

# Multiple mating opportunities boost protandry in a pied flycatcher population

David Canal · Roger Jovani · Jaime Potti

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**Abstract** Protandry, the earlier arrival of males than females to breeding areas, is widespread in birds, but its underlying mechanisms are far from well understood. The two, not mutually exclusive most highly supported hypotheses to explain avian protandry postulate that it has evolved from intrasexual male competition to acquire the best territories (“rank advantage” hypothesis) and/or to maximize the number of mates (“mate opportunity” hypothesis). We studied for two consecutive years the relative importance of both hypotheses in a population of pied flycatchers (*Ficedula hypoleuca*), a territorial songbird with a mixed mating strategy. We measured territory quality using a long-term dataset on nest occupation and breeding output, and we used molecular techniques to assess male fitness across the range of social and genetic mating options. Territory quality was unrelated to breeding date and had no influence on extra-pair paternity or social polygynous events. However, males breeding early increased their chances of becoming socially polygynous and/or of attaining extra-pair paternity and, as a consequence, increased their total reproductive success. These results support the “mate opportunity” hypothesis, suggesting that sexual selection is the main mechanism driving protandry in this population.

**Keywords** Extra-pair paternity · *Ficedula hypoleuca* · Mate opportunity hypothesis · Protandry · Rank advantage hypothesis · Social polygyny

## Introduction

Males and females emerge asynchronously, or arrive at different times at the breeding areas, in many taxa including insects, amphibians, birds, fishes and mammals (reviewed by Morbey and Ydenberg 2001). Protandry, the earlier arrival/emergence of males than females, is the most widespread pattern (e.g. Morbey and Ydenberg 2001; Kokko et al. 2006; but see Reynolds et al. 1986). Earlier males often show higher reproductive success (Thornhill and Alcock 1983; Newton 2008), especially when female fecundity decreases with time (Kleckner et al. 1995; Carvalho et al. 1998), but the mechanisms underlying protandry are not well understood.

Several hypotheses aim to explain whether selection acts directly or indirectly on the difference between male and female timing of arrival (Morbey and Ydenberg 2001). Given the diversity of the mating systems wherein protandry occurs, the different hypotheses apply to different groups. In insects, for instance, protandry may be a by-product of selection for larger (implying longer developmental time) females than males when female’s reproductive capacity increases with size (the “constraint hypothesis”; e.g. Wiklund and Solbreck 1982; Thornhill and Alcock 1983). In some lizards, however, males are incapable to reproduce immediately after emergence, and selection may act directly on the female’s timing of emergence by delaying it to reduce the odds of mating with infertile individuals (the “waiting cost hypothesis”; e.g. Olsson and Madsen 1996). In birds, where protandry is common (Rubolini et al. 2004; Coppack et al. 2006; Newton 2008) the two, not mutually exclusive, most strongly supported hypotheses explaining protandry are the “rank advantage” (Ketterson and Nolan 1976; Kokko 1999) and the “mate opportunity” hypothesis (originally conceived in butterflies; Wiklund and Fagerström 1977). The “rank

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D. Canal (✉) · R. Jovani · J. Potti  
Department of Evolutionary Ecology,  
Estación Biológica de Doñana-CSIC,  
Av. Américo Vespucio s/n,  
41092 Sevilla, Spain  
e-mail: davidcanal@ebd.csic.es

advantage” hypothesis postulates that competition for gaining the best territories is the selective force driving the sex differences in arrival schedules (Ketterson and Nolan 1976). Accordingly, an enhanced breeding success for early arriving males has been associated with acquisition of the best territories (Alatalo et al. 1986; Forstmeier 2002), and the sex defending a crucial resource for breeding (e.g. a territory or a nest site) usually arrives first (e.g. Myers 1981; Alatalo et al. 1986; Hasselquist 1998). Conversely, under the “mate opportunity” hypothesis, selection will favor protandry if males maximize their mating opportunities through an early arrival (Lozano et al. 1996; Langefors et al. 1998). This is especially important for species with a mixed mating strategy wherein early breeding may allow the consecution of additional matings via social polygyny and/or extra-pair paternity (EPP hereafter; Reudink et al. 2009). In support of this hypothesis, the chances of multiple mating either in social polygyny (Hasselquist 1998) or via EPP (Langefors et al. 1998; Coppack et al. 2006) have been shown to increase with early male arrival. In fact, the commonness of EPP (Griffith et al. 2002; Westneat and Stewart 2003) has given impetus to the “mate opportunity” hypothesis as the main mechanism underlying the evolution of protandry at both the within- and the between-species levels (e.g., Langefors et al. 1998; Rubolini et al. 2004; Coppack et al. 2006; Kokko et al. 2006; Møller et al. 2009; Reudink et al. 2009; but see Saino et al. 2010). Given that male (more than female) fitness is tightly correlated to the number of matings they achieve (Andersson 1994), males arriving simultaneously or later than females will lose as many mating opportunities as the number of females that were receptive before male arrival (Kokko et al. 2006).

