# Male decisions or female accessibility? Spatiotemporal patterns of extra pair paternity in a songbird

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Extra pair paternity is widespread in birds, but its high variability across years, populations, and species is to a great extent unresolved. Here we explored, during 2 breeding seasons, population and individual accessibility to fertile females at different spatiotemporal scales in a population of pied flycatchers (*Ficedula hypoleuca*) to understand whether individual patterns of extra pair paternity were due to adaptive individual behavior or ecological constraints. Our aim was to comprehend variation in extra pair paternity population patterns through the understanding of individual behavior. At the population level, extra pair paternity probability decayed with distance between nests. At the individual level, however, males engaged in extra pair paternity with distant (up to 390 m) females despite the fact that there were often fertile females in closer territories. Extra pair paternity cases occurred mostly during egg laying and the incubation of the extra pair male's social female despite that other neighboring females were fertile before and after these periods. Results suggest a male strategy to maximize reproductive output by guarding their social females during their peak of fertility, seeking extra pair paternity afterwards and investing in parental duties once their social nestlings hatch. This may explain why extra pair paternity rate was higher in the year with lower breeding synchrony, because this allowed early-breeding males to have more extra pair paternity opportunities after their social mate laying onset. This study highlights the necessity of considering the social contexts of individuals at the spatiotemporal scales at which extra pair paternity takes place to understand variation in extra pair paternity patterns at the individual and population levels. *Key words:* breeding phenology, *Ficedula hypoleuca*, genetic polygamy, pied flycatcher, population density, synchrony. [*Behav Ecol*]

## INTRODUCTION

Multiple paternity is common in animals (e.g. birds, Griffith et al. 2002; fish, Sefc et al. 2008; mammals, Cohas and Allainé 2009). Although monogamy is the commonest breeding system in birds (Lack 1968; Birkhead and Møller 1992; Bennett and Owens 2002), many studies in the last 2 decades in socially monogamous species have shown that genetic polygamy (i.e. extra pair paternity; EPP) is widespread (Griffith et al. 2002). Studies on EPP have typically focused on the adaptiveness of this behavior for both males and females under cost-benefit frameworks (reviewed in Jennions and Petrie 2000; Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007; Mays et al. 2008). However, the large variation in EPP rates among years and populations of the same species remains largely unexplained (Petrie and Kempenaers 1998; Griffith et al. 2002), although it strongly suggests a major role for ecological factors in shaping EPP patterns within species (Griffith et al. 2002). For instance, environmental conditions could clump breeding dates and increase the temporal overlap of the reproductive activities of different individuals, thus potentially affecting the occurrence of EPP (Westneat and Stewart 2003; Westneat and Mays 2005). Here we highlight the importance of addressing individual behavior

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in trying to explain variation in population patterns in EPP under specific ecological and social settings. Understanding how individuals make their choices in different conditions (e.g. to prioritize mate guarding vs. extra pair copulations; EPC) may help to explain why the same population displays contrasting patterns in EPP under contrasting scenarios.

Ecological factors such as breeding density or synchrony have been traditionally proposed as main determinants of EPP rates at the population level (e.g. Birkhead and Biggins 1987; Stutchbury and Morton 1995; Weatherhead 1997; Westneat and Sherman 1997; Stutchbury 1998; Richardson and Burke 2001; Johnsen and Lifjeld 2003; Lindstedt et al. 2007). However, the influence of these factors on EPP rates is not well supported in comparative studies (e.g. Birkhead and Biggins 1987; Westneat et al. 1990; Stutchbury and Morton 1995; Westneat and Sherman 1997; Stutchbury 1998). Likewise, contradictory results also abound in intraspecific studies (Dunn et al. 1994; Weatherhead 1997; Richardson and Burke 2001; Lindstedt et al. 2007). A number of studies have found a positive influence of breeding density on the frequency of EPP by enhancing the encounter rate between potential mates (Richardson and Burke 2001; Stewart et al. 2006), whereas others have not found such an effect (Dunn et al 1994; Tarof et al. 1998). Predictions on the effects of breeding synchrony on EPP rates may vary depending on the behavioral strategies followed by each sex (Stutchbury and Morton 1995; Westneat and Sherman 1997; Stutchbury 1998). When females pursue EPCs, a high number of fertile females (and hence of displaying males) would tend to increase EPP rates by enhancing the ability of females to

simultaneously assess the quality of several potential males (e.g. Stutchbury and Morton 1995; Hoi and Hoi-Leitner 1997; van Dongen and Mulder 2009). Likewise, when EPCs are initiated by males, a high synchrony should raise the probability of encountering fertile females (Stutchbury and Morton 1995). However, the effect of breeding synchrony on EPP rates would depend on whether males prioritize assuring paternity in their social nests over searching for EPP (Birkhead and Biggins 1987; Westneat et al. 1990; Stutchbury and Morton 1995), as they usually are unable to simultaneously maximize paternity outside of and within the pair bond (Kokko and Morrell 2005). Moreover, strategies may differ among males as, for instance, a high concentration of breeding individuals may incite both high quality males to invest more in seeking EPP and low quality males to guard their mates more intensively. Both circumstances would tend to obscure the association between breeding synchrony and population density with EPP (Stewart et al. 2006). Thus, besides differences due to phylogenetic history (Griffith et al. 2002), the understanding of individual behavior (or rather, its lack thereof) may play a major role in the current discrepancies between studies in EPP rates and their interpretation.

Given that EPP emerges from the interaction among at least 3 individuals—a female, its social pair, and the extra pair male—only males and females co-occurring in space and time can eventually engage in EPCs (Westneat and Stewart 2003). Thus, focusing on individual behavior demands approaches at the spatiotemporal scales at which individuals make their choices (i.e. select among available possibilities; Chuang et al. 1999; Webster et al. 2001). Importantly, this detailed individual-level information can easily translate to the understanding of population patterns. For instance, if EPP only involves individuals from neighboring territories, the overall breeding synchrony of the population may not shape EPP opportunities of individuals if it does not lead to breeding synchrony between neighbors (Chuang et al. 1999). Spatial and temporal factors could further interact, for example, a negative relationship between EPP rates and synchrony may only occur under certain breeding densities (Thusius et al. 2001). Moreover, it is important to identify the extra pair male(s) in order to consider the breeding status of all individuals involved in EPP. This is because the likelihood of an extra pair fertilization will be likely influenced not only by factors affecting the behavior of an individual alone (its costs and benefits) but also by those affecting the behavior of all individuals involved in an EPP event (Westneat 1993; Westneat and Stewart 2003).

