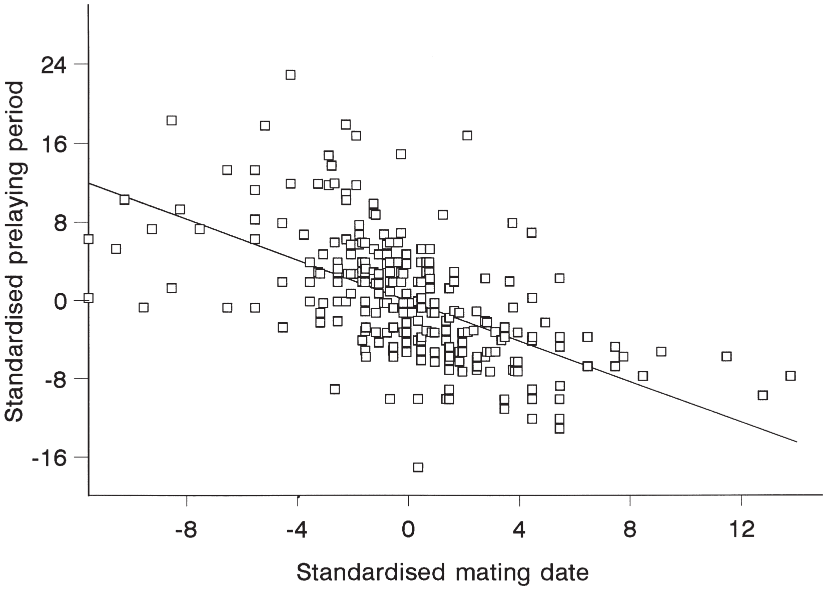

Fig. 2. Relationship between standardised mating dates and the duration of the prelaying period in female pied flycatchers. The least squares regression line is shown.

Alatalo 1992). Prelaying periods were shorter as the season advanced (regression coefficient, $b = –0.31$, $R^2 = 32.3\%$, $n = 312$, $p < 0.0001$; Fig. 2) and this relationship did not differ between young and older females (difference between slopes, $F_{1,309} = 0.08$, $p = 0.78$).

The duration of the prelaying period was unrelated to the timing of onset of incubation ($F_{3,130} = 0.34$, $p = 0.80$) or female mass ($r = 0.06$, $n = 290$, $p = 0.31$) and condition ($r = 0.04$, $n = 290$, $p = 0.47$) as scored during the incubation. Neither were prelaying periods associated to clutch size ($r = 0.02$, $n = 311$, $p = 0.70$), average volume of eggs laid ($r = –0.02$, $n = 288$, $p = 0.69$) and number of hatched young the female subsequently cared for ($r = 0.03$, $n = 280$, $p = 0.60$). Apparently, longer prelaying periods were associated to a greater number of recruits ($r = 0.19$, $n = 121$, $p = 0.04$) and to the chances of recruiting at least one young in the following years ($F_{1,120} = 4.14$, $p = 0.04$). However, this was entirely due to the fact that recruitment rate is significantly lower for late-breeding females (Potti & Montalvo 1991b; J. Potti, unpubl.) which are those with shorter prelaying periods (Fig. 2). The relationship disappeared when number of recruits was standardised for the date of the season by using residuals from the linear regression of recruit number on hatching date ($r = 0.03$, $p = 0.73$).

The duration of standardised prelaying periods was unrelated to female survival until the following year ($F_{1,311} = 0.39$, $p = 0.54$). There was an apparent significant relationship between the duration of prelaying periods and previous breeding experience ($F_{3,311} = 2.81$, $p = 0.04$). However, this was confounded by the strong relationship of prelaying period to female age and the covariation of age and breeding experience. The correlation disappeared when the test was made with old (≥ 2 years) females with variable degrees of previous breeding experience ($F_{3,236} = 0.96$, $p = 0.41$).