As pointed out by Morbey and Ydenberg (2001), studies should simultaneously consider the significance of the different selective pressures, given that hypotheses of protandry are not mutually exclusive. However, to our knowledge, no study has simultaneously analyzed, in a single species, the different factors underlying the two main hypotheses related to protandry in birds, i.e., the “rank advantage” and “mate opportunity” hypotheses, accounting for both EPP and/or social polygyny. Here, we did so studying a population of pied flycatchers (*Ficedula hypoleuca*), an interesting species in this regard because most males arrive at the breeding areas before females (Potti and Montalvo 1991), and establish a territory around a nest site and subsequently try to attract a female, thus allowing for testing of the relevance of territory quality (Lundberg and Alatalo 1992). The mating system is mainly monogamous, but 3–25% of the males acquire a second mate (secondary female, hereafter), becoming socially polygynous (reviewed in Lundberg and Alatalo 1992). Moreover, genetic polygyny is common, with percentages of extra-pair young (EPY hereafter) ranging from 4 to 24% (Table 2 in Rätti et al. 2001; Canal et al. 2011 and references

therein). Here, we studied the relative importance of the main mechanisms proposed to promote avian protandry (territory quality versus mating opportunities) by using molecular techniques to track the fitness of males through EPP and social polygyny in combination with an ongoing long-term study to estimate territory quality.

## Material and methods

### Field work

The study was carried out during the breeding seasons of 2005 and 2006 as part of a long-term study of pied flycatchers in central Spain (e.g., Potti et al. 2007; Canal et al. 2011). The study area consists of two plots (located in an oak wood and a pinewood) 1.3 km apart, including 236 nest boxes which positions have remained stable since 1995. Universal Transverse Mercator (UTM) coordinates of all nests were GPS (Global Positioning System)-referenced and distances among them calculated with Arcview (ESRI 2000is™). The average (SD) minimum distance between occupied nest boxes was 30 (14.1) m.

Field protocols have been described in detail elsewhere (Potti et al. 2007; Canal et al. 2011). Briefly, all nests were regularly checked (every 3 days before laying started 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 nest box trap while they were feeding 8-day-old nestlings. Birds were weighed (with a spring balance, to the nearest 0.1 g) and measured for tarsus length (with callipers, to the nearest 0.01 mm), height and width of the forehead patch (to the nearest 0.01 mm) and wing length (with a ruler, to the nearest 0.5 mm). The area of the forehead patch was calculated as patch height×width. Fledglings were measured and weighed at 13 days of age. Blood samples were taken from all individuals by puncturing the brachial vein and stored in ethanol.

### Molecular methods

Our sample size for parentage analyses was 1,568 individuals: 531 chicks and 212 adults (113 females and 99 males) from 113 nests in 2005 and 595 chicks and 229 adults (120 females and 109 males) from 120 nests in 2006. Within-year discrepancies in male and female numbers are due to bigamous pairings. Additional data from females lacking male assistance involving 8/21 and 8/22 females/chicks in 2005 and 2006, respectively, were excluded from analyses (see below). Individuals were genotyped at seven polymorphic microsatellite loci (*fhu1* and *fhu2* (Ellegren 1992), *fhu3* and *fhu4* (Primmer et al. 1996) and *Fhy6-126*, *Fhy1-25*, *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 having mismatches with their putative father with three additional primers (*fhy444*, *fhy466* and *fhy310*; Leder et al. 2008). We identified a given male as an extra-pair sire when an EPY had no or one mismatch and a high likelihood score with him. Paternity assignments were based on a 95% confidence level (see Canal et al. 2011 for further details on paternity analysis).

#### Mating opportunities and breeding phenology

Egg laying dates (scored as days after 1 May) were used as a proxy for arrival dates. We are confident in this approach because we have previously shown a strong correlation between both variables in the study population (Potti and Montalvo 1991), a fact also reported in other populations of pied flycatchers (Alatalo et al. 1986; Lundberg and Alatalo 1992) and in many other avian species (e.g. Møller 1994; Bêty et al. 2003; Cooper et al. 2009).