Here we studied the distribution of EPP events (EPPs) in 2 years with contrasting breeding synchrony in a Spanish population of pied flycatchers (*Ficedula hypoleuca*), a long-distance migrant passerine which establishes a territory around the nest site hole. Occurrence of EPP in this species is relatively common, with rates of extra pair young (EPY) varying across populations between 4 and 24% (Canal et al. 2011 and references therein). Thus, pied flycatchers exemplify the variation of EPP rates among populations and the discrepancies in determining the causes of that variation (Lifjeld et al. 1991; Gelter and Tegelström 1992; Rätti et al. 2001).

Here, we hypothesize a trade-off between mate guarding and seeking for EPCs in males (we assume EPCs are mainly male initiated, as suggested by previous work in pied flycatchers, Björklund and Westman 1983; Alatalo et al. 1987). Under this hypothesis, we predict that males will seek for EPCs preferably among neighboring females due to costs (loss of within-pair paternity) derived from searching for EPCs. Temporally, we predict more EPP events after the laying date of the extra pair males' social females as males would invest more in mate guarding during the fertile

period of their social female. To test this hypothesis we identified extra pair sires and analyzed the phenology of EPP events relative to the breeding stage of their social female, taking into account the spatiotemporal accessibility to fertile females for each male. Under this hypothesis, we also predict that breeding synchrony would negatively affect EPP rates at the population level. This is because if males invest in mate guarding during the fertile period of their social female a high synchrony of females' fertile period would reduce EPP rates in the population by decreasing the time available for males to engage in EPCs.

## MATERIAL AND METHODS

### Field work

The study was carried out during 2 consecutive breeding seasons (2005–2006) as part of a long-term study of pied flycatchers in central Spain (e.g. Potti and Montalvo 1991; Potti and Canal 2011). The study area consists of 2 plots 1.3 km apart, including 236 nestboxes (Figure 1). The plots are located in an old oak (*Quecus pyrenaica*) deciduous forest and a coniferous stand (mainly constituted by *Pinus sylvestris* and *P. pinaster*) with sparse old oaks. UTM coordinates of all nests were GPS referenced and distances among them calculated with Arcview (ESRITM 2000). Average (SD) distance among occupied nestboxes was 30 (14.1) m.

Field protocols have been described in detail elsewhere (Canal et al. 2011). Briefly, all nests were regularly checked every 3 days before the onset of egg laying and on a daily basis around hatching to ascertain laying date, clutch size, hatching date, and number of fledglings. Parent birds were captured with a nestbox trap while they were feeding 8-day-old nestlings. Fledglings were banded at 13 days of age. Blood samples were taken from all individuals by puncturing the brachial vein and stored in ethanol.

### Molecular methods

A total of 1,567 individuals were used in parentage analyses: 531 chicks and 212 adults (113 females and 99 males) from 113 nests in 2005, and 595 chicks and 229 adults (120 females
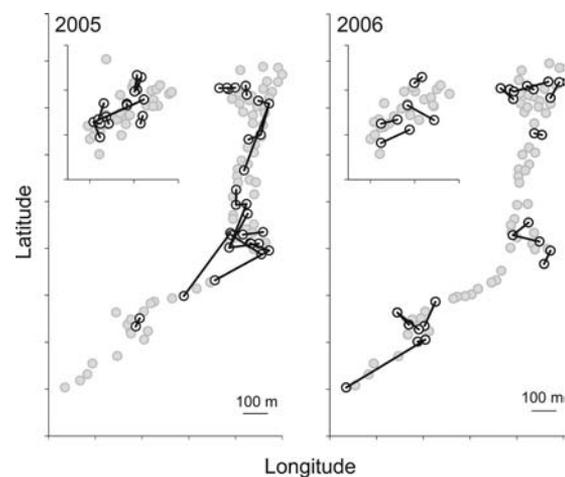


**Figure 1**
Map of the study area (inset small panels correspond to an area 1.3 km north-east to the main panels). Black circles (linked by lines) indicate territories involved in EPP, whereas gray circles represent breeding pairs without EPP. Empty territories in each year are not represented.

and 109 males) from 120 nests in 2006. Within-year discrepancies in male and female numbers are due to bigamous pairings.

Paternity assignments were performed in CERVUS 3.0 (Marshall et al. 1998) using a maximum likelihood method. Individuals were genotyped at 7 polymorphic microsatellite loci: fhu1 and fhu2 (Ellegren 1992), fhu3 and fhu4 (Primmer et al. 1996), and Fhy6-126, Fhy1-25, and Fhy3-60 (Canal et al. 2009). In addition, to increase reliability in the assignment of genetic fathers we genotyped all individuals from nests containing young which showed mismatches with their putative father with 3 additional primers (fhy444, fhy466 and fhy310; Leder et al. 2008). The combined probability of exclusion for all loci was >99.9%. A nestling was considered as an EPY when the social father was not among the most likely sires given by CERVUS, or when another male showed a significant match with him (see below). A given male was identified as extra pair sire when he had a LOD (natural logarithm of the likelihood ratio) score with an EPY higher than the critical value (which is computed by CERVUS through parentage analyses simulations) requested for assignments at 95% confidence level. Some nestlings were considered as EPY with unknown fathers, because no male showed a good match with them. Paternity assignments performed at 80% confidence level did not show any discrepancy with those at 95%, thus confirming both that unknown fathers were not sampled and that our assignments were reliable. See Canal et al. (2011) for further details on paternity analyses.

