

Behavioral Ecology (2020), XX(XX), 1-12. doi:10.1093/beheco/arz220

Original Article Socio-ecological factors shape the opportunity for polygyny in a migratory songbird

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Received 18 September 2019; revised 10 December 2019; editorial decision 12 December 2019; accepted 2 January 2020.

Why females pair with already mated males and the mechanisms behind variation in such polygynous events within and across populations and years remain open questions. Here, we used a 19-year data set from a pied flycatcher (Ficedula hypoleuca) population to investigate, through local networks of breeding pairs, the socio-ecological factors related to the probability of being involved in a polygynous event in both sexes. Then, we examined how the breeding contexts experienced by individuals shaped the spatial and temporal separation between broods of polygamous males. The probability of polygyny decreased with the distance between nests. Indeed, secondary females were often close neighbors of primary females, although the distance between both nests increased slightly with increasing synchrony between them. The probability of polygyny was also related to the breeding time of individuals because early breeding males were more likely to become polygynous with late-breeding females. Throughout the season, there was substantial variation in the temporal separation between primary and secondary broods, and this separation was, in turn, related to the breeding asynchrony of the polygamous males (in the primary nest) relative to the neighbors. Polygynous males that bred late relative to their neighbors had a short time window to attract a second female and, thus, the breeding interval between their primary and secondary broods was reduced. Overall, the spatial proximity between polygynous males' broods and, if the opportunity existed, their temporal staggering are compatible with a male strategy to maximize paternity and reduce the costs of caring for two broods, though the effect of female's interest, either primary or secondary, cannot be fully ruled out. We highlight that a comprehensive assessment of the breeding contexts faced by individuals is essential to understand mating decisions and reconcile the discrepancies raised by previous work on social polygyny.

Key words: mate choice, mating strategies, neighborhood, social polygamy, synchrony, pied flycatcher, polygyny.

INTRODUCTION

Mate choice and the evolution of mating systems are central issues in behavioral and evolutionary biology (Orians 1969; Emlen and Oring 1977; Ligon 1999; Shuster and Wade 2003). In birds, social monogamy is the predominant mating strategy, but a number of monogamous species are facultatively polygynous, with a proportion of males socially mating with two or more females (Lack 1968; Møller 1986). For males, social polygyny is assumed to be advantageous because the number of partners is closely related to their reproductive

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success (Andersson 1994; Webster et al. 2007). On the contrary, polygynous matings may entail fitness costs for females because some important resources, such as the male's territory and parental care, have to be shared with other females (Emlen and Oring 1977; Slagsvold and Lifjeld 1994; Magrath and Komdeur 2003; Ferretti and Winkler 2009). This conflict of interests between the sexes has stimulated several hypotheses on the evolution of social polygyny (see below; Orians 1969; Searcy and Yasukawa 1989; Slagsvold and Lifjeld 1994; Grønstøl et al. 2015) but, after decades of research, the debate continues about the adaptiveness of polygyny for females and the causes of its great variation across avian taxa within and among populations of the same species, across years, and among individuals

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(Searcy and Yasukawa 1989; Slagsvold and Lifjeld 1994; Shuster and Wade 2003; Halupka et al. 2014; Grønstøl et al. 2015).

Breeding strategies are likely to be context dependent: ecological (e.g., breeding synchrony by determining the number of fertile females at a particular time) and social (e.g., female aggressiveness) factors may affect mate choice and subsequent patterns of social polygyny (Emlen and Oring 1977; Searcy and Yasukawa 1989; Slagsvold and Lifjeld 1994; Shuster and Wade 2003; Grønstøl et al. 2014). Further, polygyny implies a conflict of interest between at least three parties: the polygynous male and two or more females. Thus, the relative influence of socio-ecological factors on one individual's behavior should depend on the strategies followed by all other individuals involved in a polygynous event (Slagsvold and Lifjeld 1994; Härdling et al. 2001; Grønstøl et al. 2014). For example, the benefits of mating with an already paired male early in the season (e.g., by providing superior genetic quality or territories; Alatalo et al. 1986; Forstmeier 2002; Reudink et al. 2009) may not compensate for the accompanying costs, such as aggressive encounters with the primary females and/or diminished paternal care. However, the opposite may be true late in the season due to the rapidly increasing costs of delaying breeding any further (Slagsvold et al. 1988; Slagsvold and Lifjeld 1994; Ferretti and Winkler 2009). Likewise, given that males and females have to meet each other to mate, the population-scale approach conventionally adopted in this field might not reflect the local mating opportunities for individuals, hence obscuring the determinants of social polygyny (Canal et al. 2012a; McDonald et al. 2013; Schlicht et al. 2015). For example, when males become polygynous in nearby territories, the level of breeding synchrony measured at the population scale may be too coarse to capture the actual number of accessible mates to the focal male. Thus, an approach considering all parties and the spatiotemporal scales at which individuals interact could greatly improve our understanding of the mechanisms maintaining social polygyny in natural populations (Härdling et al. 2001; McDonald et al. 2013; Schlicht et al. 2015).