When working simultaneously with EPP and social polygyny, some considerations were taken into account since the inclusion in the analyses of different types of individuals such as secondary females with or without male assistance and/or those engaging or not in EPP may be problematic. First, the secondary status may affect paternity of the offspring if males spend less time potentially guarding females during their fertile period (Lundberg and Alatalo 1992). However, data from secondary broods with male assistance were considered in the analyses concerning EPP since our aim here is to study the adaptive mechanism (s) promoting protandry and not those promoting EPP (i.e., we aimed to assess male fitness accrued from EPP and not the reasons for female promiscuous behavior). Second, data from females lacking male assistance were excluded from analyses as they could, in fact, be secondary females or either have been deserted by their mates or widowed after pairing. To confirm that those cases did not bias our conclusions in polygynous contexts, we made the analyses including and excluding data from nests lacking male assistance and results remained unchanged (data not shown).

#### Temporal patterns of EPP and social polygyny

The probabilities of males and females being involved in EPP (coded as 0/1) during the breeding season were modeled in each year with generalized linear models (binomial distribution) and laying dates as explanatory variables. Likewise, the probabilities of a male becoming socially polygynous or a female becoming secondary were modeled in each year.

The influence of laying date on male fitness was tested with general or generalized linear models. In

these analyses, the reproductive success of males (number of fledglings sired) was divided into several components: fitness attributable to the social pair (once those fledglings lost by EPP were deducted from their own nests (normal distribution)), that due to additional matings (Poisson distribution), and overall realized reproductive success (normal distribution).

#### Territory quality

The long-term quality of territories (nest boxes;  $n=236$ ) was calculated using information from a period of 16 years (1995–2010). To this end, we computed an index of nest occupancy (following Sergio and Newton 2003; see also Askenmo 1984) as the proportion of years a nest box was occupied by pied flycatchers in relation to those it was available (i.e., not occupied by other species). The index thus shows the preference of the species for each nest box since, on average (range), 34 (5–56) % of the nest boxes were not occupied but available to the flycatchers each year and the proportion of nest boxes used by other species is relatively low (on average, 12 (3–31) %). We also computed two additional indices indicative of territory quality based on the mean numbers of nestlings fledged and of those recruited from each nest box in the following years, thus summarizing all the factors potentially shaping the breeding success in a given territory, and the survival expectancies of the chicks reared there. As the three indices were intercorrelated but not fully redundant (occupancy–number of fledglings:  $r_s=0.15$ ,  $P=0.017$ , occupancy–number of recruits:  $r_s=0.17$ ,  $P=0.007$ , number of fledglings–recruits:  $r_s=0.32$ ,  $P<0.001$ ), we made a Principal Component Analysis to summarize overall variation in territory quality. PC1 explained 48.2% of the total variance in territory quality with similar and positive contribution of each index (factor loadings: occupation rate 0.56, number of fledglings 0.75, number of recruits 0.76) and its scores were used as an index of territory quality in further analyses (tests done with each index separately gave similar results, results not shown).

We used a general linear model to test whether territory quality was related to breeding date or annual reproductive success (numbers of fledglings and recruits). A generalized linear model was run to see whether males that attained EPP (binomial distribution) occupied the best territories wherein male identity was introduced as a random factor (as some males bred in both years). Wilcoxon tests were used to see if promiscuous females engaged in EPP with males established in better territories than those of their social males. Likewise, in contexts of social polygyny, the relationship between female mating status (primary, secondary or monogamous) and the quality of her (social male's) territory was modeled with a generalized linear model where female

status was introduced as a multinomial dependent variable, territory quality as an explanatory variable and female identity as a random factor. Primary and secondary territories of polygynous males were also compared with pairwise tests.

An association between territory and male quality could be an important and potential confounding source of variation concerning conclusions on the ranking advantage hypothesis of protandry. To explore this possibility, we calculated the average size of male forehead patches and tarsus lengths (two traits positively related to success in intrasexual competition for territories; see Lundberg and Alatalo 1992; Sanz 2001) for males occupying a given nest box, and related them to the scores of territory quality with general linear models. In addition, we related long-term territory quality with male traits in the two study years separately.

Statistical analyses were made in SAS 9.1 (SAS Institute 2004) and Statistica 7 (StatSoft, Inc. 2004).

## Results

### Patterns of EPP and social polygyny

In 2005, 40% (45/113) of the nests and 33% (70/212) of the adults were involved in EPP episodes with 20% (106/531) of the offspring being EPY. Respective figures in 2006 were a bit lower: 27% (32/120), 21% (48/228) and 11% (68/595), respectively. Excluding secondary females, these rates were: 19% (101/517), 33% (65/198) and 40% (40/99) in 2005 and 28% (30/108), 21% (46/216), and 12% (65/546) in 2006. Regarding social polygyny, we were able to identify the bigamous male parent in 14 and 11 nests in 2005 and 2006, respectively.

