Origin and outcome of social polygyny in the Blue Tit

Emmi Schlicht & Bart Kempenaers[*]

Classic explanations for polygyny consider habitat, genetic makeup and paternal care, but little attention has been paid to social inertia. We studied facultative social polygyny in a population of Blue Tits *Cyanistes caeruleus* with a low rate of polygyny (3% of males across 12 years). Occurrence of polygyny was best predicted by social turnover after the disappearance of one or more individuals; habitat quality and individual phenotypic traits were unimportant. Females settled as secondary females with a male and in an area they had previously associated with, indicating a role of familiarity in the formation of polygyny. Females mated to polygynous males received less help feeding nestlings. Reduced paternal care is potentially costly, because these females survived less well than females mated to monogamous males. Reduction in care occurred at both primary and secondary nests although polygynous males rarely divided their care between nests. On any given day during the nestling period, polygynous males were more likely than monogamous males to not feed nestlings at all and – as a consequence – polygynous males provided less care in total than monogamous males. Polygynous males rarely intermingled visits at both nests, suggesting a cost of switching between feeding locations. Both primary and secondary nests had reduced fledging success, even after controlling for variation in habitat quality and paternal care, due to a higher rate of nest failure. Paternity loss was higher at secondary nests, presumably because the secondary female copulated with a previous mate that disappeared. Due to increased paternity loss and reduced fledging success polygynous males did not sire more fledglings than monogamous males in a given season. Thus, the benefit of social polygyny for males seems limited. Social polygyny in our population probably arises as a by-product of widowed females settling as secondary mates with a familiar male or in a familiar area, thereby making the best of a bad situation.
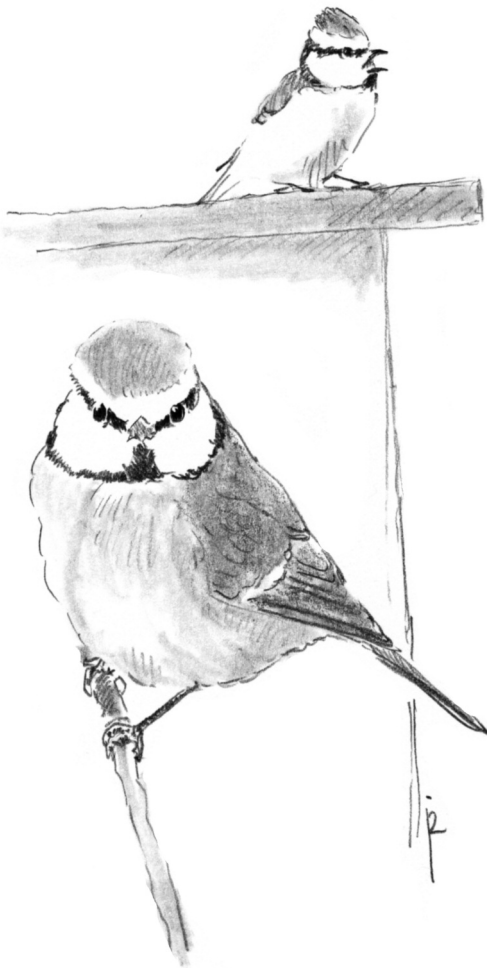
Key words: Blue Tit, *Cyanistes caeruleus*, extra-pair paternity, facultative polygyny, familiarity, fledging success, mating system, parental care, polygyny, social instability

Department of Behavioural Ecology & Evolutionary Genetics, Max Planck Institute for Ornithology, Seewiesen, Germany;
*corresponding author (b.kempenaers@orn.mpg.de)

In many passerine species social monogamy dominates, but social polygyny, i.e. a male breeding with more than one female in his territory, occurs regularly (Ford 1983, Møller 1986). Such facultative social polygyny (in the following referred to simply as polygyny) typically arises when a mated male and female are joined by another (secondary) female (e.g. Orians 1969, Bensch 1997). Males are thought to benefit from polygyny, because they can increase their seasonal reproductive success (e.g. Orians 1969, Jungwirth & Johnstone 2019). However, males only benefit if indeed they are able to sire and successfully raise more

offspring than they would with a single female and if this is not outweighed by a survival cost. Males may face a trade-off between securing additional mates as social partners and protecting paternity with their mate(s) (Bollinger & Gavin 1991, Hasselquist & Bensch 1991). In several facultatively polygynous species, polygynous males had a higher rate of paternity loss than monogamous males (reviewed in Vedder *et al.* 2011). Furthermore, clutches laid by females of polygynous males are often smaller than clutches of females mated to monogamous males, especially for secondary females that breed late (Slagsvold & Lifjeld 1994,

Czapka & Johnson 2000, Komdeur *et al.* 2002). Finally, fledging success of nests from polygynous males, in particular secondary nests, is often reduced (Ligon 1999, Huk & Winkel 2006). Taken together, these effects may considerably reduce benefits of polygyny for males, even to the extent that reproductive success of polygynous males can be lower than that of monogamous males (Dunn & Robertson 1993). Polygyny may also have immediate costs for males. Parental care is strenuous and caring for more than one brood may have adverse effects on male health and survival. In addition, for an already mated male establishing and maintaining another pair bond may require additional investment in terms of courtship, territory defence and mate guarding (Komdeur *et al.* 2002). Yet, a comprehensive assessment of costs and benefits of polygyny for males is rarely performed, perhaps because benefits of polygyny appear obvious for males, at least when compared to females (Searcy & Yasukawa 1989).