In this study, we fill this gap by using a spatially explicit model to investigate how the current socio-ecological context relates to the spatial and temporal patterns of polygyny within local networks of breeding pairs. A key advantage of this approach is that, unlike the use of population-wide measurements, it allows modeling the local breeding contexts, as well as the male, female, and pair characteristics simultaneously so that their relative effects can be simultaneously assessed (Schlicht et al. 2015). As a model organism, we used the pied flycatcher (Ficedula hypoleuca), a songbird whose mating system has been widely studied and that exemplifies the discrepancies on the mechanisms underlying the evolution of social polygyny. The pied flycatcher is a long-distance migratory passerine that establishes a small territory around a nest hole (Lundberg and Alatalo 1992). Males arrive from the wintering areas before females, search for a suitable cavity, and compete for its possession. Although the species has a predominantly monogamous mating system, some males (<25%; Lundberg and Alatalo 1992) occupy a second nest cavity, attract a second female, and become socially bigamous (Alatalo et al. 1984; Lundberg and Alatalo 1992; Potti and Montalvo 1993; Canal et al. 2012b). Secondary flycatcher females often receive less assistance from the male than primary females and, as a result, their direct and indirect reproductive success is diminished in relation to monogamous and/or primary females. This contradicts a main prediction of the polygyny threshold model (Orians 1969), one of the most popular models to explain avian polygyny in resource defense mating systems. The lack of empirical support for this model has led to the emergence of alternatives to explain the maintenance and variation of polygyny in this (Alatalo et al. 1981;

Breiehagen and Slagsvold 1988) and other taxa (reviewed in Searcy and Yasukawa 1989; Slagsvold et al. 1992). For example, the deception hypothesis (Alatalo et al. 1981) states that males conceal their mating status by deceiving secondary females into believing that they remain unmated. By contrast, the female aggression hypothesis (Breiehagen and Slagsvold 1988) states that the spatiotemporal separation of the polygynous male's broods is explicitly caused by the aggressive behavior of primary females, whereas the asynchronous settlement model (Leonard 1990) predicts that the asynchronous settlement of secondary females will reduce the competition with the primary females for male assistance and food. These hypotheses mainly focus on the behavior of the male only (the deception hypothesis) or of one of the females, either the primary (female aggression hypothesis) or the secondary female (asynchronous settlement model). However, individuals may follow different strategies and may even shift them along the breeding cycle as a result of the interactions with the other players involved in the polygynous event and the potential competitors (Slagsvold and Lifjeld 1994; Grønstøl et al. 2014). Understanding how the social settings in a spatiotemporally structured environment influence individual decisions could, thus, help to reconcile the discrepancies raised by previous work on social polygyny.

Based on previous studies on pied flycatchers, we constructed a set of hypotheses from both the male's and the female's point of view. Pied flycatcher males are assumed to face a trade-off on paternity (Canal et al. 2012a, 2012b). On one hand, males should be selected to acquire an additional nest site and become polygynous to increase their reproductive success. On the other hand, males should invest heavily into their primary nest, both guarding their primary mate to assure paternity (extra-pair paternity rate in the study population [Canal et al. 2012a] is among the highest reported for the species; see Rätti et al. 2001; Slagsvold et al. 2001 and references therein) and, subsequently, providing brood care to increase the chances of offspring recruitment (Lifjeld and Slagsvold 1989; Magrath and Komdeur 2003). It is likely that only high-quality males are able to solve this trade-off optimally and acquire a secondary female. Because high-quality males typically breed early (e.g., Møller 1994; Kissner et al. 2003; Møller et al. 2004), we expect early breeding males to be more likely to acquire secondary females than late breeders. Additionally, males would preferentially become polygynous after the primary female's fertile period and before the eggs hatch. By doing so, they would avoid loss of paternity in the primary nest and could reduce the overlap between broods to invest in feeding the nestlings after hatching at both nests. Spatially, in contrast to what has been reported in Scandinavian populations (Lundberg and Alatalo 1992), we predict that males would try to acquire a second female in neighboring territories. We have shown that extra-pair paternity in the study population occurs between relatively close neighbors (Canal et al. 2012a). Thus, it is reasonable to expect that social polygyny, which implies energetic and time costs associated with the defense and maintenance of two broods, also occurs in neighboring nests (Adams 2001; Hinsch and Komdeur 2010; Veiga et al. 2014). Nonetheless, the optimum time and distance for pairing with a second female should be contingent on breeding synchrony and density because these two parameters widely vary between years in this population (Canal et al. 2012b; Camacho et al. 2013) and may ultimately determine mate availability. For example, a high breeding synchrony, where fertile females are temporally concentrated, is expected to reduce the time interval between polygynous male's broods, whereas a high density will increase their distance as a result of male-male competition and the aggressiveness of primary females (Slagsvold et al. 1992). Regarding females, being a secondary mate entails important disadvantages (e.g.,

aggressiveness of the primary female, reduced male care) in comparison to the primary females. Thus, females unable to find a mate providing exclusive assistance (assuming they are able to detect the male pairing status) are expected to postpone reproduction until the costs of delaying breeding exceed those of being secondary. Spatially, secondary females are expected to avoid aggression from the primary female by breeding farther away, while breeding close enough to receive sufficient assistance from the male.

These hypotheses as a whole suggest that early breeding males are more likely to pair with late-breeding females, ideally, while the male's primary female is incubating. The distance between the nests of the primary and the secondary female likely depends on whether the male capacity to defend a secondary nesting site (shorter distance) or the aggressiveness of the primary female (larger distance) is driving the settlement patterns of the secondary female. To test the predictions above (summarized in Table 1), we 1) focus on the spatiotemporal scale at which polygynous interactions occur; 2) disentangle the particular breeding contexts experienced for each male–female combination in the population (e.g., breeding synchrony with other individuals in the neighborhood); 3) analyze how these particular contexts affect the probability of polygyny; and 4) examine how this is reflected in the temporal and spatial distribution of primary and secondary broods at the population level.