In 2005, the probability of a male engaging in EPP was highest at the beginning of the breeding season, decreasing afterwards ( $\chi_1^2=8.2$ ,  $P=0.004$ ). The same trend was observed in 2006, but the relationship was not statistically significant ( $\chi_1^2=0.18$ ,  $P=0.67$ ; Fig. 1). The probability of females engaging in EPP was unrelated to breeding date in both years ( $\chi_1^2=0.01$ ,  $P=0.98$  and  $\chi_1^2=1.26$ ,  $P=0.26$ , in 2005 and 2006, respectively; Fig. 2).

In both years, the probability of a male becoming socially polygynous decreased as the season advanced ( $\chi_1^2=11.46$ ,  $P<0.001$  and  $\chi_1^2=4.15$ ,  $P=0.041$ , in 2005 and 2006, respectively; Fig. 1). In contrast, the probability of becoming a secondary female increased throughout the season ( $\chi_1^2=8.70$ ,  $P=0.003$  and  $\chi_1^2=3.79$ ,  $P=0.05$ ; Fig. 2).

Male fitness decreased with laying date in both years ( $\chi_1^2=19.07$ ,  $P<0.001$  and  $\chi_1^2=9.75$ ,  $P=0.002$ , in 2005 and 2006, respectively). This was explained in part by the number of young attributable to the social pair ( $\chi_1^2=6.89$ ,  $P=0.008$  and  $\chi_1^2=9.99$ ,  $P=0.002$ ), but particularly because

early breeding males increased their fitness by siring young through EPP and/or by becoming polygynous in other nests ( $\chi_1^2=13.72$ ,  $P<0.001$  and  $\chi_1^2=3.3$ ,  $P=0.069$ ; Fig. 3).

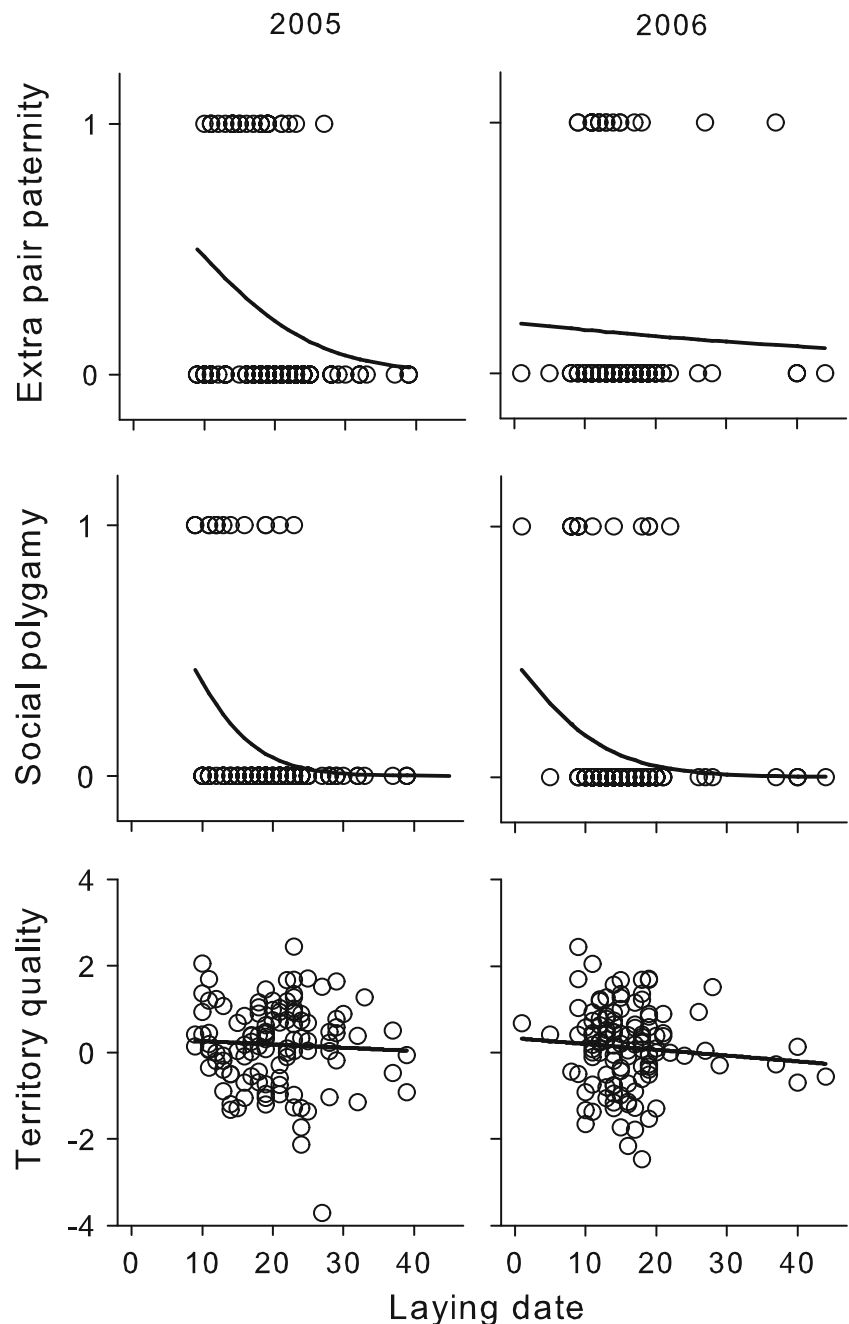
### Extra-pair mating, social polygyny and territory quality