Females sharing a partner suffer a cost, mainly because they each secure less paternal care (Searcy & Yasukawa 1989, Bensch 1997). Why females sometimes mate with an already mated male has therefore become a classic topic in research on avian mating systems (reviewed in Ligon 1999). Initially, focus was on the benefits obtained by females choosing freely to mate with a mated male. These benefits include resources from high quality territories (polygyny threshold model; Verner 1964, Verner & Willson 1966, Orians 1969), efficient nest defence (Knight & Temple 1988), high quality paternal care (Sejberg *et al.* 2000), inclusive fitness benefits due to kinship among females mated to the same male (Grønstøl *et al.* 2015) or genetic benefits obtained from the polygynous male (Weatherhead & Robertson 1979, Santoro 2020). Later studies on social polygyny incorporated limitations of free female choice of mates such as a female-biased sex ratio (Smith *et al.* 1982, Kempenaers 1994, Mulvihill *et al.* 2002, Kus *et al.* 2017, Artemyev 2018), females being unaware of the mated status of the male (Alatalo *et al.* 1981, Alatalo & Lundberg 1984), aggression of competing females (Slagsvold & Lifjeld 1994), costs of mate sampling (Stenmark *et al.* 1988, Slagsvold & Dale 1994) and variation in female quality or condition (Forstmeier *et al.* 2001, Griggio *et al.* 2003). In some species polygyny appears to arise as a consequence of strong site attachment of females, whereby the males available at the preferred location are already mated (Eliason 1986, Mulvihill *et al.* 2002). Furthermore, polygyny in predominantly monogamous species often arises when a female has lost her initial mate and an already mated neighbouring male replaces him (Smith

et al. 1982, Ford 1983, Kempenaers 1994, Mulvihill *et al.* 2002). This may reflect a combination of time constraints and female attachment to a specific local and social environment. For example, in the European Starling *Sturnus vulgaris*, females mated to the same polygynous male were socially associated before breeding (Henry *et al.* 2013), suggesting that social attachment plays a role. Hence, females may additionally be restricted in their choice of a mate and breeding site by effects of site fidelity and social inertia. Although a role of familiarity for breeding success is well described (Forslund & Pärt 1995, Bruinzeel & van de Pol 2004, Snell-Rood & Cristol 2005, Brown *et al.* 2008, Piper 2011, Firth *et al.* 2018, Beck *et al.* 2020), the fact that familiarity with a site, social environment or mate may influence the occurrence of polygyny has received relatively little attention.

The aim of this study is to describe in detail both the origin and outcome of polygyny in a population of Blue Tits *Cyanistes caeruleus* and then use this information to consider costs and benefits of polygyny for polygynous males, primary females and secondary females. Blue Tits are predominantly socially monogamous, but 3–20% of males breed with more than one female (Dhondt *et al.* 1983, Kempenaers 1994, Vedder *et al.* 2011, Schlicht & Kempenaers 2013). First ('origin i'), we used automatically collected data about presence of individuals at nestboxes and feeders to distinguish between three ways polygyny can originate in Blue Tits (based on Kempenaers 1994). (1) Females that have settled in the breeding area may become secondary mates after they lose their original partner, if by staying in the area an association arises with a neighbouring male that is already mated and takes over the territory of the deceased male (replacement polygyny). (2) Females that fail to settle early in the breeding season may still have the option to breed at a given location, even if it is fully occupied by already mated males, if they settle as secondary females (successive polygyny). (3) Occasionally, males seem to form pair bonds with two females simultaneously, sometimes across several seasons. Kempenaers (1994) referred to this as 'year-round polygyny'. However, because we do not always have information about the presence of individuals in winter, we here use the term 'parallel polygyny'. It occurs, for example, when a male loses its mate and the vacancy is filled by two females simultaneously.

Following previous studies (e.g. Bruun *et al.* 1997, Pribil 2000, Moreno *et al.* 2002), we classified the two females of a polygynous male as primary and secondary female based on the start of laying, assuming that laying date reflects the order of mating. In a second

step ('origin ii'), we use behavioural data on mating order and on the intensity of pre-breeding interactions to test this assumption.

Third ('origin iii'), we examine whether variation in habitat quality and the spatial distribution of breeding attempts influence the emergence of polygyny. The polygyny threshold model predicts that secondary females actively choose high-quality sites for breeding (Verner 1964, Verner & Willson 1966, Orians 1969). We therefore compare the number and diameter of oak *Quercus* spp. trees (a proxy of habitat quality) surrounding primary nests, secondary nests and nests of females mated to monogamous males. We also assess whether secondary females choose generally preferred locations for breeding (Kempenaers 1995) by testing whether secondary females settle in areas of high local density. Alternatively, secondary females may try to reduce interference with other females by settling in areas of low local density. To assess whether secondary females are successful at reducing interference with the primary and neighbouring females we also examine the spatial distribution of breeding events that results after the settlement of secondary females.

Fourth ('origin iv'), we consider the timing of polygynous breeding attempts in terms of the start of egg laying and the duration of the incubation period. Theory predicts that polygyny may arise to avoid delayed breeding of secondary females (Jungwirth & Johnstone 2019), suggesting an importance of time constraints for the emergence of polygyny. Secondary females often breed late (Slagsvold & Lifjeld 1994, Czapka & Johnson 2000, Komdeur *et al.* 2002), which affects the reproductive value of their broods and the probability of receiving male help with nestling feeding (Kempenaers 1995), unless they accelerate the process of breeding after having settled.

Fifth ('origin v'), we used the automatically collected data to inspect male-female interactions among individuals that did or did not end up breeding together. We establish mating order of polygynous males with their two females (i.e. which is the primary female and which female is joining later) and we describe how interactions and familiarity among breeding partners develop as egg laying approaches. We also explore whether the disappearance of interacting individuals plays a role in the establishment of polygyny.

Sixth ('origin vi'), we assess whether male and female traits that have been reported to influence breeding success in Blue Tits (body size, age and arrival date; Schlicht *et al.* 2015a, Amininasab *et al.* 2017, Gilsenan *et al.* 2020) are linked to the occurrence of polygyny.