## Patterns of EPP

Laying dates were scored as days after the 1st of May. Laying date differences between the social and the extra pair mate of a given male (hereafter $\Delta LD$) were calculated by subtracting the social female's laying date from that of the extra pair female. For instance, $\Delta LD$ was +5 days for a male whose social and extra pair females laid their first egg (day 0) on 15th and 20th of May, respectively. Likewise, we calculated the difference in laying dates and the linear distances between all breeding pairs in the population. An index of synchrony (SI; Kempenaers 1993), indicating the average proportion of fertile females per day in the population, was also calculated for each year.

Female birds can store sperm up to several weeks, although early EPCs have a reduced chance of success due to last-male sperm precedence (Birkhead and Møller 1992; Birkhead 1998; Michl et al. 2002). In pied flycatchers, however, females seem to store sperm only from day −2 onwards (Birkhead et al. 1997). Thus, we define the fertile period as starting at day −2 until the day the penultimate egg was laid (Birkhead and Møller 1992; Lifjeld et al. 1997; Birkhead 1998). Moreover, the highest insemination rate in pied flycatchers and its sister species, the collared flycatcher (*F. albicollis*), occurs between days −2 and +1 (Lifjeld et al. 1997; Michl et al. 2002). In fact, Lifjeld et al. (1997) showed that male pied flycatchers removed from their territories before day −3 did not sire any young in the clutch, whereas those removed on day +1 fertilized the entire clutch. Therefore, we assumed that most inseminations should have occurred between days −2 and +1 and thereby that an EPP event is an accurate proxy of the moment wherein an EPC occurred.

The secondary status of a brood may affect paternity of the offspring if males spend less time potentially guarding females during their fertile period (Lundberg and Alatalo 1992). To confirm that data from secondary females engaging in EPP (2005: 4 out of 14 cases; 2006: 1 out of 11) did not bias our conclusions, we repeated all analyses excluding the cases of secondary females engaging in EPP, but results remained unchanged (data not shown).

## Spatiotemporal patterns and EPP opportunities

To analyze whether the probability of EPP (presence vs absence of EPY in a nest) was spatially influenced, we coded the distance between nests (obtained from pairwise comparisons; see above) by stretches of 30 m (i.e. the average distance between nests in the population). Thus, for a given focal breeding pair, all pairs breeding at distances lower than 30 m were included in group 1, those from 31 to 60 m in group 2, etc. Then, the probability of EPP between 2 nests of a given stretch (number of EPPs/ number of breeding pairs) was modeled with a generalized linear model (GLM) with binomial distribution and the midpoint distance of the section as an explanatory variable.

The probability of EPP (presence vs absence of EPY in a nest) in relation to the number of accessible females was modeled with a GLM with binomial distribution. We only considered as accessible females for a given male those fertile females (see above) breeding within the spatiotemporal scale (i.e. distance between nests and $\Delta LD$) at which EPPs occurred in each year (see Results).

We also tested whether the distribution of EPPs relative to the breeding status of each extra pair male's social female was the consequence of a male's strategy to maximize paternity (by mate guarding before their social female's egg laying and engaging in EPP afterwards) or if, in contrast, EPPs were a mere outcome of female accessibility. For each male, the $\Delta LD$ and distance in relation to each female in the population were computed and only accessible females for each male were considered. Finally, we tested with Fisher's exact tests whether observed and expected frequencies of realized EPP differed from those of accessible females before and after the social female's egg laying onset.

Data from both study plots were grouped for analyses. This is justified because breeding synchrony was consistently higher in 2006 than in 2005 in both areas (2005: 29.8 and 28.6% in the oak and pine plots, respectively; 2006: 40.5 and 52.9%). Also, neither breeding density (2005: 8.5 and 8.1 pairs/ha, $P = 0.81$; 2006: 8.5 and 7.5 pairs/ha, $P = 0.52$), distance between EPP mates (GLM: $\chi^2_1 = 1.74$, $P = 0.18$ and $\chi^2_1 = 0.23$, $P = 0.63$ in 2005 and 2006, respectively) or frequency of EPP events (Fisher's exact tests: $P = 0.36$ and $P = 0.22$) differed between plots. Statistical analyses were done in SAS 9.1 (SAS Institute 2004) and Statistica 7.

## RESULTS

In 2005, 40% ($N = 113$) of the nests and 33% ($N = 212$) of the adults were involved in EPP, with 20% ($N = 531$) of the offspring being EPY. Respective figures in 2006 were lower than in 2005: 27% ($N = 120$; $\chi^2_1 = 4.55$, $P = 0.03$), 21% ($N = 229$; $\chi^2_1 = 8.17$, $P = 0.04$), and 11% ($N = 595$; $\chi^2_1 = 16.64$, $P = 0.001$). The genetic father was identified for 67% ($N = 106$) and 66% ($N = 68$) of the EPY in 2005 and 2006, respectively. Breeding synchrony was higher in 2006 (SI = 39.7%) than in 2005 (SI = 27.7%, Figure 2A, 2B).

## Spatiotemporal patterns in EPP at the population level

Females engaging in EPP laid consistently later than the females of their extra pair males: an average (range) of 3.9 (−13, +17) days later in 2005 (Paired t-test: $t = 3.06$, df = 29, $P = 0.004$) and 2.7 (−5, +8) days later in 2006 ($t = 2.8$, df = 17, $P = 0.012$). In other words, males usually attained EPP after their social female had started to lay (Figure 2C, 2D and
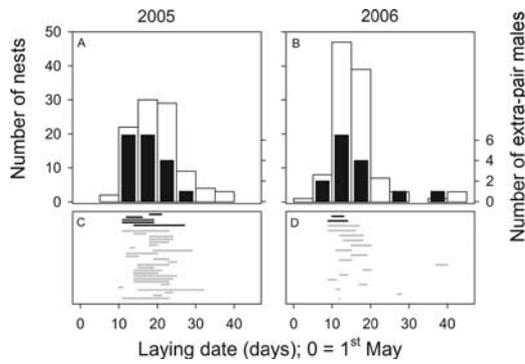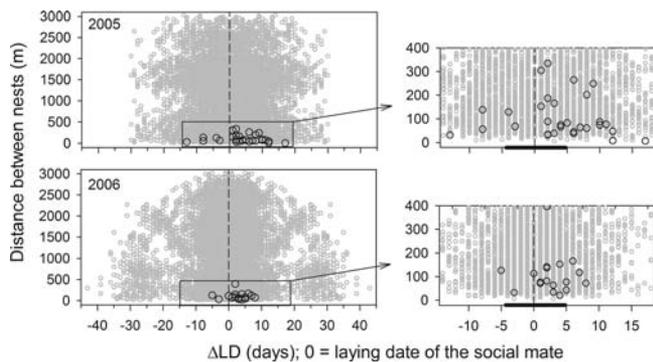
**Figure 2**
(A-B) Frequency distribution of all laying dates in the population (white bars, left y-axis) and laying dates of the social female of those males involved in EPP (black bars, right y-axis). (C-D) Lines link the laying dates of the social female of males engaging in EPP to those of their extra pair female(s); black lines stand for males that engaged in EPP before their social females started to lay whereas gray lines indicate males engaging in EPP after their social females' laying date.