3.2. Ontogenetic and genetic variation in the prelaying period

The stability of prelaying periods across subsequent (yearly) breeding attempts was examined by repeatability analyses. There is a significant repeatability of female laying dates ($R = 0.15$, J. Potti, unpubl.). As prelaying periods are bound by mating and laying dates, I first examined if there is a significant consistency of mating dates within individual females. The repeatability of mating dates within individual females, standardised for yearly and female age variation, was significant ($R = 0.29$, S.E. $= 0.17$, $F_{76,169} = 1.88$, $n_0 = 2.21$, $p = 0.002$). However, there was no significant resemblance in the mating dates of mothers and daughters, the heritability being $h^2 = 0.41 \pm$

(S.E.) 0.38 ($p = 0.29$, $n = 36$ families).

Given that mating and laying dates are consistent within females across years, I expected to find a significant repeatability of prelaying periods within females. While the consistency of raw data was nil ($F_{76,169} = 0.69$, $R = –0.16$, S.E. = 0.10, $p = 0.95$) when data were standardised for variation with year and female age, there was a low but statistically significant within-female repeatability of prelaying periods ($R = 0.16$, $F_{76,169} = 1.43$, S.E. = 0.10, $p = 0.049$). In conclusion, female identity only explains about 16% of the between-year individual variance in the duration of the prelaying period, the main source of variation in the prelaying period lying in unaccounted variation besides female identity.

There was no significant resemblance between the prelaying periods of mothers and daughters, the estimate of heritability being not significantly different from zero ($h^2 = 0.57 \pm$ (S.E.) 0.50, $p = 0.27$, $n = 36$).

4. Discussion

As in Lundberg and Alatalo's (1992) study of Scandinavian pied flycatchers, I also observed that the time elapsed from mating to laying in pied flycatcher females in a southern European population was shorter for late breeders. I expected that longer prelaying periods would be reflected in improved female condition and/or enhanced breeding performance, as scored by laying date, clutch size and/or recruitment. However, the duration of this period was unrelated to all these surrogates for fitness. Older females had longer prelaying periods than young females due to their earlier arrival from migration, the most strong correlate of a long prelaying period. I also detected a high within-female plasticity in both mating dates and the duration of the prelaying period of females as they age. Consistent with the low repeatabilities (Falconer 1986; but *see* Aragaki & Meffert 1998), no significant heritabilities could be found in either female mating dates or duration of prelaying periods.

No support for the hypothesis that longer prelaying periods would be reflected in improved female condition, as scored by mass scaled to size, was found. Theoretically, a longer period from mating to laying should give females increased experience with nesting and foraging areas and more time to gather reserves, which could be reflected in enhanced performance afterwards. This could be especially important for females lacking previous breeding experience or knowledge of the area. However, there were no clear advantages, in terms of female condition, to the longer periods elapsed from mating to laying that were characteristic of the first females to arrive from spring migration, irrespective of their previous experience. Those females were in fact most successful, but this was due to their age and nesting phenology (Winkler & Allen 1996), not to their relative delays between mating and laying.

There were no obvious correlates of variation in prelaying periods apart from those derived from the age of the female, permanent genetic and/or environmental variation, and those due to the season's date *per se*. As the American Tree Swallows (*Tachycineta bicolor*) studied by Winkler and Allen's (1996), the studied population of pied flycatchers does not seem to fulfill one of the key underlying assumptions of Rowe *et al.*'s (1994) model, namely condition-dependent breeding time, at least when female body condition is scored as mass or size-independent mass (J. Potti, unpubl.; cf. Askenmo 1982, Andersson & Gustafsson 1995). Moreover, the extent to which that model may apply to passerines in general (Winkler & Allen 1996) is unclear, where most species could be near the "income" end of the avian life-history continuum (Drent & Daan 1980) which goes from "income" breeders (those using resources ingested near laying time) to "capital breeders" (those basing their breeding on resources stored in advance to laying). Pied flycatchers form their eggs on direct input from foraging (Ojanen 1983) and thus should be nearer the "income" group in this spectrum. Food is usually thought to directly influence the onset of laying by affecting the bird's energy balance (Perrins 1970), and there exists now ample, yet controversial, experimental evidence for a role of food as a proximate trigger of laying date in some bird populations (reviewed by Winkler & Allen 1996, Nager *et al.* 1997). As the latter authors point, however, feeding experiments with pre-laying great tits (*Parus major*) showed that birds provided with supplemental food waited a considerable time before starting the laying, and many of them laid even later than birds without additional food (Nager *et al.* 1997; *see* also Svensson & Nilsson 1995). Therefore other factors than food evidently affected the decision to start breeding. Nager *et al.* (1997) hypothesised that in great tits the natural pattern of changes in food availability may provide important cues to the most suitable time to rear young (Lack 1954). Although even pied flycatchers, unlike Great Tits, are long-distance migrants presumably hard-pressed by the short duration of their breeding season (Ojanen 1982), a similar explanation could also apply to them. In addition, variation in prelaying periods in the pied flycatcher might also reflect to some degree a variation related to the stochasticity of environmental factors — weather (Järvinen & Väisänen 1984), phenological state of development of the breeding habitat (Slagsvold 1977, 1982), and constraints due to sociosexual interactions (e.g., Breiehagen & Slagsvold 1988, Dale & Slagsvold 1995) for which there exists circumstantial evidence that they may lead to delays in egg laying in this species (Lundberg & Alatalo 1992: p. 80).