MATERIAL AND METHODS

Study system and general procedures

Data were obtained from a pied flycatcher population breeding in nest boxes in central Spain (ca. 41°4′42″ N, 3°25′55″ W, 1200–1300 m asl) during a long-term study conducted from 1995 to 2016. Sampling intensity was limited in the years 1996, 2002, and 2003 and, therefore, these years were excluded from analyses. In total, we use data from 19 study years.

The study system consists of two nearby (1.1 km) plots: a mature oak (*Quercus pyrenaica*) forest of 9.3 ha and a mixed pine (dominated by *Pinus sylvestris*) plantation of 4.8 ha, separated by unsuitable breeding habitat for pied flycatchers. The area includes 237 georeferenced next boxes (156 and 81 in the oak and pine forest, respectively) at a mean distance of 30 (standard error [SE] 14.1) m. Nest boxes were provided in 1984 (oak forest) and 1988 (pine plantation) and maintained until nowadays. See Camacho et al. (2015) for a detailed description of the study area.

Field protocols have been described in detail elsewhere (Canal et al. 2011; Camacho et al. 2015). Briefly, the breeding season in our population typically lasts from mid-April (with the arrival of males) until the beginning of July (when last nestlings fledge). All nest boxes were checked regularly to ascertain the onset of laying (laying date, hereafter), clutch size (typically, 5-6 eggs), hatching date (of the first hatchling), and number of fledglings. Parent birds were captured while incubating (females) or feeding nestlings (both sexes) with a swing trap (Friedman et al. 2008) placed inside the nest box. Birds were individually marked with a numbered metal band and a unique combination of color bands. For those males that were not captured with the swing trap during the first trapping attempt (when nestlings aged 8-days old), the nest was monitored during periods of 30-60 min on successive days until fledging (approx. 15-days old), unless a male assisting the brood was seen before. Nest observations were mainly conducted during the dawn and dusk peaks of feeding activity to maximize the chances of male detection. When we observed a male assisting the brood, we recorded his unique color-band combination and, if possible, captured him. Identification and subsequent capture efforts were similar for all the cases in which males were not caught in routine trapping sessions.

Determination of breeding status

A male was considered socially polygynous when it had been observed and/or captured while feeding nestlings in another nest. All polygynous males were bigynous. Four categories of social mating status were assigned to females and their broods (note that, along this study, we only discuss social behaviors, not genetic mating patterns, which were investigated in: Canal et al. 2011, 2012a, 2012b): 1) females of socially monogamous males (n = 2358); 2) primary females of polygynous males (n = 105); 3) secondary females of polygynous males (n = 105), defined as those with a later laying date in relation to the primary female and with relatively frequent assistance of the male in chick feeding; in six cases, primary and secondary females had the same laying date and the brood status was assigned according to the level of assistance of the male in each social brood (lower in secondary broods; Alatalo and Lundberg 1984; Lifjeld and Slagsvold 1989; Lundberg and Alatalo 1992; Potti and Montalvo 1993); 4) females without any confirmed male assistance, where no male was ever observed feeding the nestlings (n = 59). These females may have been either secondary females, deserted by

Table 1

$Hypotheses \ (H) \ and \ predictions \ (P) \ concerning \ the \ parameters \ potentially \ related \ to \ the \ occurrence \ of \ polygyny \ in \ the \ study \ population$

	Hypothesis	Prediction
Laying date and	(Locally) early breeding males (= high quality)	(Locally) early breeding males are more likely to
breeding asynchrony	should be more likely to become polygynous.	become polygynous with (locally) late-breeding females
	Males should temporally separate their broods	The importance of the laying date of the opposite sex
	to allocate resources.	should be strongest for late (polygynous) males and
	Females suffer costs from being polygynous.	early secondary females (= asynchrony; interaction of
	Therefore, only low-quality females (= [locally]	laying date male and laying date female).
	late breeders) should become polygynous.	, , , , , ,
Breeding distance	Energy and time costs of holding two territories increases with distance	Probability of polygyny decreases with distance
Number of	The proportion of polygynous events depends	The number of polygyny events will change
neighbors	on the availability of males	proportionally with the number of neighbors

Male-female combination

their mates, or become widowed after pairing. Because male identity and female mating status were uncertain, data from these nests cannot be used to explore questions on polygyny (see below). The exclusion of unassisted females might bias our analyses if most of the unassisted females are indeed secondary females of males with a different spatiotemporal pattern (e.g., breeding far from the primary nest) from that found in the confirmed cases of polygyny (see Results). However, genetic data from a 2-year study on paternity in this population (Canal et al. 2012a) argue against such possibility since the offspring from nests without observed male assistance were sired by either: 1) unknown individuals (i.e., nonbreeding in other nests; 58%), which can be floaters (which by definition are neither monogamous nor polygynous) or have presumably been depredated before sampling (the population is sampled entirely and breeding outside the study area is an extremely rare event; pers. obs., Potti and Montalvo 1991a), or (ii) males from a nearby nest (42%; <50 m), which can be either extra-pair fathers or polygynous males that provided no or little assistance to the females. In the latter case, the spatial (<50 m) and temporal separation (range: 6-18 days) between the broods (i.e., the genetically identified and that observed in the field) of these males was also similar to that found for the confirmed polygynous males (see Results). Thus, it is unlikely that the exclusion of unassisted females would bias the results of this study; if any such bias occurs, it is expected to be minimal because, for most females, their pairing status is clear (98%, on average, for the whole study period).