Regarding the outcome of polygyny, we first ('outcome i') compare paternal feeding rates between monogamous, primary and secondary broods. Many studies report that polygynous males do not provide full care at both nests (Dyrcz 1986, Lifjeld & Slagsvold 1989, Johnson *et al.* 1993, Pinxten & Eens 1994, Kempenaers 1995, Rodrigues 1996, Sandell *et al.* 1996, Sejberg *et al.* 2000, Forstmeier *et al.* 2001, Moreno *et al.* 2002), but it is unknown whether polygynous males work harder than monogamous males. We compare total male investment using data on feeding rates at both nests across the entire nestling period.

We next ('outcome ii') compare reproductive success of monogamous, primary, and secondary broods, accounting for extra-pair paternity. Finally ('outcome iii'), we compare survival of males and females involved in monogamous and polygynous matings.

METHODS

General Methods

STUDY AREA AND SPECIES

We studied a population of Blue Tits in a 40-ha oak rich plot within a mixed-deciduous forest close to Landsberg am Lech, Germany ('Westerholz', 48°08'26"N, 10°53'29"E), from 2007 to 2018. The study area contains 277 nestboxes, each of which is permanently equipped with an RFID antenna around the entrance hole and with two light barriers (one on the outside and one on the inside; see Loës *et al.* 2019a). Each Blue Tit carrying a passive-integrated transponder (PIT-tag) is automatically recorded when it passes through the nest hole, with data on bird identity, date, time and box entry or exit based on information from the light barriers. During the winter months (November–March) of 2014/15–2017/18 we collected information about visits at feeders using similar technology (Loës *et al.* 2019b). The first three winters, 16 feeders were installed 150 m apart along three edges of the study area. In autumn 2017, 20 feeders were installed at distances of 200 m throughout the study area. Blue Tits are small (c. 10–12 g) cavity-nesting passerines that are socially monogamous with occasional social polygyny and regular extra-pair paternity. In our population, 43% of nests contain extra-pair young and 11% of young are not sired by their social father (Table 1). Mean clutch size is 9.8 (Table 1). Pairs produced one clutch per season, except for replacement attempts after clutch or brood failure (about 3% of males and 2% of females; Table 1). Blue Tits are non-migratory, but in our study

area not all individuals are resident throughout the year and early arrival on the study site is positively related to reproductive success (Gilsenan *et al.* 2020). Between-year local survival is relatively low: of 1201 female and 1197 male breeders included in this study, 41% of females and 45% of males were observed again in the next spring. In the following, polygyny and monogamy refer to the social mating system, not to males that sire extra-pair young (or not) by copulating with females other than their social mate. The term "monogamous females" is used as shorthand for the females of socially monogamous males.

FIELD PROCEDURES

Each year we monitored breeding activity in all nest-boxes from early March until the end of June. We visited every nestbox at least weekly (daily around egg laying and hatching) to record the stage of nest building, the start of laying (laying date), clutch size, and the date of hatching and fledging. We banded nestlings and took a blood sample when they were 13–14 days old. For a more detailed description of field procedures and ethical implications see Schlicht *et al.* (2012, 2015b). Permits were obtained from the Bavarian government and the Bavarian regional office for forestry (LWF).

Adult Blue Tits were captured throughout the year, either at the nestbox during nestling feeding (majority of captures until spring 2013) or with mist nests

between September and March (majority of captures since winter 2014). A few birds were caught roosting in nestboxes or with snap traps. Birds were banded, measured and aged (yearling or older). We also took a 5–10 µl blood sample and implanted a PIT-tag under the skin on the back. For molecular sex determination and parentage analysis we extracted DNA from all blood samples and, when possible, from embryo or nestling tissue. For genotyping, we used 14 microsatellite markers: ADCYAP1_bm, ClkpolyQ, Mcµ4, PAT MP 2-43, Pca3, Pca4, Pca7, Pca8, Pca9, Phtr3 (until 2017), PK11, PK12, PmaTAGAn71 (from 2018 onwards), POCC1 and POCC6. Microsatellite amplifications were performed in multiplexed PCRs using the Qiagen Type-it Microsatellite PCR Kit with primer mixes containing two to five primer pairs (Table S1). Each 10-µl multiplex PCR contained 20–80 ng DNA (see footnotes to Table S1 for PCR cycling conditions). The PCR products were analysed on an ABI 3130xl Genetic Analyzer. We compared the genotypes of parents and their offspring following Delhey *et al.* (2003) and Schlicht *et al.* (2012) using the software Cervus (v. 3.0; Kalinowski *et al.* 2007).

DEFINITION OF POLYGYNY

We used the following information to identify the social parents of a nest: observations of individuals defending the box or feeding nestlings, box visits based on the automated recording system, individuals caught at the

Table 1. Yearly breeding parameters of the Blue Tit population in Westerholz (southern Germany). Shown are the number of nests and the number of individuals of different sex and mating status, the frequency of extra-pair paternity and measures of reproductive success (means ± SD). Polygynous males are males that bred simultaneously with two females. Replacement males or females are those that bred with the same or another partner after failure of an initial attempt (in parentheses: number of individuals where replacement attempt is with the same partner). EPY = extra-pair young.