Figure 3). This occurred in 83% ($N = 30$) and 88% ($N = 18$) of the EPPs in 2005 and 2006, respectively. Spatially, EPPs occurred on average (range) at 107 (17–334) m and 99 (18–395) m from the social nest, in 2005 and 2006, respectively (Figure 1 and 3). Thus, overall, EPPs occurred at a shorter spatiotemporal scale than that imposed by breeding phenology (Fig. 2) or the extension of the study area (Figure 1 and 3).

### EPP patterns within realized spatiotemporal scales

Within the spatiotemporal scale (see above) at which EPP interactions occurred, the probability of EPP decreased with the distance between nests (GLM: $\chi^2_1 = 38.01$, $P < 0.001$; Figure 4A). However, at the individual level, 75% of the males did not engage in EPP with the closest accessible fertile female but did so with females breeding at more distant territories in both years (median [range] = 5th [1–29] and 3rd [1–23] territory in 2005 and 2006, respectively; Figure 5).

Temporally, the probability of EPP was strongly dependent on the number of accessible fertile females in both years (GLM: $\chi^2_1 = 71.32$, $P < 0.001$; year × number of accessible females: $\chi^2_1 = 0.58$, $P = 0.44$). When both the number
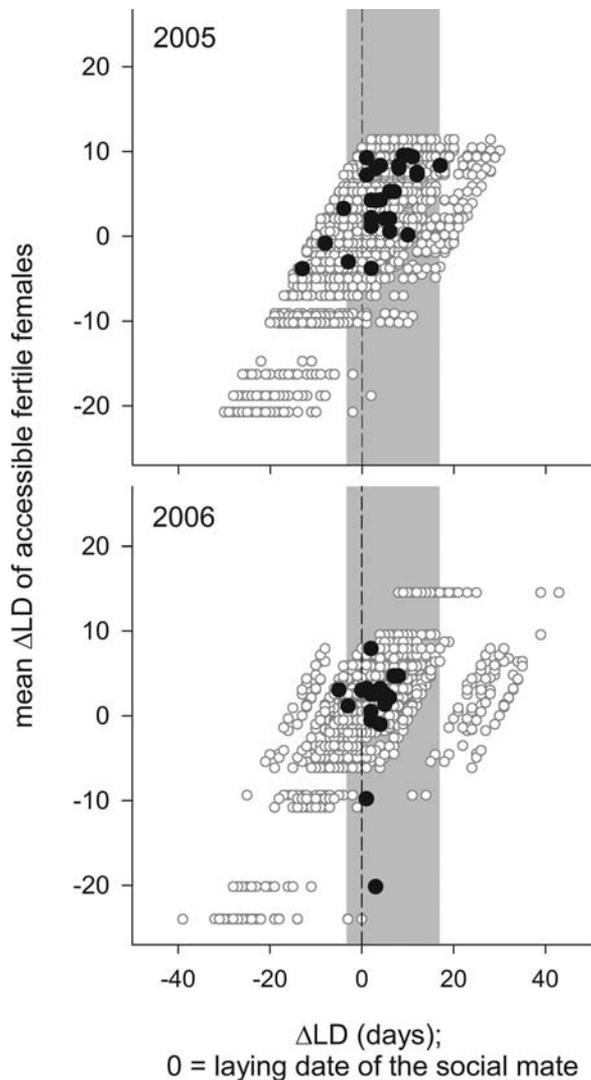


**Figure 3**
Spatial (distance) and temporal (difference in laying dates, ΔLD) relationship between pairs of individuals involved (black circles) or not (gray circles) in EPP at the population level (left panels) and at the spatiotemporal scale at which interactions occurred (right panels). Bold lines on the x-axis of the right panels indicate the fertile period of the extra pair's social females.
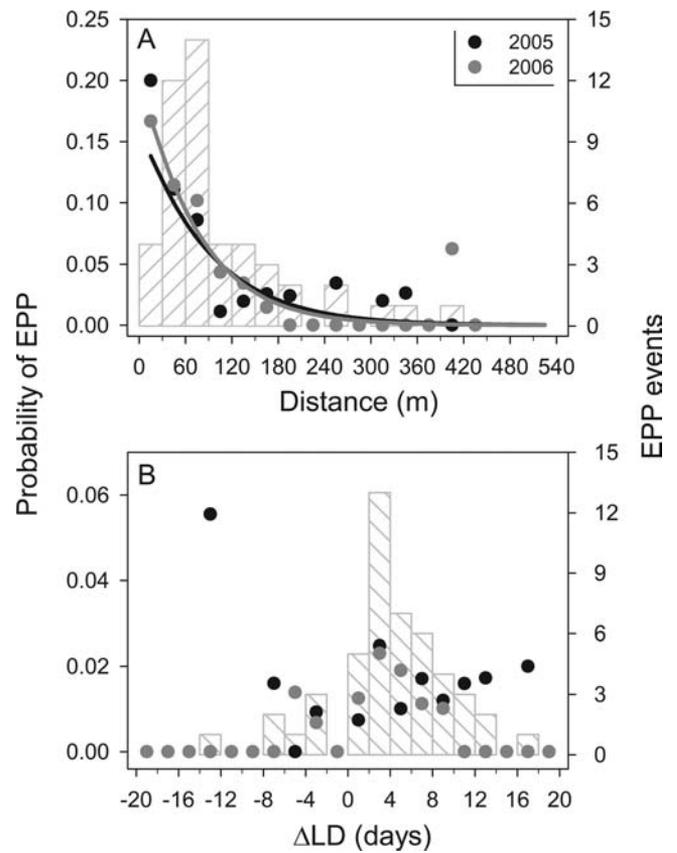