Spatiotemporal model of polygyny

To investigate the factors underlying the spatiotemporal distribution of polygyny, we adapted a spatially explicit method proposed by Schlicht et al. (2015). This approach, originally developed in the context of extra-pair paternity, can be easily adapted to investigate other types of individual interactions, such as polygyny. In our study case, male pied flycatchers arrive at the breeding areas before females and females visit several males before settling (Dale and Slagsvold 1996; Canal et al. 2012b). Similar as for extra-pair paternity, all individuals, therefore, make a choice about whether or not and with whom to pair up in a polygynous situation. The method proposed by Schlicht et al. (2015) allows, thus, examining which specific individuals become polygynous with each other within local networks of breeding pairs.

Under this approach, all the male-female combinations that may occur in a population are taken into account such that all breeding females (except the primary females) are considered as potential secondary mates for each focal male. For every male-female combination, it is possible to investigate different types of features: 1) attributes of the pair, for example, the distance between nests, 2) attributes of the male, for example, the laying onset of the male's primary female, and 3) attributes of the female, for example, the laying onset of the secondary female. These attributes can then be used to explain the probability of polygyny for the focal male-female combination, that is, the probability that this specific male becomes polygynous with this specific (secondary) female. This information is analyzed using a generalized linear mixed model (GLMM; binomial distribution). For every male-female combination, the occurrence of polygyny (no/yes; the latter coded for the combination between the polygynous male and the secondary female) is the response variable and their attributes are included as the explanatory variables. The advantage of this approach is that it allows testing simultaneously multiple variables related to the breeding contexts of each individual (and, thus, multiple hypotheses) in one single model by including the information of all other potential mates in the population, regardless of their success in becoming polygynous. In addition, by considering the breeding distance in the model, it is possible to identify correlations due to the underlying spatial structure of the data and to distinguish local effects from population-wide effects. Importantly, as shown by Schlicht et al. (2015), when male and female identities are modeled as random effects, considering all male–female combinations in a model does not reduce the power of the tests nor inflates the type I error rate.

For the aim of this study, we have focused exclusively on socioecological parameters potentially affecting the probability of polygyny, such as laying date, breeding distance, number of neighbors, and breeding synchrony (specific hypotheses and predictions for these variables are outlined in Table 1). We defined breeding distance as the straight-line distance in meters between the focal male and female. Further, we assessed the spatial distribution of territories within each breeding season using Thiessen polygons, which were estimated with the packages *expp* (Valcu et al. 2018) and *spatstat* (Baddeley and Turner 2005) in R version 3.3.2 (R Core Team 2019). Thiessen polygons partition the breeding area into regions, hereafter, the territories, based on the Euclidean distance between occupied nest boxes, so individuals were coded as first-order (direct), second-order neighbors, and so on. As key advantages, the partition by Thiessen polygons is sensitive to variation in breeding densities (e.g., territories will be smaller at high densities) and also allows defining the identity of neighbors for all the individuals (for details, see Valcu and Kempenaers 2010; Schlicht et al. 2015). We used the term "neighborhood" to refer to all the individuals breeding both closer and at the same territory of distance as that between the focal male and female. Therefore, if any specific male-female combination was constituted by individuals breeding at a distance of two territories, the variables at the neighborhood level (e.g., local synchrony) were calculated in relation to all the direct and second-order neighbors of the male (male neighborhood) and all the direct and second-order neighbors of the female (female neighborhood). Results (not shown) remained similar if the second-order neighborhood included only the second-order neighbors as originally described by Schlicht et al. (2015). Note that the male and female neighborhoods are by definition not identical. Depending on the position of the nest of a focal individual within the area, some neighbor identities may be shared between the focal male and focal female.

Breeding density was defined as the number of neighbors of the focal male–female combination. To account for differences in the number of neighbors among breeding distances, this variable was centered using the mean number of neighbors found at the respective distance throughout the population each year (see Schlicht et al. 2015).

Breeding synchrony is often defined as the proportion of fertile females per day in a population (Kempenaers 1993). To obtain an analogous variable at the local level for each female–male combination, we calculated the "relative breeding asynchrony," defined as the mean difference in laying (first egg) dates between the focal male–female combination and all alternative potential pairs in the neighborhood (Schlicht et al. 2015). Relative breeding asynchrony was calculated from the focal male's perspective (relative to all other potential pairs surrounding a given male) and from the focal female's perspective (relative to all other potential pairs surrounding a given female). This variable, therefore, reflects if a given individual breeds early or late in relation to his/her neighbors.