Long-term territory quality was not associated with average size (tarsus length;  $\chi_1^2=1.57$ ,  $P=0.21$ ) or forehead patch size ( $\chi_1^2=0.01$ ,  $P=0.97$ ) of the males occupying the nest boxes. The same was true when limiting the analysis to 2005 and 2006 (tarsus length:  $\chi_1^2=1.74$ ,  $P=0.18$  and  $\chi_1^2=0.01$ ,  $P=0.93$ ; forehead patch size:  $\chi_1^2=1.22$ ,  $P=0.26$  and  $\chi_1^2=0.14$ ,  $P=0.7$ ). These results suggest that an association between male quality and prime territory sites (see Alatalo et al. 1986) is not likely to be biasing our results herein. Territory quality was independent of laying date as early breeders did not occupy better territories (all nests  $\chi_1^2=0.03$ ,  $P=0.86$  and  $\chi_1^2=0.99$ ,  $P=0.31$ ; after removing secondary nests:  $\chi_1^2=0.15$ ,  $P=0.7$ , and  $\chi_1^2=1.14$ ,  $P=0.28$ , in 2005 and 2006, respectively, Fig. 1). Territory quality did not influence EPP or social polygyny events, as extra-pair males did not occupy better territories than males not involved in EPP ( $\chi_1^2=0.07$ ,  $P=0.79$ ), neither did females engage in EPP with males holding better territories than those of their social mates ( $Z=0.24$ ,  $P=0.8$ ). Also, there were no differences in the quality of the territories between monogamous, primary or secondary females ( $\chi_1^2=0.29$ ,  $P=0.59$ ) and the primary and secondary territories of polygynous males were of similar quality ( $Z=0.29$ ,  $P=0.76$ ). Long-term territory quality was unrelated to the annual production of fledglings (2005:  $\chi_1^2=0.24$ ,  $P=0.62$ ; 2006:  $\chi_1^2=1.3$ ,  $P=0.25$ ) and recruits (2005:  $\chi_1^2=0.09$ ,  $P=0.76$ ; 2006:  $\chi_1^2=0.01$ ,  $P=0.91$ ).

## Discussion

Breeding early was advantageous for males as their chances to become polygynous and engaging in extra-pair matings declined through the season, even though for the latter there was annual variation in the significance of arriving early to the breeding grounds. Although males increased their reproductive output by breeding early, the increase was higher for males siring young in several nests. Conversely, females were not constrained to maximize their EPP opportunities through early breeding as their likelihood to engage in EPP was unrelated to date, though their chances of becoming secondary increased throughout the season. Remarkably, territory quality was not related to breeding date, nor was it influenced by EPP or polygynous events; EPP males did not occupy better territories than the males they cuckolded and the same was true for primary and secondary territories of polygynous males. Since by breeding

**Fig. 1** Male probability of attaining extra-pair paternity (*top*) or becoming socially polygynous (*middle*), and territory quality achieved (*bottom*) according to the laying date (as days after 1 May) of their social pair