**Figure 4**
Probability (dots) and number of EPP (bars) events in relation to (A) the distance between nests and (B) the difference in laying dates (ΔLD) between the nest of the male and the female engaging in an EPP. EPP probability = number of EPPs/number of breeding pairs in each stretch of 30 m or period of two days.
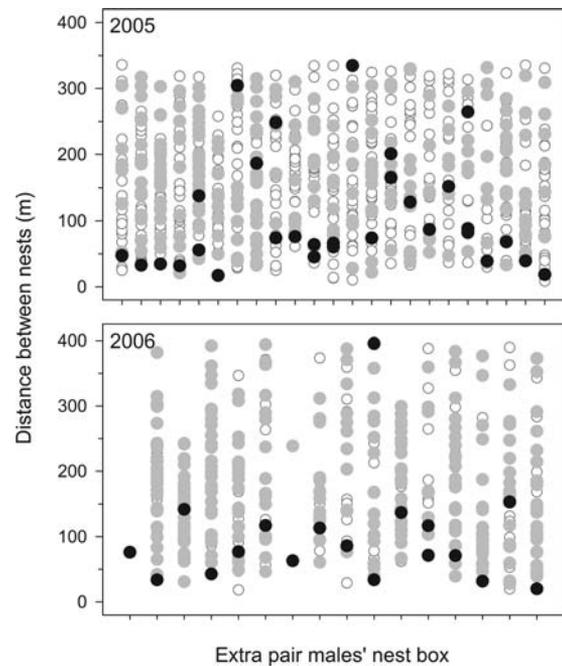


**Figure 5**
Spatial distribution of the EPP events (black circles) in relation to the accessible mates for extra pair males. White circles indicate accessible females, whereas gray circles indicate highly synchronous females with respect to the extra pair male's social female (i.e. −3 to +4 days).

**Figure 6**
Temporal distribution of EPP (black dots) and accessible females for males (gray dots) in relation to their social female's laying date. The gray area indicates the fertile and incubation period of a male's social female (i.e. −3 to +17 days).

of accessible females and the breeding status of the extra pair male's social female were considered, most males which attained EPP did so once their social females had already laid the first egg (Fisher's exact tests: $P = 0.004$ and $P = 0.044$ in 2005 and 2006, respectively) despite there were accessible females before those dates (Figure 6). Moreover, the frequency of EPP decreased during the days prior to the social female's laying date (none of 48 EPPs occurred in days −2 and −1) whereas 85% of them occurred during the egg laying and incubation periods (Figure 4B and 6) and none afterwards, suggesting that males were engaged in chick rearing afterwards.

## DISCUSSION

The probability of EPP at the population level was temporally tied to the number of accessible fertile females. Spatially, the occurrence of EPP decreased with the distance between the nests. As a consequence, EPPs occurred at a shorter scale than that possible according to the population breeding

phenology and spatial extent. Most EPPs occurred after the social females of extra pair males had started laying (i.e. after their peak of fertility) and before the eggs hatched. These patterns suggest a male's strategy to maximize paternity by guarding their females during the critical period of inseminations, searching for EPC during egg laying and incubation, and focusing on rearing their chicks on hatching. At the population scale, therefore, our results suggest that, spatially, individuals tried to remain as close as possible to their nests when engaging in EPP and, temporally, that EPP was (obviously) restricted by breeding phenology. However, when simultaneously taking into account the individual accessibility to fertile females and the scale at which EPPs occurred (i.e. at the local scale), the spatial picture changed as males usually did not engage in EPP with the closest accessible females.

The accessibility to fertile females shaped the distribution of EPPs along the breeding season. The between-year differences in EPP rates could thus be explained by differences in synchrony, because a more synchronous breeding season (i.e. 2006 as compared with 2005; Figure 2A, 2B) should impose additional time constraints on EPP. This is because males face a conflict over paternity, as the chances of gaining it (e.g. through exploratory behaviors for EPCs) reduce those of lowering cuckoldry in their own nests (e.g. through mate guarding), and both activities can hardly be simultaneously maximized (Hasselquist and Bensch 1991; Kokko and Morrell 2005). Thus, when EPCs are mainly male initiated, as suggested by previous work in pied flycatchers (Björklund and Westman 1983; Alatalo et al. 1987), a negative relationship between synchrony and EPP rates would occur when males prioritize avoiding cuckoldry over seeking paternity outside the pair bond (Birkhead and Biggins 1987; Westneat et al. 1990). Accordingly, when the risk of cuckoldry is high, fairy martin males (*Petrochelidon ariel*) guard their mates more intensively, (Hammers et al. 2009) whereas golden whistler males (*Pachycephala pectoralis*) are more aggressive towards intruders and remain closer to their mates (van Dongen 2008).