Year	Nests	Males	Females	Polygynous males	Replacement males	Replacement females	% Nests with ≥ 1 EPY	% EPY	Clutch size	Number of hatchlings	Number of fledglings
2007	88	84	86	2	2 (2)	2 (2)	50.6	12.4	10.7 ± 1.7	9.6 ± 3.0	8.2 ± 3.0
2008	98	96	96	0	2 (2)	2 (2)	38.1	8.9	9.9 ± 2.0	7.9 ± 3.3	6.2 ± 3.3
2009	62	60	61	1	1 (1)	1 (1)	54.0	13.2	10.8 ± 2.0	9.5 ± 3.3	8.4 ± 3.3
2010	102	98	98	1	3 (3)	4 (3)	36.6	9.4	10.0 ± 2.0	8.8 ± 3.2	5.6 ± 3.2
2011	79	74	77	3	2 (2)	2 (2)	46.2	11.5	10.5 ± 2.0	9.3 ± 3.4	8.0 ± 3.4
2012	149	136	148	11	2 (1)	1 (1)	44.9	10.7	9.4 ± 2.3	7.8 ± 3.2	6.1 ± 3.2
2013	99	95	97	1	3 (2)	2 (2)	45.9	10.2	10.2 ± 2.1	8.9 ± 3.2	6.3 ± 3.2
2014	79	77	78	1	1 (1)	1 (1)	43.0	9.0	11.1 ± 1.4	8.3 ± 3.3	7.6 ± 3.3
2015	114	105	113	4	5 (0)	1 (0)	33.9	8.2	9.4 ± 1.9	8.5 ± 2.6	7.0 ± 2.6
2016	125	119	123	1	5 (2)	2 (2)	41.0	10.7	9.1 ± 2.2	7.5 ± 3.3	6.0 ± 3.3
2017	186	160	176	6	20 (9)	10 (9)	43.9	12.5	9.0 ± 2.3	6.2 ± 3.8	3.8 ± 3.8
2018	135	126	133	4	5 (2)	2 (2)	41.4	10.9	9.2 ± 2.1	8.8 ± 1.8	8.5 ± 1.8

box during nestling feeding and genetic parentage data. Males were classified as polygynous if (1) they were assigned as the social male to more than one nest, (2) different females were assigned to those nests and (3) the nesting periods overlapped to some extent, i.e. the later-laying female started laying before the brood of the earlier-laying female fledged or failed. The 24 cases where the third condition was not met were not classified as polygyny, because we cannot exclude that males renested after failure, for example after their first mate died (Table 1). These nests, as well as two cases where the social male could not be unambiguously assigned as polygynous, were excluded except in the analyses of breeding distances (see below).

The two females mated to a polygynous male are defined as primary and secondary female based on their laying date. In most cases, this operational definition reflects mating order, the number of male-female pre-breeding interactions and the division of male feeding investment, as shown in detail below. The male and the two females form the 'polygynous trio'. Thirty females laid a replacement clutch after their initial breeding attempt failed (Table 1). The two nests were usually either in the same or in neighbouring boxes. In this study no male was polygynous with more than two females. In 2017, two males were assigned as the social male to three breeding attempts. One of them was renesting twice after two successive failures with two females that each disappeared. The other male was polygynous and had a replacement attempt with the primary female after her first clutch failed. Both clutches of the primary female were in the same nestbox and both were abandoned during egg laying (possibly due to a wasp nest). In comparisons of the timing of breeding, we used the laying date of the earlier of the two clutches of the primary female. We did not include her later clutch in analyses involving replacement broods.

ASSIGNING NESTBOX VISITS OF PIT-TAGGED INDIVIDUALS

We used two methods to extract nestbox visits. First, we considered all transponder reads at a nestbox that were more than 30 s apart as separate visits. This method will overestimate visit number whenever individuals stay in the nestbox longer than 30 s and underestimate visit number whenever individuals perform more than one visit in 30 s. Note that during periods of peak feeding activity, the latter occurs for less than 8% of visits (Santema *et al.* 2017, Iserbyt *et al.* 2018). Second, we used the light barrier information to establish the most likely action of the bird when the transponder was read: flying in, flying out, at the

entrance hole while staying outside of the box or at the entrance hole while inside the box. We considered consecutive in- and out-actions as one visit. This method may count a single visit as multiple visits, when a bird's visit is associated with back-and-forth-movement in the light barriers' fields. We then summed visits on a daily basis for each method and compared the results. Daily visits from both methods were highly correlated (Pearson $r = 0.83$, $n = 9842$ individual-days). Daily visits obtained with the first method were higher than those obtained with the second method for 91% of days (and lower for 8% of days), suggesting that light barrier information rarely counted single visits as multiple visits, whereas individuals often stayed in the nestbox longer than 30 s. We therefore use daily visit data obtained with the second method in all following analyses. Using visit data based on the first method gave qualitatively similar results.

We excluded (1) days preceding PIT-tagging of an individual, (2) the day of capture and (3) days with partial data due to transponder loss or malfunctioning of the recording system. When an individual was not detected at a nestbox on a given day and both the transponder reading unit of that box and the individual's transponder were working in the relevant time period (as indicated, respectively, by reads of other individuals at that box or by reads of the same individual at other boxes), we inferred that that individual conducted zero visits at that box on that day.

STATISTICAL ANALYSES

All analyses were performed with the package MCMCglmm (v. 2.29; Hadfield 2010) in R v. 3.6.2 (R Core Team 2019). Models are either linear or generalized linear mixed-effect models (GLMM). We used the default prior for the fixed effects, which is a diffuse normal prior. MCMCglmm uses an inverse Wishart prior for the (co)variances of the random effects and residuals. For these, we specified weakly informative priors with a low degree of belief ($V = 1$, $nu = 0.002$). We checked the robustness of our results using alternative priors where residual variances were fixed at 1 or 10 and parameter-expansion was used for random variances with $V = 1$, $nu = 1$, $alpha.mu = 0$ and $alpha.V = 1000$. In models with a binary or proportion response, we always used fixed residual variances.

Convergence of parameter estimates (i.e. mixing of chains) was inspected visually by plotting the trace of parameter estimates used throughout the MCMC sampling process. We checked for autocorrelation among 100 consecutive samples (acf-function in R). The level of auto-correlation was considered acceptable

if smaller than 0.05 in all cases. Models were run for 1.8 to 20 million iterations with a burn-in of 6000 to 30,000 and a thinning interval of 800 to 80,000. Higher number of iterations were chosen to generate effective sample sizes > 1000. Models are numbered and their details are summarized in Table S2. Data used for the models and the analytical script are provided in Schlicht & Kempenaers (2020; Table S3).