The results here reported suggest a considerable degree of individual plasticity in the duration of the prelaying period in pied flycatchers. Female pied flycatchers may fine-tune laying time, i.e. start laying in the date of the season so that one component of fitness (recruitment) is maximised. Some females, usually the earliest, may “elect” to postpone laying (Winkler & Allen 1996, Nager *et al.* 1997) even though being physiologically capable of doing so (cf. Perrins 1970), therefore having longer prelaying periods, in the face of selection against a “too early” start of breeding (Nilsson 1994), i.e. stabilizing selection on laying date (Svensson 1997, J. Potti, unpubl.). On the contrary, the latest females to settle to breed are under strong directional selection, due to the steadily diminishing chances of recruitment for late breeders (Hochachka 1990, Lindén *et al.* 1992), which also holds in this species (Potti & Montalvo 1991b). One may argue that the condition-constrained component of lay date determination might apply to late-arrived females, who are likely to be those in poorest condition. However, in my population, where this correlation is also observed, this is entirely due to they pertaining to both the youngest and oldest age classes (J. Potti, unpubl.). Furthermore, females settling late to breed probably have plenty of food in their territories and, all else being equal, should have few constraints on attaining breeding condition, “allowing” themselves short prelaying periods. The evidence here presented, however, supports instead the hypotheses that food availability at prelaying and laying times (Nager & van Noordwijk 1995, Nager *et al.* 1997), and/or factors correlated with temperature (e.g., bud burst, leaf phenology, caterpillar abundance; Nager & van Noordwijk 1995, Svensson & Nilsson 1995), give information on the environment allowing birds to anticipate conditions later in the season rather than physiologically restricting egg and clutch formation.

The low consistency of individual females in their prelaying periods likely reflects the high general environmental variation sketched above, while leaving open the possibility for the existence of a genetic variation for the duration of prelaying periods (Falconer 1986). As defined in this study, these are bound by laying and mating dates, hence genetic and environmental variation in one or both of these dates are added in the route to their genetic determination: environmental variance is added at each step, so that even though there may be a genetic component to the prelaying period via its connection with heritable traits this should be small (Price and Schluter 1991, Roff 1997). In fact, laying dates may retain a heritable component in my pied flycatcher population (J. Potti, unpubl.), as it has been demonstrated for other bird populations (e.g., van Nooordwijk *et al.* 1981, Blondel *et al.* 1990). Nevertheless, a result common to this study and a previous one (Potti 1998a), that the repeatability of male and female arrival date from spring migration is, at most, low, indicates that the heritability of traits related to settlement from spring migration also should be low (Falconer 1986). Very large sample sizes will thus be required to estimate them with reasonable degrees of accuracy (*see* Boake 1994, Potti 1998a). As this study has shown, a further challenge to understand individual decisions on breeding time is to incorporate aspects of phenotypic quality as age and experience into models of lay date and clutch size optimization in birds to make them more realistic (Clutton-Brock 1988, Newton 1989, Sæther 1990, Desrochers & Magrath 1993, Forslund & Pärt 1995, Winkler & Allen 1996).

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