Most EPPs occurred while the extra pair male's social females were laying or incubating, despite the presence of a great number of fertile females before and after this period (Figure 6). This strongly suggests that males favored both securing their paternity and engaging in parental duties in their social nests over gaining paternity in other nests. However, the key factor here is that successful males in EPP usually bred early in the season (Canal et al. 2012; Figure 2C, 2D) and thereby many females were still fertile after their social females' laying onset. Successful males in EPP could thus have solved the conflict over paternity, because when female's fertility is asynchronous within the population, guarding the social female during her fertile period and searching afterwards for additional paternity seems to be an evolutionarily stable strategy (Birkhead and Biggins 1987; Kokko and Morrell 2005). For instance, wood thrush males (*Hylocichla mustelina*) search for EPC after the fertile period of their social females (Evans et al 2008) and experimentally induced late broods of house sparrows (*Passer domesticus*) contained more EPY sired by early males whose females were already incubating (Václav and Hoi 2007). Therefore, a high synchrony may lessen the population rate of EPP by decreasing the effective time to attain it but, at the same time, may increase the variance in EPP opportunities between males, because those which breed early relative to their neighbors should enjoy more EPP opportunities (and lower costs of cuckoldry) than the other males (Birkhead and Biggins 1987; Václav and Hoi 2007). However, it could also be argued that protandry (often associated with earlier breeding) may have evolved because of the benefit males gain

by increasing female accessibility after their social females lay, thus boosting their chances of EPCs (Coppack et al. 2006; Canal et al. 2012). From a female's point of view, engaging in EPP with early males could report some type of either direct (Lozano et al. 1996) or genetic (Akçay and Roughgarden 2007) benefit, as arrival date is often reported as being a reliable signal of male quality in migrant birds of temperate regions (e.g. Lozano et al. 1996; Smith and Moore 2005). We emphasize that accounting for the timing of breeding relative to others may increase our ability to comprehend individual decisions related to EPP and thereby the effects of breeding synchrony on EPP rates at the population level.

Remarkably, the frequency of EPP dropped in the days previous to the extra pair males' social female laying onset (days −2 and −1). Although this could be taken as an anecdotal evidence, it is also in agreement with a males' decision about when it would pay to pursue EPCs (Birkhead and Biggins 1987; Birkhead 1998). This is because those are the days when most fertilizations occur in birds (see Birkhead and Møller1992 for a review) and thereby when males should increase their efforts to avoid loss of paternity. Thus, for instance, red-winged blackbird (*Agelaius phoeniceus*) males copulate more often during the days prior to the onset of egg laying (Westneat 1993) and in superb fairy wrens (*Malurus cyaneus*), a species where females foray outside the territory more commonly during their peak of fertility, males more intensively pursue their mates (Double and Cockburn 2000). Accordingly, previous studies in pied flycatchers have shown that males seem to prioritize mate guarding before egg laying (Björklund and Westman 1983), because most copulations occur in days −2 and −1 (von Haartman 1956; Alatalo et al. 1987; Lifjeld et al. 1997), and males experimentally switched in day +1 fertilized the whole clutch (suggesting that inseminations fertilizing last eggs occur several days before; Lifjeld et al. 1997). However, the effectiveness of mate guarding is uncertain (Birkhead 1998; Stutchbury and Neudorf 1998), because there is evidence showing that females may sometimes circumvent the constraints imposed by male behavioral strategies (e.g. Kempenaers et al. 1995; Johnsen et al.1998). We cannot discard the possibility that the low probability of EPP observed before egg laying could also be due to other factors such as aggressiveness among females (Slagsvold et al. 1999).

Further evidence for EPP being male initiated comes from the absence of EPPs after nestlings hatch in social nests, despite sustained opportunities for additional matings. At the same time, this also supports the idea that engaging in EPP is a costly behavior. In fact, investment in EPP is expected to trade-off against parental care duties (Magrath and Komdeur 2003). For instance, pursuing EPCs could have a large negative impact on nestling fitness (and hence, on male reproductive success), especially in the early stages of nestling development, if such behavior implies a reduction in males' chick-feeding rates due to the time spent away from the territory (Magrath and Komdeur 2003).

Spatially, the pattern of EPP found here contrasts with that most common in passerines, wherein extra pair males usually are the nearest or the next-to-nearest neighbors (e.g. Gibbs et al. 1990; Yezerinac et al. 1995; Stutchbury et al. 1997; Freeman-Gallant et al 2005; Pedersen et al. 2006; van Dongen and Mulder 2009). However, it is similar to that found in scarlet rosefinches (*Carpodacus erythrinus*; Albrecht et al. 2007), red-winged blackbirds (Westneat and Mays 2005) or in a northern population of pied flycatchers (Rätti et al. 1995; but see Björklund and Westman 1983). Several non mutually exclusive circumstances could explain why males often did not attain EPPs with the closest accessible females.

For instance, a low willingness of the neighboring female to accept EPCs (e.g. if they are mated with a higher-quality male) or an effective behavior (e.g. mate guarding) of the social mate to prevent loss of paternity could explain this pattern. Experimental approaches addressing male/female readiness to engage in EPC (e.g. in relation to social mate presence; Lindstedt et al. 2007) and radio-tracking studies (Pedersen et al. 2006) are needed to improve our understanding of the population consequences of variation in individual behavior on EPP spatiotemporal patterns.

In summary, EPP was not constrained to closest neighbors. Despite often having females closer to them, males sired young up to 390 m away from their nests, implying a high mobility of individuals. Variation in the time window of accessibility to fertile females was a major factor underlying patterns in EPP. A high proportion of extra pair males gained paternity during the egg laying and incubation periods of their social females, despite the fact that there were fertile females accessible before and afterwards. These patterns suggest a male's strategy to optimize paternity through EPP and provide an explanation for why the year with higher breeding synchrony was the year with lower EPP occurrence. Therefore, our work encourages studies on EPP to be carried out at the spatiotemporal scale at which the individual behavior takes place while simultaneously considering the social contexts of all players involved in an EPP event.

## REFERENCES

Akçay E, Roughgarden J. 2007. Extra-pair paternity in birds: review of the genetic benefits. Evol Ecol Res. 9:855–868.

Alatalo RV, Gottlander K, Lundberg A. 1987. Extra-pair copulations and mate-guarding in the polyterritorial pied flycatcher (*Ficedula hypoleuca*). Behaviour. 101:139–155.

Albrecht T, Schnitzer J, Kreising J, Exnerova A, Bryj J, Munclinger P. 2007. Extrapair paternity and the opportunity for sexual selection in long-distant migratory passerines. Behav Ecol. 18:477–486.

Arnqvist G, Kirkpatrick M. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. Am Nat. 165:S26–S37.

Bennett P, Owens I. 2002. Evolutionary ecology of birds. Life histories, mating systems, and extinction. Oxford: Oxford Univ. Press.