Types of polygyny (origin i)

We used the nestbox visit data to graphically inspect the behaviour of all individuals involved in polygynous breeding events (see Figures S2–S8 for examples). We included visits by other individuals if they visited a box on the same day as one of the focal individuals. Based on these data, we (1) identified other individuals associated with one of the focal individuals (the polygynous trio) and (2) established likely days of disappearance of individuals. We then used this information to (3) classify the type of polygyny (replacement, successive, parallel). We classified a polygynous event as replacement polygyny when another male associated with the secondary female before breeding (joint visits at nestboxes and feeders), when records of that male stopped abruptly with no later reappearance and when the secondary female was observed increasing her association with the polygynous male after disappearance of the initial male. We classified a polygynous event as successive polygyny when the polygynous male associated earlier and more intensively with the primary than with the secondary female and there was no involvement of additional individuals. We classified a polygynous event as parallel polygyny when the polygynous male associated with the primary and the secondary females at similar times and with similar intensity, for example when the polygynous male was associated with both the primary and the secondary female early on in the season without the involvement of additional individuals (year-round polygyny sensu Kempenaers 1994). Additional individuals could be involved, for example, when a male lost its initial mate and the vacancy was filled by two females at the same time, or when two neighbouring females both lost their initial mate at similar times and then both mated with the same previously unmated male. In 26 of 35 cases, data were too sparse to allow classification (key individuals without transponder or receiving transponder too late in the season).

We tested whether variation in the frequency of polygyny between years was related to annual variation in overall breeding density using a generalized linear model in which the proportion of polygynous males

(dependent variable, binomial error structure, logit-link function) was related to the total number of breeding males (model 1a in Table S2). We further compared the probability to renest with the same male (yes or no, dependent variable) between primary and monogamous females using a GLMM with a categorical error structure (binary data, logit-link function) and female identity as random factor (model 1b).

Classification of primary and secondary females (origin ii)

We used data from 17 polygynous males which were sufficiently detailed to test the assumption that the primary and secondary female can be classified based on their laying date. We compared order of laying date with mating order, the intensity of pre-breeding interactions and relative male parental investment (see details in the relevant sections below).

Polygyny, breeding density and habitat quality (origin iii)

RELATING POLYGYNY TO VARIATION IN LOCAL BREEDING DENSITY

To inspect the effects of the spatial distribution of breeding events on settlement decisions of secondary females, we first assessed variation in local breeding density before settlement of the secondary female of a polygynous male, i.e. excluding secondary nests. To evaluate how the spatial distribution of breeding events varied as a result of settlement of secondary females we also assessed variation in local breeding density after the settlement of the secondary female, i.e. including secondary nests. First, we assigned territories to the relevant breeding pairs via Thiessen polygons using the R-package expp v. 1.2.4 (Valcu 2019). We excluded replacement nests, but used the position of the original (failed) nest. We then defined neighbouring territories as those that shared a boundary. As a measure of local breeding density, we calculated distances (in meters) between the nests of neighbouring breeding events. Before settlement of secondary females, neighbouring nests could either both be from monogamous pairs (category 1) or they could be the primary nest of a polygynous male neighbouring the nest of another (monogamous or polygynous) male (category 2). We assessed whether secondary females settled in areas of higher local density (preferred areas) or lower local density (reduced competition with other females) by comparing the distances of neighbourhoods belonging to category 1 with those of category 2. We used a model with distance between two breeding events as the dependent variable (Gaussian error structure) and

with neighbourhood category as the explanatory variable. We ran two versions of this model. In the first version we only added year as random intercept to account for population-wide between-year variation in breeding density and in the occurrence of polygyny (model 2a). In the second version we also included the identity of the two neighbouring boxes as random intercepts to account for consistent local variation in breeding density at the level of nestboxes (e.g. due to habitat characteristics; model 2b).

After settlement of secondary females, we distinguished between four categories of neighbouring nests: (1) both nests were from monogamous males, (2) the primary nest of a polygynous male neighboured the nest of another (monogamous or polygynous) male, (3) the secondary nest of a polygynous male neighboured the nest of another (monogamous or polygynous) male, (4) the primary and secondary nest of one polygynous male neighboured each other. In two cases, the two breeding boxes of a polygynous male were assigned as second-order neighbours (based on the Thiessen polygons), but we treated them as direct neighbours in the analysis (excluding these cases did not qualitatively affect the results). We assessed whether local breeding density at locations of polygyny is higher after settlement of secondary females (secondary females 'squeezing in') by comparing distances of neighbourhoods belonging to category 3 with those belonging to categories 1 or 2. We also compared distances of neighbourhoods belonging to category 4 with those belonging to 1–3, to assess whether the two social mates of polygynous males bred closer together or further apart than females mated to different males. The former would be expected if polygynous males do not have territories large enough for their females to maintain the same distance as two females mated to different mates, while the latter might arise if secondary females avoid interference with primary females by maximizing their distance to them (Canal *et al.* 2020). We used the same model structure as before (i.e. random intercepts for year only or for year and the identity of the two neighbouring nestboxes). Because both versions of the model gave similar results, we only show the results including year as random intercept (model 2c).

RELATING POLYGYNY TO LOCAL VARIATION IN HABITAT QUALITY

We used vegetation data to assess whether the occurrence of polygyny is related to habitat quality. In 2013 and 2014 all trees in our study site with a diameter (at breast height) > 25 cm were mapped by a botanist who identified the species and measured the diameter. In this manner, 5741 trees of 15 species were mapped. The four most common species were: Small-leaved Lime *Tilia cordata* (49% of trees, average diameter 38 cm), Common Oak *Quercus robur* (24%, diameter 68 cm), European Ash *Fraxinus excelsior* (9%, diameter 68 cm) and Sycamore *Acer pseudoplatanus* (7%, diameter 48 cm). Given the ecological significance of oak trees for Blue Tits (Cramp & Perrins 1993), we focus on *Quercus* spp. in the analyses. We defined habitat quality in a given area based on the number of oak trees and their diameter. Following Wilkin *et al.* (2007), Cole *et al.* (2015) and Hinks *et al.* (2015), the area relevant for a given breeding attempt was calculated in two ways: (1) a circular area within 75 m of a breeding attempt or (2) the territory as defined by the Thiessen polygons, as described above. Because the results of both methods were similar (details not shown), we only present the results of the first method. Thus, we used the number of oak trees or the average diameter of oak trees within 75 m of a nest as dependent variables and mating category (monogamous/primary/secondary) as the explanatory variable. The two models had a Gaussian error structure and included year as random intercept (model 3a, b).