One might argue that the pair needs to be established before egg laying occurs and that our approach, which is based on laying dates, might, therefore, not be representative of the contexts experienced when pair-bonding occurred. However, we argue that individuals from the same neighborhood experience similar environmental and social conditions before and during pair formation. Therefore, it is likely that pair formation dates and laying dates are strongly correlated within neighborhoods. That means that differences in laying dates between the females (hereafter, ΔLD) within the neighborhood are equivalent to their differences in pairing dates and, thus, suitable for this analysis. However, environmental factors, such as temperature, precipitation, or food availability, may cause between-individuals differences in the prelaying period (days from mating to first egg date; Slagsvold et al. 1988; Bêty et al. 2003; Jonzén et al. 2007). Accordingly, late females are expected to have shorter prelaying periods than earlier ones as the latter would have more time to optimize their breeding date according to the environmental conditions (Potti 1999; Bêty et al. 2003). As a result, we might be overestimating the prelaying interval of secondary females as compared with earlier primary females and, therefore, their laying date differences, particularly, in early cases of polygyny. Despite this potential issue, we are confident that our approach is reliable because: 1) using prelaying periods available for a subset of years, we showed that there are no differences in the prelaying period according to the female's mating status (monogamous, primary, and secondary females; Tukey contrasts, Global test: $\chi^2_2 = 3.1$, P = 0.21; 2) the laying intervals between broods of early polygamous males were large (highest frequency of Δ LD was between 10 and 15 days; see below), so even if the Δ LD is overestimated, most polygamous bonds would possibly be established within the primary female's incubation period (see Results); 3) given that late polygamous males had short laying intervals between broods, the potential bias resulting from our assumption is low. Furthermore, if any, this potential bias would reinforce the evidence pointing out mate choice constraints in those late neighborhoods (see below).

Statistical analyses

Socio-ecological contexts and the probability of polygyny

To analyze how socio-ecological factors are related to the probability of polygyny, we fitted a GLMM (binomial distribution and logit scale) wherein all possible male-female combinations in the population were considered (see above). The occurrence of polygyny (yes/no) for each pair was included as the response variable, whereas six parameters defining the male's and female's breeding contexts were included as predictors: breeding distance (defined for the male-female combination), male's breeding date and his number of neighbors, female's breeding date and her number of neighbors, and the interaction between male's and female's breeding date. This interaction can be interpreted as the overall time span between primary and secondary broods. Exploratory analyses showed that male and female local asynchronies were strongly correlated with breeding date in males (r = 0.79, P < 0.001) and females (r = 0.83, P < 0.001), respectively. Thus, individuals breeding early in the population also bred early (i.e., asynchronously) relative to their neighbors and vice versa. Since strong collinearity may bias the model output, we excluded male and female local asynchronies from the model above. Male and female identities were included as random factors in the model to account for repeated observations of the same individuals because we considered all possible

male-female combinations in each year and a fraction of adults (41% of males and 43% of females) bred in two or more seasons. Initially, year was also included as a random factor, but the models did not converge, possibly, due to the low or null occurrence of polygyny in some study years (see Supplementary Table 1).

Socio-ecological contexts and the spatial separation between the broods of polygamous males

To explore whether the distance between the nests of polygynous males was related to the breeding context, we used a GLMM (Gaussian distribution). In these analyses, we restricted the data to the cases of polygyny exclusively. Distance between nests of a polygamous male (log-transformed to meet normality) was included as the response variable. Laying dates of the primary and secondary females and the number of neighbors relative to both the primary and secondary female were included as explanatory variables, whereas year was included as a random factor. Note that asynchrony between broods resulted from the difference between the primary and secondary female's laying dates and, thus, the three parameters could not be included together in a model. For this reason, we fitted another model on distance with the exception that asynchrony between polygynous male's broods (rather than the male's and female's laying date) was included as a predictor. By doing so, on one hand, we aimed to test whether the distance between primary and secondary broods was independently affected by the breeding dates of the male and the female. On the other hand, we directly tested whether asynchrony between broods of polygynous males was related to their distance.

Socio-ecological contexts and the temporal separation between the broods of polygamous males

To explore whether the degree of asynchrony between primary and secondary broods (as a response variable) was related to the breeding context, we used a GLMM (Gaussian distribution). As in the spatial model, this analysis only considered male–female combinations that resulted in polygynous matings. The breeding date of the polygynous male's primary female, the number of neighbors relative to both the primary and secondary female, and the distance between both nests were included as predictors, whereas year was included as a random effect. Because asynchrony between broods resulted from the difference between the primary and secondary female's laying dates, secondary female's laying date was not included as a predictor in this model.

Before interpreting any model outcome, we systematically performed several model diagnostics statistics (e.g., distribution of residuals, multicollinearity, and influential data points) to avoid misleading results based on statistical artifacts. These analyses did not show any obvious deviations from the assumptions of linear models.

Statistical analyses were performed using R version 3.3.2 (R Core Team 2019) with the packages *lme4* (Bates et al. 2014) and *lmerTest* (Kuznetsova et al. 2017). Package *DHARMa* (Hartig 2016) and VIF function, available in package *car* (Fox and Weisberg Sanford 2011), were used for model diagnostics.

RESULTS

Overall, there were 105 cases of social polygyny with male assistance during the 19 breeding seasons under study, with a rate of polygyny ranging from 9.5% (13/135 nests) in 2005 to 0% in 1997 and 2001 (141 and 101 nests, respectively; Supplementary Table 1). The probability of polygyny decreased with breeding distance (Figure 1a and Table 2) and was independently affected by the male's and female's breeding dates (interaction male × female breeding date: P = 0.12; Table 2). Males breeding early in the season increased their probability of becoming polygynous, whereas females breeding late increased their probability of mating with an already mated male, thus becoming secondary females. Overall, polygynous pairs were, therefore, most likely to occur between early breeding males and late-breeding females. Neither male's nor female's number of neighbors affected the probability of polygyny (Table 2).