Birkhead TR. 1998. Sperm competition in birds: mechanisms and function. In: Birkhead TR, Møller AP, editors. Sperm competition and sexual selection. San Diego (CA): Academic Press. p. 579–622.

Birkhead TR, Biggins JD. 1987. Reproductive synchrony and extra-pair copulations in birds. Ethology. 74:320–334.

Birkhead TR, Briskie JV, Lifjeld JT, Slagsvold T. 1997. Breeding cycle patterns of sperm storage in the pied flycatcher (Ficedula hypoleuca). Auk. 114:792–796.

Birkhead TR, Møller AP. 1992. Sperm competition in birds: Evolutionary causes and consequences. London; Academic Press.

Björklund M, Westman B. 1983. Extra-pair copulations in the pied flycatcher (*Ficedula hypoleuca*). A removal experiment. Behav Ecol Sociobiol. 13:271–275.

Canal D, Dávila JA, de Nova PJC, Ferrero E, Potti J. 2009. Polymorphic microsatellite markers isolated from a southern European

population of pied flycatcher (*Ficedula hypoleuca iberiae*). Mol Ecol Res. 9:1375–1379.

Canal D, Jovani R, Potti J. 2012. Multiple mating opportunities boost protandry in a pied flycatcher population. Behav Ecol Sociobiol. 66:67–76. doi: 10.1007/s00265-011-1253-8.

Canal D, Potti J, Dávila JA. 2011. Male phenotype predicts extra pair paternity in pied flycatchers. Behaviour. 148:691–712.

Chuang HC, Webster MS, Holmes RT. 1999. Extrapair paternity and local synchrony in the Black-throated Blue Warbler. Auk. 116:726–736.

Cohas A, Allainé D. 2009. Social structure influences extra-pair paternity in socially monogamous mammals. Biol Lett. 5:313–316.

Coppack T, Tottrup AP, Spottiswoode C. 2006. Degree of protandry reflects level of extrapair paternity in migratory songbirds. J Ornithol. 147:260–265.

van Dongen WFD. 2008. Mate guarding and territorial aggression vary with breeding synchrony in golden whistlers (*Pachycephala pectoralis*). Naturwissenschaften. 95:537–545.

van Dongen WFD, Mulder RA. 2009. Multiple ornamentation, female breeding synchrony, and extra-pair mating success of golden whistlers (*Pachycephala pectoralis*). J Ornithol. 150:607–620.

Double MC, Cockburn A. 2000. Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. Proc R Soc B. 267:465–470. doi 10.1098/rspb.2000.1023.

Dunn PO, Whittingham LA, Lifjeld JT, Robertson RJ, Boag PT. 1994. Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. Behav Ecol. 5:123–129.

Evans ML, Stutchbury BJM, Woofenden BE. 2008. Off-territory forays and the genetic mating system of the wood thrush. Auk. 125:67–75.

Ellegren H. 1992. Polymerase-chain-reaction (PCR) analysis of microsatellites – a new approach to studies of genetic relationships in birds. Auk. 109:886–895.

Freeman-Gallant CR, Wheelwright NT, Meiklejohn KE, States SL, Sollecito SV. 2005. Little effect of extrapair paternity on the opportunity for sexual selection in savannah sparrows (*Passerculus sandwichensis*). Evolution. 59:422–430.

Gelter HP, Tegelström M. 1992. High frequency of extra-pair paternity in Swedish pied flycatchers revealed by allozyme electrophoresis and DNA fingerprinting. Behav Ecol Sociobiol. 31:1–7.

Gibbs HL, Weatherhead PJ, Boag PT, White BN, Tabak LM, Hoysak DJ. 1990. Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. Science. 250:1394–1397.

Griffith SC, Owens IPF, Thuman AK. 2002. Extra-pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol. 11:2195–2212.

von Haartman L. 1956. Territory in the pied flycatcher *Muscicapa hypoleuca*. Ibis. 98:460–475.

Hammers M, von Engelhardt N, Langmore NE, Komdeur J, Griffith SC, Magrath MJL. 2009. Mate-guarding intensity increases with breeding synchrony in the colonial fairy martin, *Petrochelidon ariel*. Anim Behav. 78:661–669.

Hasselquist D, Bensch S. 1991. Trade-off between mate guarding and mate attraction in the polygynous great reed warbler. Behav Ecol Sociobiol. 28:187–193.

Hoi H, Hoi-Leitner M. 1997. An alternative route to coloniality in the bearded tit: females pursue extra-pair fertilizations. Behav Ecol. 8:113–119.

Jennions MD, Petrie M. 2000. Why do females mate multiply? A review of the genetic benefits. Biol Rev. 75:21–64.

Johnsen A, Lifjeld JT. 2003. Ecological constraints on extra-pair paternity in the bluethroat. Oecologia. 136:476–483.

Johnsen A, Lifjeld JT, Rohde PA, Primmer CR, Ellegren H. 1998. Sexual conflict over fertilizations: female bluethroats escape male paternity guards. Behav Ecol Sociobiol. 43:401–408.

Kempenaers B. 1993. The use of a breeding synchrony index. Ornis Scand. 24:84.

Kempenaers B, Verheyen GR, van den Broek M. 1992. Extra pair paternity results from female preference for high quality males in the blue tit. Nature. 357:494–496.

Kempenaers B, Verheyen GR, Dhondt AA. 1995. Mate guarding and copulation behaviour in monogamous and polygynous blue tits: do males follow a best-of-a-bad-job strategy? Behav Ecol and Sociobiol. 36:33–42.

Kokko H, Morrell LJ. 2005. Mate guarding, male attractiveness, and paternity under social monogamy. Behav Ecol. 16:724–731.

Lack D. 1968. Ecological adaptations for breeding in birds. London: Methuen.

Lindstedt ER, Oh KP, Badyaev AV. 2007. Ecological, social, and genetic contingency of extrapair behavior in a socially monogamous bird. J. Avian Biol. 38:214–223.

Leder EH, Karaiskou N, Primmer CR. 2008. Seventy new microsatellites for the pied flycatcher, *Ficedula hypoleuca* and amplification in other passerine birds. Mol Ecol Res. 8:874–880.