Timing of polygyny (origin iv)

First, we compared the laying dates (mean-centred within year) of primary, secondary and monogamous females. Because yearling females start laying later (Amininasab *et al.* 2017), female age (categorical) was included as covariate (model 4a). Second, we compared the laying dates of secondary females with those of replacement clutches (model 4b). The mean laying date of primary and secondary females might be respectively earlier and later, than the mean laying date of monogamous females, simply because we categorized females as primary and secondary based on laying date. To take this into account, we used the 'sample'-function in R to randomly choose two clutches from monogamous breeding attempts in a given year (excluding replacement clutches) and sort the two by laying date until all (or all but one) clutches of the year were paired. We did this 1000 times for each year of the study. The resultant data set contains 564,000 paired breeding attempts, sorted into an 'early' group and a 'late' group. We then compared the laying dates between primary females and females from the early group and between secondary females and females from the late group. We used models with a Gaussian error structure and with year and female identity as random intercepts (model 4c, d). Finally, we compared

the difference in laying dates between the primary and secondary female of a polygynous male and between the early and late clutches of the randomly paired events, using a model with a Poisson error structure (log-link function) and with year as random intercept (model 4e).

After the start of laying, secondary females may speed up breeding by decreasing the laying period (i.e. clutch size) or the incubation period (i.e. the period between clutch completion and hatching), because this may increase the probability that they receive male help (Kempenaers 1995). We tested this, using pair-wise comparisons between the primary and secondary nest of polygynous events. Clutch size and the duration of the incubation period (in days) were the dependent variables (model 5a, b). We also performed a population-level comparison of clutch size of primary, secondary and monogamous nests. Here, we included laying date (mean-centred within year) as a covariate. To account for effects of habitat quality, we also included the number and average diameter of oak trees within 75 m of the nestbox (model 6).

Mating order and pre-breeding interactions (origin v)

Based on interactions between males and females we (1) established the mating order of polygynous males, (2) compared how pairs of different mating status (monogamous, primary or secondary) develop an association before the onset of laying and (3) examined whether the number and disappearance of social partners plays a role in the establishment of polygyny. A male and a female were considered interacting on a given day if they were registered at the same location (box for (1), box or feeder for (2) and (3)) within 10 minutes (arbitrary cut-off for temporal proximity, results are qualitatively similar when using 5 min and 60 min). We only considered interactions where both pair members (1, 2) or the focal individual (3) had received a PIT-tag at least three weeks before the onset of laying in the nest of the focal individual or pair. For (1), we defined mating order based on the date of the first interaction of the focal male with each female at a nestbox. For (2) and (3), we considered a 60-day period before the start of laying in the nest of the focal individual or pair. The cut-off of 60 days is arbitrary, but earlier interactions among pair members were rare (Figure 2), indicating that pairs typically associate during this period.

For (2), we describe the number of interactions between a male and a female that bred together over the 60-day period at the breeding site, at other nest-

boxes and at feeders (for the latter, observations ended at the end of March, when feeders were removed). We compared the development of these interactions for the three types of breeding pairs: socially monogamous pairs, polygynous males and their primary female, and polygynous males and their secondary female. As dependent variable we modelled the probability (presence/absence) of an interaction for each day during which both pair members carried a transponder. As explanatory variables, we included the type of breeding pair (monogamous, primary, secondary), days to first egg (first egg day is defined as day zero), location (breeding box, other nestbox, feeder) and the interaction between pair type and location. The model has a categorical error structure with year, male identity and female identity as random intercepts. In addition, we allowed for different slopes of individual males and females as egg laying approached (random slopes of days to first egg for male and female identity; Schielzeth & Forstmeier 2009; model 7).

For (3), we examined interactions of breeding individuals (monogamous and polygynous males, monogamous, primary and secondary females) with individuals of the opposite sex other than their breeding partners. As a measure of social association, we counted for each focal breeding individual the number of opposite-sex individuals it interacted with. To ensure that 'chance encounters' between otherwise unfamiliar individuals were excluded, we only counted the opposite-sex individual if there were interactions on at least three days in a given season (using a minimum of two or five days gave qualitatively similar results). To investigate the role of mate loss and social instability, we calculated the proportion of these interacting individuals that disappeared (i.e. were no longer detected) before the start of laying in the nest of the focal individual. We ran separate models for males and females, with the number of interacting individuals (Poisson error structure) or the proportion of interacting individuals that disappeared (binomial error structure) as dependent variables. We included mating status (polygynous or monogamous for males, primary, secondary or monogamous for females) as the explanatory variable of interest, the number of days for which data were available as covariate (range: 21–60) to account for potential biases arising from variation in when individuals had been PIT-tagged, and breeder identity and year as random intercepts (model 8a–d).

Traits of males and females involved in polygyny (origin vi)

We compared body size (tarsus in mm, average of all

measurements for an individual), age (yearling or older) and arrival date (first detection on the study site in a given season) between monogamous and polygynous males, and between monogamous, primary and secondary females. Individuals were defined as present if their first registration in a given season was earlier than 60 days before the first egg of the population in a given year. The cut-off of 60 days is arbitrary, but conclusions do not differ when using 50 or 100 days instead (details not shown). Presence was only assigned for individuals that had received a transponder before the start of the 60-day-period. We used models with a Gaussian (tarsus) or categorical (age, presence on study site) error structure and with male or female identity and year as random intercepts (model 9a–c, e–g).