Most (93.3%) polygynous pairings occurred before nestlings of the primary brood had hatched, and the frequency of polygyny peaked during the primary female's incubation period, that is, after the primary female fertile period (Figure 1b,c). To visualize these results in the Figure 1b,c, note that 1) egg formation in small passerines take less than 5 days (and environmental cues may stimulate ova development before pairing; Williams 2012), 2) the period from mating to laying is expected to be shorter in late females relative to earlier ones (Potti 1999), 3) the fertile period in the study species ranges from day -2 until the day the penultimate egg is laid (Birkhead and Møller 1992; Lifjeld et al. 1997), and 4) incubation often begins the day the penultimate egg is laid (Potti 1998). On average, the laying date interval between the primary and secondary females of polygynous males was 9 (range = 0-23) days (Figure 1b), but it was tightly related to the breeding phenology of individuals: ΔLDs decreased throughout the season (Figure 2), that is, polygynous males breeding early (thus, asynchronously to their neighbors) had large laying date intervals with their secondary females relative to later polygynous males, possibly, due to fertile females being available for a longer time span. Further, breeding intervals between females of polygynous males increased with the number of neighbors surrounding the primary female's nest, perhaps, as a result of male competition for breeding sites or fertile females (Table 3).

In 82% of the cases of polygyny, the secondary female was the nearest or next-to-nearest neighbor (Figure 3) and only four cases occurred further than two territories away. On average, the distance between the primary and secondary nests of a polygynous male was 39.6 m (range = 19–166; 90th percentile = 65.6 m). The distance between primary and secondary nests was related to the laying date of both the primary and the secondary females (Figure 4 and Table 4). In particular, the distance between broods of polygynous males increased with the primary female's laying date. The distance between primary and secondary broods also increased with the overlap between the two broods (note that Δ LDs decreased along the season; see above). Neither the number of neighbors of the primary female nor that of the secondary female was related to the distance between broods of polygynous males.

DISCUSSION

By using a spatially explicit model that considers local networks of breeding pairs, we have shown how the specific breeding contexts faced by individuals shaped their mating strategies and, subsequently, the spatial and temporal separation between the broods of polygamous males. As we will discuss below, the spatial proximity between polygynous male's broods (most secondary nests were in the nearest or next-to-nearest territory) and, if the opportunity existed, their temporal staggering could arise as a male strategy to maximize paternity and reduce the costs of caring for two broods. However, the interest of (primary and secondary) females could also have contributed to these patterns.



Figure 1

Probability of engaging in polygynous mating (dots; percentages from the raw data) and cases of polygyny (bars) according to (a) the distance between nests and (b) the time interval between the laying date of the primary and secondary female of polygynous males. (c) Temporal distribution of cases of polygyny in relation to the laying dates of the neighbors. Secondary females (black dots), as well as all other females surrounding the neighborhood (white dots), are shown in relation to the primary female's laying date (dashed line). The x axis indicates whether neighboring females bred before (negative values; not accessible females) or after (positive values; accessible females) the primary female. Neighborhoods are sorted by increasing asynchronies of the male's primary female regarding the neighbors in the y axis. The shaded area indicates the fertile and incubation periods of the male's primary female.

The probability of polygyny for a male–female combination decreased rapidly with the distance between nests. From the male's perspective, this was a somewhat expected result because males first have to monopolize a second nest box to become polygynous. Thus, occupying neighboring territories would allow males to reduce the costs of holding two territories, such as those associated with defense and parental care (Adams 2001; Hinsch and Komdeur 2010; Veiga et al. 2014). The interest of females could also have shaped this spatial pattern as, for example, secondary females could receive more

Table 2	2
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Results of the GLMM analyzing the probability of polygyny in relation to the breeding contexts experienced by individuals

Random effects	Variance	SD		
Female	0.000	0.000		
Male	1.00E-14	1.00E-7		
Fixed effects	Estimate	SE	z	P
Intercept	-3.334	0.247	-13.482	< 0.001
Distance (meters)	-0.047	0.005	-8.866	< 0.001
Female's breeding date	0.061	0.010	6.300	< 0.001
Male's breeding date	-0.114	0.018	-6.366	< 0.001
Female's × male's breeding dates	0.002	0.002	1.527	0.127
Female's number of neighbors	0.003	0.035	0.081	0.935
Male's number of neighbors	-0.040	0.034	-1.181	0.238

SD, standard deviation.



Figure 2

Breeding date in relation to the local asynchrony (days) of males (a) and females (b). Negative values indicate individuals breeding early relative to all birds of the population (*y* axis) or their neighbors (*x* axis). (c) Difference of laying dates between primary and secondary females of polygynous males in relation to breeding date of polygynous males in the primary territory.

parental care by nesting close to the primary female. In either case, the close proximity between broods of polygynous males questions some of the theories explaining polygyny in the species, such as the "male deception" and "female aggressiveness" hypotheses, as discussed below. Otherwise, given that nest boxes are a limited resource in our population, males have to compete intensively, intraspecifically and interspecifically (with tits [*Paridae*], treecreepers [*Certhia brachydactyla*], and nuthatches [*Sitta europaea*]) for nesting sites (Camacho et al. 2013). Thus, our findings suggest that males becoming polygynous should be of intrinsic high quality (Canal et al. submitted) to be able to occupy and defend two nesting sites according to their own interests (Hinsch and Komdeur 2010; Veiga et al. 2014), that is, in close proximity.