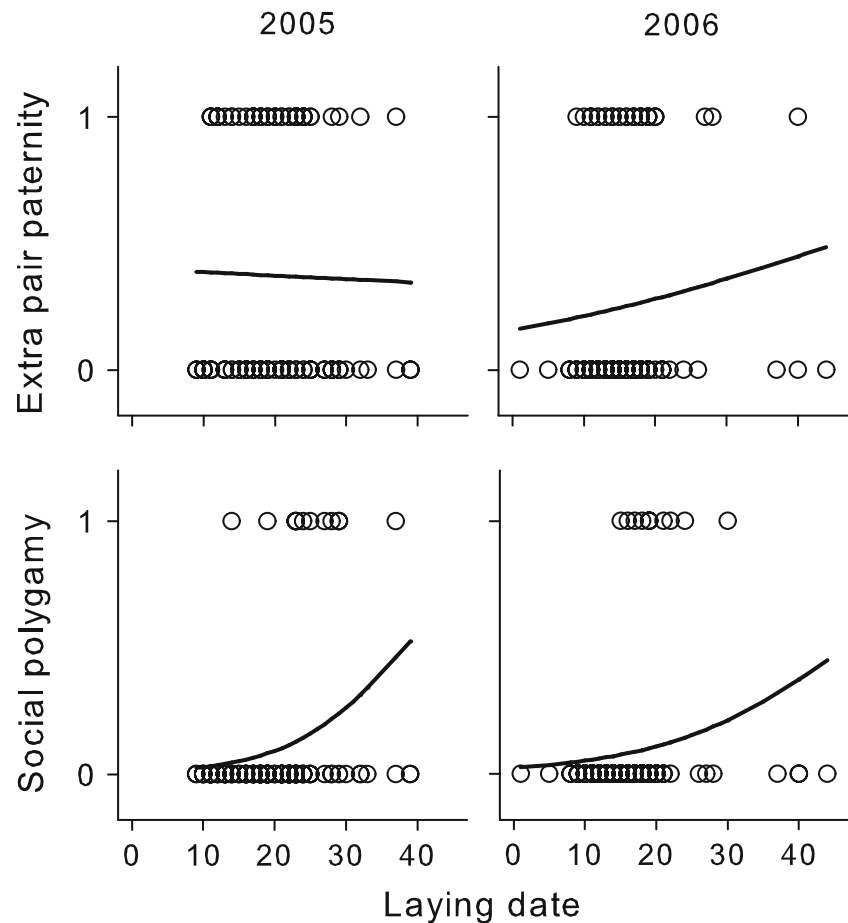
early males improved their prospects for multiple matings and, in turn, their fitness, it follows that sexual selection may be underlying protandry in this population.

The exact moment when extra-pair fertilizations occur may seem uncertain since female birds are known to store sperm from a few days to several weeks (Birkhead and Møller 1992; Birkhead 1998). However, due to sperm competition, early extra-pair copulations (EPC) have reduced chances of success since any subsequent copulation with the social male seems to decrease the fertilization success from prior inseminations via last-male sperm precedence (Birkhead and Møller 1992; Birkhead 1998; Michl et al. 2002). In fact,

the highest rate of pair copulations and fertilizations in pied flycatchers occurs between days  $-2$  and  $-1$  (Lifjeld et al. 1997) whereas experimental work with the sister species (the collared flycatcher, *Ficedula albicollis*; Michl et al. 2002), suggests that females may be selectively timing EPC to the period comprised between days 0 and +1 (Michl et al. 2002). For these reasons, we consider any potential effect of that uncertainty on our conclusions small.

A plethora of studies has shown that an early reproduction is one of the main determinants of breeding success in seasonally breeding taxa (e.g. mosquitoes, Kleckner et al. 1995; butterflies, Carvalho et al. 1998; birds, Table 14.2 in

**Fig. 2** Female probability of engaging in extra-pair paternity (*top*) or becoming secondary (*bottom*) in relation to laying date (as days after 1 May)