Parental care and polygyny (outcome i)
We used transponder data to extract visits to the active nestbox as described above and considered each visit by a parent during the nestling period as a feeding event (Santema *et al.* 2017). Broods of monogamous males were only included from 2012 onwards, because higher data quality in later years reduced the work required for compilation. Because individuals may feed less on the day of hatching, we excluded this day for analysis. We also excluded visits that occurred more than 18 days after hatching, because this coincides with the start of fledging. If a nest failed during the nestling period, we only included days before feeding rates dropped (based on visual inspection). Replacement broods were included in the analysis if the male was socially monogamous.

First, we compared the number of feeds per nestling per day between nests of monogamous, primary and secondary females. The number of visits performed by a parent on a day was divided by brood size to obtain the number of feeds per nestling per day. Brood size on a given day was assumed to be the number of nestlings observed at hatching (for days preceding ringing of nestlings) or at ringing (from the day of ringing onwards) unless more accurate information was available. The dependent variable was the number of feeds per nestling per day, square-root-transformed. Models were run separately for males and females. We controlled for the non-linear relationship with nestling age by including age as a log-transformed covariate. To control for the time of season we also included relative hatch date (mean centred within year). We further included year, and both parents' identities as random intercepts. We allowed for different slopes of the feeding individuals as young grew older, by including a

random slope of log-transformed nestling age for feeding parent identity (model 10a, b).

Second, we compared the total number of feeds per day delivered by monogamous and polygynous males. Sample sizes are lower, because feeding data had to be available for the primary and secondary brood of a given polygynous male. In this analysis, we did not account for brood size, because we were interested in comparing the total effort of polygynous and monogamous males, independent of the number of young they cared for. We excluded days after one of the two nests had fledged. We included relative hatch date and log-transformed nestling age from the nest where the male fed more on a given day (95% of feeding days of polygynous males are at a single nest). The dependent variable was the total number of feeds per day, square-root-transformed. We also included year, and both parents' identities as random intercepts. Female identity refers to the female from the nest where the male fed more on a given day. We allowed for different slopes of feeding males as young grew older by including a random slope of log-transformed nestling age for male identity (model 10c). We repeated this analysis excluding for each male the days where it did not feed at all (model 10d).

Third, we tested whether the proportion of all male feeding visits at the secondary nest depended on the difference in hatch date between the primary and secondary nest (Kempenaers 1995). We used the feeding data of polygynous males, but included only days during which both nests contained nestlings. We summed up all visits of a given male across all days for each nest. We then ran a model with a binomial error structure with year as random intercept, where the number of visits to the secondary nests was the dependent variable and the total number of visits the binomial denominator (model 11).

Fourth, we compared the feeding patterns of monogamous and polygynous males. Feeds of polygynous males were pooled across their two nests. We compared the following two parameters. (1) The inter-visit interval, i.e. the time between two successive visits (at the same or a different nest) on the same day. The dataset included 882,476 inter-visit intervals and we constructed a model with a Poisson error structure. We included nestling number, relative hatch date and log-transformed nestling age as covariates, year, and male and female identity as random intercepts and nestling age (log-transformed) as random slope (for male identity). Parameters are taken from the nest which was visited at the end of the inter-visit interval (model 12a). (2) The proportion of the nestling period (day 1–18 after hatching) during which the male fed. For each day

when nestlings were present (for polygynous male in either the primary or secondary nest) and data available, we assessed whether the male visited one of his nests (yes/no). We constructed a model with a binomial error structure with the number of days when males visited their nest(s) as the dependent variable and the total nestling period as the binomial denominator. We included brood size and relative hatch date (from the nest where the male fed more often in total) as covariates and year, male identity and female identity (from the nest where the male fed more) as random intercepts (model 12b).

Breeding success and mating status (outcome ii)

We compared hatching success (probability of hatching of an egg), mean nestling body mass at day 14 after hatching, fledging success (yes/no and offspring probability of fledging) and recruitment rate (fledgling probability to subsequently breed, i.e. have a nest with at least one egg, in the study area) between nests of monogamous and those of polygynous males (primary and secondary nests separately and combined). The lower fledging success of polygynous nests (see results) could be due to the reduced investment in feeding by polygynous males. To test this, we repeated the analysis of fledging success while controlling for variation in male feeding. We first modelled the number of male feeds per nestling per day as described above, but for monogamous males only. We then calculated the difference between the number of feeds per nestling per day predicted by the model and that performed by the male. For each nest, we averaged that difference across all days for which feeding data were available. This variable was then included as a covariate in the model explaining variation in fledging success. The lower fledging success of polygynous nests may also be due to variation in habitat quality (food availability or quality). Thus, we also included the number and average diameter of oak trees in a 75-m radius around the nestbox as covariates. We also investigated whether complete nest failure was responsible for reduced fledging success by repeating the analysis of fledging success excluding failed nests.

Next, we considered reproductive success taking extra-pair paternity into account. We compared the occurrence of extra-pair young (presence/absence, and the proportion of extra-pair young for all nests, and for the subset of nests that contained at least one extra-pair young). For males, we compared both paternity loss, i.e. the proportion of all nestlings that were sired by other males, and paternity gain, i.e. extra-pair siring success (yes/no, and the number of extra-pair young

sired for all males, or only for those that sired at least one extra-pair young). To assess the overall effect of polygyny on reproductive success, we compared the total number of fledglings sired (in any nest) by monogamous and polygynous males. We ran models with a Gaussian (total number of fledglings sired), Poisson (average nestling weight, total number of fledglings sired) or categorical (all other models) error structure and included year and male and female identity (where applicable) as random intercepts (model 13a–f, 14a–i, 15a–h).

Survival of males and females involved in polygyny (outcome iii)

We compared local survival of individuals of different mating status. We defined an individual as having survived if it was recorded (based on automated data, direct observation, capture or parentage) after 15 March of the year following the focal breeding season. We ran models – for males and females separately – with a categorical error structure, with age (yearling or older) as covariate and with year and individual identity as random intercepts (model 9d, h).