Breeding date was another factor related to the probability of being involved in a polygynous event in both sexes. For males, the likelihood of acquiring a secondary female decreased as the season advanced, whereas for females the probability of mating with an already mated male increased throughout the season. In both sexes, these effects were mediated by the level of asynchrony of individuals relative to their neighborhood because individuals bred progressively later in relation to their neighbors as the season advanced (Figure 2a,b). Thus, by breeding early in the primary nest, males would maximize their chances of acquiring multiple nesting cavities and additional matings via social polygyny (but also through extra-pair paternity; Canal et al. 2012b) because many fertile females would still be accessible afterward (Hasselquist 1998; Coppack et al. 2006; Kokko et al. 2006). Indeed, in species with a mixed-mating strategy, the opportunity of additional paternity seems to be the main mechanism underlying the earlier arrival (a proxy of breeding date) of males to the breeding areas compared to females (Rubolini et al. 2004; Coppack et al. 2006; Kokko et al. 2006). On the other side of the coin, late females would encounter numerous mated males but few or no unmated males in the area, thus increasing their chances of becoming secondary. Interestingly, we found that the probability of polygyny for a male-female combination was independently related to the breeding dates of the male and the female. This suggests that either 1) only early breeders were able to hold a second nesting site or 2) that the polygynous events resulted from the active behavior of males, but also of females, which would prefer to mate with an early-and presumably high-quality-breeder over a late-arrived-and presumably low-quality-male (Møller 1994; Kissner et al. 2003; Møller et al. 2004). By doing so, secondary females could obtain some type of indirect benefit, such as an enhanced fitness of the offspring if, for example, sons inherit the quality of their father (Weatherhead and Robertson 1979; Huk and Winkel 2006). This could indeed be a plausible scenario in the study population as several traits indicating individual quality, such as the plumage blackness or the forehead patch size, are related to the breeding date of individuals and, hence, to the probability of polygyny (Canal et al. submitted).

Table 3

Results of the GLMM analyzing the relation between the breeding contexts experienced by individuals and the breeding date intervals between females of polygynous males

Random effects	Variance	SD			
Year	5.841	2.417			
Residual	18.51	4.302			
Fixed effects	Estimate	SE	df	t	P
Intercept	7.380	1.327	61.856	5.562	< 0.001
Distance (meters)	-0.034	0.025	90.341	-1.351	0.180
Male's breeding date	-0.556	0.095	86.396	-5.869	< 0.001
Male's number of neighbors	-0.519	0.169	94.192	-3.067	0.003
Female's number of neighbors	0.141	0.174	86.635	0.806	0.422

SD, standard deviation.



Figure 3

Spatial distribution of cases of polygyny (black dots) in relation to accessible (gray dots) and nonaccessible (by breeding earlier; white dots) females around the male's nest. Temporal thresholds to qualify a female as accessible or not were adjusted annually based on the largest laying date interval between broods of a polygamous male in each year. Each tick on the *x* axis (and, therefore, each series of vertical of dots) shows a case of polygyny, for example, two polygynous cases in 1999. Note that, in 1997 and 2001, there were no cases of polygyny and that years 1996, 2002, and 2003 were excluded from analyses (see Methods). For illustrative purposes, the maximum distance shown (*y* axis) is 108 m as, only in one case, polygynous male's broods were located further (166 m).

Other social factors, such as the male and female number of neighbors (i.e., breeding density), did not have a significant effect

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Figure 4

(a)

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Distance between primary and secondary females of polygynous males in relation to (a) the breeding date of the primary female and (b) the difference in their breeding dates. Negative values in breeding dates indicate individuals breeding early relative to all birds in the population. in the model assessing the probability of polygyny. In our statistical model, we corrected the number of polygynous events for the number of available mates by repeatedly introducing the identity of individuals as many times as potential mates are present in the population. The nonsignificant effect of breeding density suggests, therefore, that the number of polygynous events increased proportionally with the availability of mates in both sexes (see Schlicht et al. 2015), which may occur, for example, when an increased number of neighbors favors the settlement of females as secondary females.

The synchrony between primary and secondary broods increased throughout the season. Several factors related with the contrasting interests of the individuals involved in polygyny could lead to the greater temporal separation between the broods of polygynous males in early neighborhoods. High numbers of surrounding fertile females early in the season may augment the aggressiveness of already mated females to hinder their males from attracting a new mate (Slagsvold et al. 1992; Grønstøl et al. 2014) and/or the competitiveness among males for fertile females. However, these two possibilities seem not to apply in our study system since the time interval between polygynous male's broods decreased (instead of increasing) with the male's number of neighbors. Alternatively, secondary females may have either 1) unsuccessfully attempted to become a primary female or 2) deliberately delayed breeding to reduce the overlap with the primary brood as a strategy to benefit from increased male parental care (Leonard 1990; see below) and/ or to avoid agonistic interactions with the primary female (Slagsvold and Lifjeld 1994). However, as occurs in other migratory species (Newton 2008), reproductive success in pied flycatchers decreases rapidly as the breeding season progresses (Lundberg and Alatalo 1992; Canal et al. 2012b). Thus, it seems unlikely that this possibility fully explains the temporal distribution of primary and secondary broods. Finally, as reported in the context of extra-pair paternity (Canal et al. 2012a), early males may postpone their search for additional paternity as a strategy to optimize the trade-off between costs and benefits of additional matings. First, that strategy would allow males to maximize the certainty of paternity in the primary nest by guarding the primary female during her fertile period because many females will still be fertile afterward. Second, it might enhance the breeding success in both the primary and secondary broods because the asynchrony between the two mates would allow males to allocate parental care to both broods, avoiding the negative consequences of reduced attendance on recently hatched nestlings (Slagsvold and Lifjeld 1994; Magrath and Komdeur 2003; but see Lifjeld and Slagsvold 1989). Under this view, "late" polygynous males may be time constrained to find fertile females (Figure 1c),