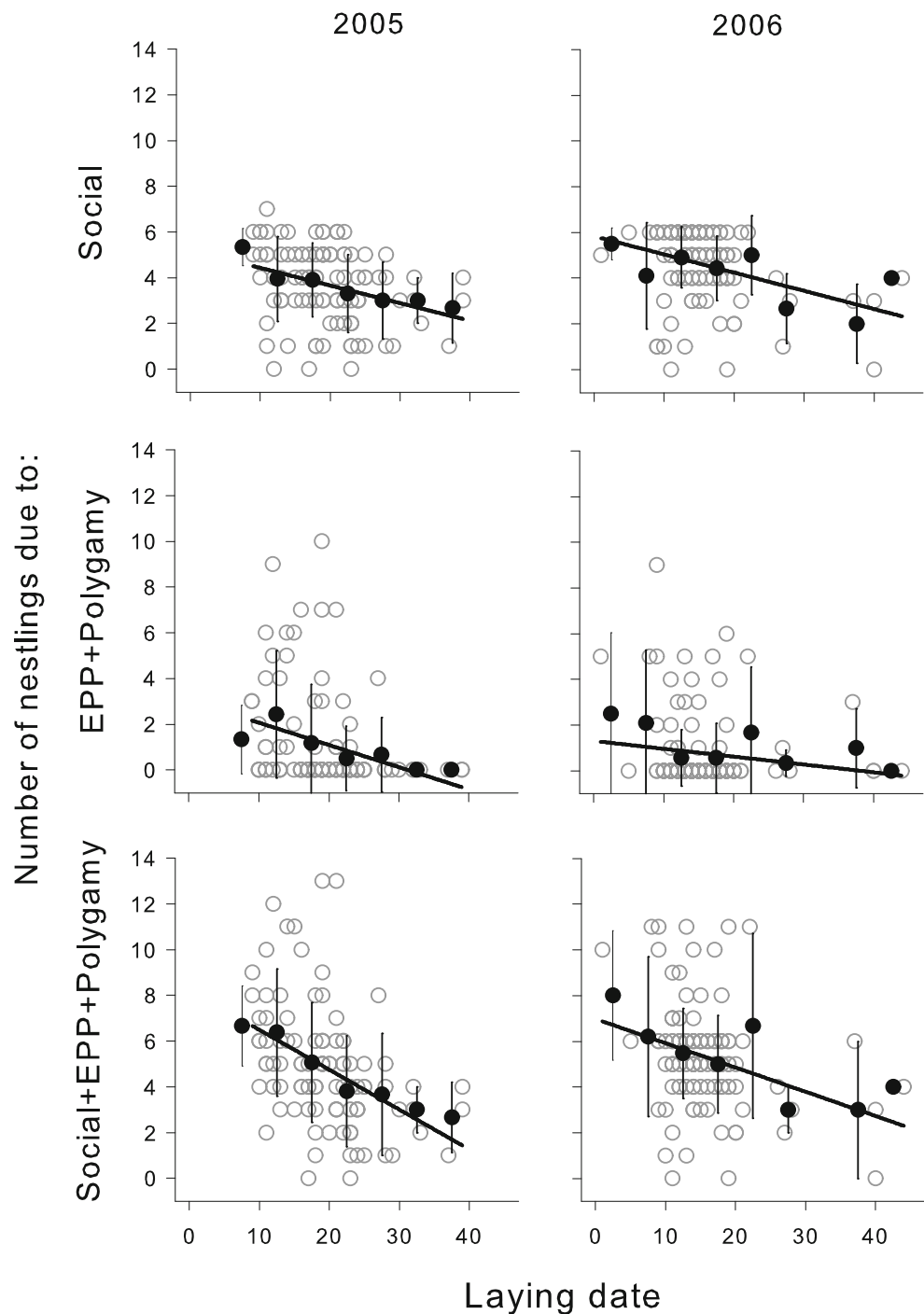


Newton 2008). However, an early phenology could impose costs due to adverse environmental conditions in the breeding areas at the beginning of the season (e.g. Morton and Sherman 1978; Crecco and Savoy 1985; Newton 2008). In birds, early arrival has been suggested to provide reliable information of male quality for females because only males in good condition can afford to arrive early (e.g. Arvidsson and Neergaard 1991; Lozano 1994; Møller 1994; Kissner et al. 2003, Møller et al. 2003, Smith and Moore 2005) due, for instance, to the risk of mortality by harsh environmental conditions (Brown and Brown 2000; Møller 2004; see also Table 4 in Newton 2006). Males, therefore, face a trade-off between the advantages and risks associated with an early arrival so that protandry should only appear when benefits for early arriving males outweigh costs derived from natural selection (Kokko 1999; Spottiswoode et al. 2006).

Both theoretical and empirical studies imply that competition for the best territories and increased mating success EPP strengthens selection for an early arrival in males as compared with females (Thornhill and Alcock 1983; Morbey and Ydenberg 2001; Kokko et al. 2006 and references therein). In some wasps and butterflies, protandry via mate opportunity is favored when females mate once, when most eggs are laid after the first mating or when sperm

precedence of the first male occurs (Wiklund and Fagerström 1977; Thornhill and Alcock 1983; Hastings 1989). Likewise, in some fishes and newts first males increase their chances of multiple matings and/or of siring more offspring (Morbey 2000; Tennessen and Zamudio 2003). In territorial birds, however, the acquisition of the best territories or resources selects for the earlier arrival of the territorial sex (Ketterson and Nolan 1976). In our population, early breeders enjoyed greater chances of additional matings than late breeders. By contrast, territory quality was unrelated to breeding date. Further, females did not attain EPP with males holding better territories nor did secondary females occupy worse territories than their male's primary territory. Similarly, at the population level extra-pair males did not occupy better territories than males not engaging in EPP, nor did territory quality vary across the range of social mating types (monogamous, primary or secondary pairings). Thus, habitat features seem not to be heterogeneous enough in our study area to promote protandry through competition for the best territories. Alternatively, if territory quality fluctuates widely from year to year, long-term quality measures (of occupancy and/or productivity) may not reflect territory quality in a particular year (Sergio and Newton 2003) as suggested by the lack of correlation between our long-term quality indexes and yearly reproduc-