Lifjeld JT, Slagsvold T, Lampe HM. 1991. Low frequency of extrapair paternity in pied flycatcher revealed by DNA fingerprinting. Behav Ecol Sociobiol. 29:95–101.

Lifjeld JT, Slagsvold T, Ellegren H. 1997. Experimental mate switching in pied flycatchers: Male copulatory access and fertilization success. Anim Behav. 53:1225–1232.

Lozano GA, Perreault S, Lemon RE .1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. J Avian Biol. 27:164–170.

Lundberg A, Alatalo RV. 1992. The pied flycatcher. London: Poyser.

Magrath MJL, Komdeur J. 2003. Is male care compromised by additional mating opportunity? TREE. 18: 424–430.

Marshall TC, Slate J, Kruuk LEB, Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Mol. Ecol. 7:639–655. doi: 10.1046/j.1365-294x.1998.00374.x

Mays HL, Albrecht T, Liu M, Hill GE. 2008. Female choice for genetic complementarity in birds: a review. Genetica. 134:147–158.

Michl G, Török J, Griffith SC, Sheldon BC. 2002. Experimental analysis of sperm competition mechanisms in a wild bird population. Proc Natl Acad Sci USA. 99:5466–5470.

Pedersen MC, Dunn PO, Whittingham LA. 2006. Extraterritorial forays are related to a male ornamental trait in the common yellowthroat. Anim. Behav. 72:479–486.

Petrie M, Kempenaers B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends Ecol Evol. 13:52–58.

Potti J, Canal D. 2011. Heritability and genetic correlation between the sexes in a songbird sexual ornament. Heredity. 106:945–954.

Potti J, Montalvo S. 1991. Male arrival and female mate choice in Pied Flycatchers (*Ficedula hypoleuca*) in central Spain. Ornis Scand. 22:45–54.

Primmer G, Anders M, Ellegren H. 1996. New microsatellites from the pied flycatcher Ficedula hypoleuca and the swallow *Hirundo rustica* genomes. Hereditas. 124:281–283.

Rätti O, Hovi H, Lundberg A, Tegelström H, Alatalo RV. 1995. Extra-pair paternity and male characteristics in the pied flycatcher. Behav Ecol Sociobiol. 37:419–425.

Rätti O, Lundberg A, Tegelström H, Alatalo RV. 2001. No evidence for effects of breeding density and male removal on extrapair paternity in the pied flycatcher. Auk. 118:147–155.

Richardson DS, Burke T. 2001. Extra-pair paternity and variance in reproductive success related to breeding density in Bullock's orioles. Anim Behav. 62:519–525.

Sefc KM, Mattersdorfer K, Sturmbauer C, Koblmüller S. 2008. High frequency of multiple paternity in broods of a socially monogamous cichlid fish with biparental brood care. Mol Ecol. 17:2531–2543.

Smith RJ, Moore FR .2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behav Ecol Sociobiol. 57:231–239.

Stewart IRK, Hanschu RD, Burke T, Westneat DF. 2006. Tests of ecological, phenotypic, and genetic correlates of extra-pair paternity in the house sparrow. Condor. 108:399–413.

Slagsvold T, Dale S, Lampe HM. 1999. Does female aggression prevent polygyny? An experiment with pied flycatchers (*Ficedula hypoleuca*). Behav Ecol Sociobiol. 45:403–410.

Stutchbury BJM. 1998. Female mate choice of extra-pair males: breeding synchrony is important. Behav Ecol Sociobiol. 43:213–215.

Stutchbury BJM, Morton ES. 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. Behaviour. 132:675–690.

Stutchbury BJM, Neudorf DL. 1998. Female control, breeding synchrony and the evolution of extra-pair mating strategies. In: Parker PG, Burley N, editors. Avian reproductive tactics: female and male perspectives. Am Ornithol Union Monogr. vol 49. p. 103–122.

Stutchbury BJM, Piper WH, Neudorf DL, Tarof SA, Rhymer JM, Fuller G, Fleischer RC. 1997. Correlates of extra-pair fertilization success in hooded warblers. Behav Ecol Sociobiol. 40:119–126.

Tarof SA, Stutchbury BJM, Piper WH, Fleischer RC. 1998. Does breeding density covary with extra-pair fertilizations in hooded warblers? J Avian Biol. 29:145–154.

Thusius KJ, Dunn PO, Peterson KA, Whittingham LA. 2001. Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. Behav Ecol. 12:633–639.

Václav R, Hoi H. 2007. Experimental manipulation of timing of breeding suggests laying order instead of breeding synchrony affects extra-pair paternity in house sparrows. J Ornithol. 148:395–400.

Weatherhead PJ. 1997. Breeding synchrony and extra-pair mating in red-winged blackbirds. Behav Ecol Sociobiol. 40:151–158.

Webster MS, Chuang-Dobbs HC, Holmes RT. 2001. Microsatellite identification of extra-pair sires in a socially monogamous warbler. Behav Ecol. 12:439–446.

Westneat DF. 1993. Temporal patterns of within-pair copulations, male mate-guarding and extra-pair events in eastern red-winged blackbirds (*Agelaius phoeniceus*). Behaviour. 124:267–290.

Westneat DF, Mays HL. 2005. Tests of spatial and temporal factors influencing extra-pair paternity in red-winged blackbirds. Mol Ecol. 14:2155–2167.

Westneat DF, Sherman PW. 1997. Density and extra-pair fertilizations in birds: a comparative analysis. Behav Ecol Sociobiol. 41:205–215.

Westneat DF, Sherman PW, Morton ML.1990. The ecology and evolution of extra-pair copulations in birds. In: Power DM,editor. Current ornithology. New York: Plenum Press. p. 331–370.

Westneat DF, Stewart IRK. 2003. Extra-pair paternity in birds: Causes, correlates, and conflict. Annu Rev Ecol Evol Syst. 34:365–396.

Yezerinac SM, Weatherhead PJ, Boag PT. 1995. Extra-pair paternity and the opportunity for sexual selection in a socially monogamous bird (*Dendroica petechia*). Behav Ecol Sociobiol. 37:179–188.