Table 4

Results of the GLMM analyzing the relation between the breeding contexts experienced by individuals and distance between nests of polygynous males

Random effects	Variance	SD			
Year	0.000	0.000			
Residual	0.2675	0.5172			
Fixed effects	Estimate	SE	Df	t value	Р
Intercept	3.695	0.097	95	38.024	< 0.001
Male's breeding date	0.022	0.011	95	2.098	0.0386
Female's breeding date	-0.024	0.011	95	-2.267	0.0257
Male's number of neighbors	-0.017	0.020	95	-0.842	0.4019
Female's number of neighbors	0.013	0.020	95	0.639	0.5245

SD, standard deviation.

leading them to remate immediately after the primary female's egg laying. The fact that the chances of polygyny were mostly concentrated during the primary female's incubation period also concurs with a male's decision about when it would pay to search for an additional mate, that is, after the primary females' fertile period to avoid paternity loss and before egg hatching because males will be focused on parental duties afterwards (Magrath and Komdeur 2003; Kokko and Morrell 2005; Canal et al. 2012a).

The spatial pattern found here, with most secondary females being close neighbors of the primary ones, is in sharp contrast with that reported in other populations (Alatalo et al. 1990; but see von Haartman 1951). In fact, the pied flycatcher is the classic example of polyterritorial polygyny, with bigamous males usually holding distant territories (Alatalo et al. 1981; Breiehagen and Slagsvold 1988; Alatalo et al. 1990; Lundberg and Alatalo 1992), separated on average by 200-250 m. Nonetheless, secondary nests farther than 1 km from the primary nest have also been recorded (Table 1 in Alatalo et al. 1990; Artemyev 2018). Concerning the main hypotheses postulated to explain polygyny in the pied flycatcher, our findings suggest that males did not try to conceal their mating status from secondary females (as suggested by the deception hypothesis; Alatalo et al. 1981) and/or that primary females were not aggressive enough to prevent their male from mating again (as suggested by the aggressiveness hypothesis; Breichagen and Slagsvold 1988). However, a scenario of secondary nests adjacent to primary territories is still compatible with a male deceptive and/or female aggressive behavior when males are able to stagger their broods. This may occur, for example, because polygynous males are early breeders and still have a good chance to acquire a second female (Bensch and Hasselquist 1991; Kokko et al. 2006; Canal et al. 2012a) as seems to occur in our population. By doing so, males may 1) take advantage of the long time the primary females spend incubating (Lundberg and Alatalo 1992) to hide their reproductive status to prospecting females, even if this requires behaving like an unmated male (Searcy et al. 1991) and/or 2) reduce aggressiveness of the primary, already unfertile, female because aggressiveness drops over the females' reproductive cycle (see Tables 1 and 2 in Slagsvold and Lifield 1994). Indeed, we found that the distances between the primary and secondary nests slightly increased with the overlap between broods, suggesting that the aggressive behaviors of the primary female could possibly have contributed to the spatial distribution of bigamous nests. Further, time-related constraints may lead females to remain with a polygynous male, even if the female finds out the male's mating status or the latter clearly reveals it (Alatalo et al. 1981; Stenmark et al. 1988). Time-related constraints may also lead to a higher resilience of late, secondary females to potential aggressions from primary females (Slagsvold and Lifjeld 1994), thereby favoring the closeness between primary and secondary broods.

Concluding remarks

We have shown that the probability of polygyny decreased with the distance between broods and that it was related to the breeding time of individuals. Breeding date was also a crucial factor shaping both the spatial and temporal separation between primary and secondary broods. The spatiotemporal patterns of polygyny described here are compatible with the male's breeding strategies (according to actual availability of mates) to maximize fitness, but the behavior of the primary (aggressiveness toward prospecting females) and secondary (ability to avoid aggressiveness or costs of delaying breeding) females possibly contributed to shape these patterns. Given the correlational nature of our study, we cannot determine the relative contribution of male and female interests to the observed patterns of social polygyny. However, we emphasize the importance of accounting for the breeding contexts of all the players involved in polygynous liaisons because, as suggested by theoretical and empirical work, several models on the evolution and maintenance of social polygyny may operate together under different ecological contexts.

SUPPLEMENTARY MATERIAL

Supplementary data are available at Behavioral Ecology online.

FUNDING

This work was supported by grants from the Spanish Governments between 1987 and 2019, most recently by projects CGL2014-55969-P and CGL2015-70639-P. D.C. was supported by a grant from the Spanish Ministry of Education and Science (grant number I3PBDP2005). C.C. received financial support from the Spanish Ministry of Economy and Competitiveness (grant number SVP-2013–067686).

We thank all those persons, too numerous to name individually, who helped with data collection throughout the years.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Canal et al. (2019)

Handling editor: Ulrika Candolin

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