**Fig. 3** Relationship between male fitness and the laying date (as days after 1 May) of their social pair. Male fitness is divided into two components: fitness attributable to the social pair (*top*), and fitness due to additional matings (*middle*). Overall reproductive output is also shown (*bottom*). Grey empty dots show raw data (one dot for each male); black dots show the mean (SD) in bins of 5 days (i.e., laying date 1–5, 6–10, 11–15, etc.), showing that the data followed the overall linear trend along the entire laying date range



tive success in the territories. Experimental settings (e.g. Alatalo et al. 1986; Lifjeld and Slagsvold 1988; Sirkiä and Laaksonen 2009) will surely provide further insights into female choice of male(s) characteristics and territory quality and their consequences for multiple mating. Recently, Kokko et al. (2006) have shown that the rank advantage hypothesis per se may fail to explain protandry in migrant birds since females are also expected to advance their arrival date (even more than males) when arriving late affects their fitness (e.g., by occupying poor territories). In fact, empirical work at both

within- and between-species levels has confirmed that competition for mates rather than territories positively influences protandry (Rubolini et al. 2004; Coppack et al. 2006; Møller et al. 2003, 2009). In accordance with these studies, the prospects of additional paternity seem to be the main factor promoting selection for an early social mate acquisition and thus an early male arrival in our population. Additionally, a male-biased adult sex ratio could be operating together with social polygyny and EPP in strengthening selection for protandry by accentuating within-sex competition

for mates (Kokko et al. 2006). However, as in other previous studies (e.g. Rubolini et al. 2004; Coppack et al. 2006; Saino et al. 2010), this association was not studied here due to the difficulty in obtaining reliable estimates of tertiary sex ratios in wild populations.

At least two factors, i.e., availability of fertile females and scarcity of competitors for mates, may influence multiple matings opportunities for early breeding males (Thornhill and Alcock 1983; Hastings 1989; Holzapfel and Bradshaw 2002). In our pied flycatcher population, most females were likely either arriving or still fertile when early males had already paired, which should increase the males' chances of multiple matings. Further, as few competitors for additional (genetic/social) matings would be present in the early stages of the breeding season this would increase the chances of gaining paternity while at the same time reducing those of cuckoldry (Birkhead and Møller, 1998; Fishman et al. 2003). From the female point of view, mating with early (i.e., high quality) males in extra-pair contexts could provide some type of direct/indirect benefits (e.g. Møller 1994; Lozano et al. 1996; Møller et al. 2003; Smith and Moore 2005). In fact, a number of studies, including one in this population (Canal et al. 2011), shows that EPP success covaries with male traits signaling quality (plumage ornamentation or song repertory; e.g. Weatherhead and Boag 1995; Kempenaers et al. 1997; Cordero et al. 1999; Bitton et al. 2007; Neto et al. 2010, see also Appendix 2 in Griffith et al. 2002). On the other hand, females mated with (early) polygynous males could benefit in future generations by the enhanced fitness of their offspring (e.g. by inheriting their fathers attractiveness; Weatherhead and Robertson 1979) despite suffering direct costs in their current reproductive success. Empirical studies dealing with the latter prediction have nonetheless reported contrasting results (Huk and Winkel 2008, see also Ligon 1999).

Phenological trends of genetic polygyny varied slightly between both study years. In 2006, a marked advancement (6 days) in the mean population breeding date with respect to the historical population mean ( $t=9.42$ ,  $P<0.001$ ) caused a decrease in the effective time to attain EPP. By contrast, the opportunities of becoming socially polygynous were not apparently affected by such advancement, likely because secondary females usually breed late in the season (Lundberg and Alatalo 1992; Fig. 2), contrary to the case of females engaging in EPP (Fig. 2). Since the variance in the number of mates strongly affects male fitness (Andersson 1994; Webster et al. 2007), our study highlights the adaptive importance of an early breeding (and hence, arrival) for males. Males should settle especially early in years wherein females rapidly become a scarce resource since a delay in their arrival may generate great loss of fitness opportunities (Kokko et al. 2006). The optimal arrival moment for males should depend on the interaction between individual phenotype

(its physical condition) and environment (changing ecological factors) since mortality rates are high early in the season and the onset of breeding likely matches food availability (Brown and Brown 2000; Jonzén et al. 2007). In contrast, males arriving simultaneously or later than females will lose mating prospects at a rate proportional to the number of females becoming infertile in the population each day, i.e., late-arrived males will not be able to mate with those females already incubating or rearing their chicks (Kokko 1999; Kokko et al. 2006).

To conclude, we found little support for territory quality favoring the evolution of patterns in breeding phenology or in (social and/or genetic) polygyny in this pied flycatcher population (i.e., the “rank advantage” hypothesis). However, our data provide supporting evidence for an increase in reproductive output for the earliest arriving males through higher success in both socially and genetically polygynous settings (i.e., “mating opportunity” hypothesis). Since EPP and social polygyny confer great advantages in male reproductive success, sexual selection may be underlying the different schedules in the arrival dates of males and females in this population.

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