RESULTS

Types of polygyny (origin i)

We observed a total of 35 instances of polygyny across 12 years. Twelve polygynous males were observed again in the next breeding season, but no male was polygynous in more than one year. One female was primary female in two breeding seasons. The frequency of polygyny was low (3% of males) and highly variable between years (0–8% of males; Table 1). This variation was not related to breeding density (number of breeding males; estimate on logit-scale = 0.01, 95% CI: –0.002 to 0.03, $P = 0.08$, $n = 12$, model 1a). In nine cases, sufficient data were available to trace the origin of polygyny (Table S3). In five cases the polygynous trio formed after a monogamously paired female lost her mate (replacement polygyny; Figures S2, S3). In one case (β in Table S3), the primary and secondary female were each associated with a different male, both of which disappeared a few days apart and the polygynous trio formed with a third male (parallel polygyny, but replacement from female perspective; Figure S4). In one case (γ) the female of a monogamous male disappeared and the vacancy was filled with two females simultaneously (parallel polygyny; Figure S5). In the two final cases, no associations with individuals other than those of the polygynous trio were observed.

In one case (δ) the male first formed an association with the primary and then with the secondary female (successive polygyny; Figure S6), while in the other case (ε) the male first interacted with both females around the same time, but interacted more often with the primary female. Interestingly, the secondary female had bred with the same male in the previous year at the same location (parallel polygyny with previous mate; Figure S7). Eight primary females had also bred with the same male in previous seasons (in six cases once, in two cases twice). Breeding with a previous mate was more common among primary than among monogamous females (44.4 % vs. 19.8%; model 1b, effect on logit-scale: 2.63 (0.33–4.85), $P = 0.02$, $n = 443$ females with breeding experience, of which 18 are primary females).

Classification of primary and secondary females (origin ii)

For 14 out of 17 cases of polygyny (82%) for which the relevant information was available, the earlier laying female was the first to mate, had more pre-breeding interactions with the male and received more male help with feeding nestlings, in agreement with the classification of primary and secondary female (Table S3, Figure S1). In the other three cases, the assignment based on laying order did not match with the male's behaviour towards both females. In case α (Figure S3), the male started interacting with the secondary (later-laying) female 44 days before he first interacted with the primary female and he interacted more often with the secondary female. The primary (earlier-laying) female was initially paired to another male, who later disappeared (replacement polygyny). During the nestling period, the male initially visited the nest of the secondary female more often, but later switched to feeding more at the primary nest (Figure 5B). This is the only clear case where the classification based on laying date did not reflect mating order. Excluding this case in analyses did not qualitatively affect any of the results. In case β (Figures 5C, S4), the male behaved similarly towards both females and nests. In case η (Figure 5A), the male switched focus from the primary to the secondary nest during the nestling period. In these three cases, the difference in laying date between the two females was maximally 3 days (Table S3), suggesting that classification of primary and secondary females based on laying date is biologically meaningful when laying dates are further apart (Figure S1).

Laying started at least seven days apart for 16 of 18 cases of polygyny (89%) for which no behavioural information is available (Figure S1D). In one case laying started five days apart, but the male visited the nestbox of the earlier-laying female earlier and more often than that of the later-laying female. This leaves only one case (difference in laying date one day) without further behavioural data where classification based on laying date is potentially misleading. Excluding this case in analyses did not qualitatively affect the results.

Polygyny, breeding density and habitat quality (origin iii)

Before settlement of secondary females, direct neighbours bred on average 70.0 ± 28.0 m apart (neighbours identified based on Thiessen polygons, see Methods). Primary females bred at similar distances to their neighbours as monogamous females (Table S4). After settlement of secondary females, distances between breeding boxes of monogamous and polygynous males remained similar to the distance between two monogamous broods (distance to monogamous neighbour 66.9 ± 24.5 m for primary and 63.1 ± 23.9 m for secondary broods compared to 69.4 ± 27.9 m for monogamous broods), but the primary and secondary female bred significantly closer to each other (51.3 ± 22.9 m; Table S4).

Oaks were equally common around nests of monogamous, primary and secondary females (Table S5), but they were smaller in diameter around primary and secondary nests than around nests of monogamous females (Table S5). However, effect sizes were small (around 3 cm for an average oak diameter of 70.3 ± 8.4 cm) and not significant for secondary females.

Timing of polygyny (origin iv)

Laying date of primary and monogamous females was similar, but secondary females started laying significantly later and later than expected from sorting of two randomly chosen monogamous breeding attempts (Figure 1A, Table S6). However, secondary attempts were not as late as replacement attempts (Table S6). The laying dates of the primary and the secondary female were 2.7 (95% CI: 2.1–3.4) times further apart than predicted from randomly chosen monogamous nests (10.7 ± 8.9 days, range 1–44; for polygynous events compared to 4.0 ± 4.6 days for randomly paired clutches; Figure S1D, Table S6).

The difference in timing between the two broods of polygynous males decreased, because secondary females laid a smaller clutch than primary females (pair-wise comparison, mean difference: –1.4 eggs, 95% CI: –2.5 to –0.3, $P = 0.02$, $n = 35$, model 5a) and had a shorter incubation period (–1.4 days, 95% CI: –2.9 to –0.03, $P = 0.06$, $n = 23$, model 5b).

Mating order and pre-breeding interactions (origin v)

Of eight polygynous males for which data were available, six started interacting earlier with the primary than with the secondary female (on average 41.0 ± 28.9 days apart, range: 5 to 69 days; Table S3). Two males started interacting earlier with the later laying female (82 and 3 days apart, cases α and β; Figure S1A). Laying dates of the primary and secondary female were close together in these two cases (one and three days apart; Figure S1A).

The probability that (future) pair members interact with each other increased over the course of the pre-breeding period, especially at the breeding box (Table S7, Figure 2). The pattern was similar for primary and monogamous females, but secondary females were less likely to interact with their polygynous mate at both the breeding box and at other boxes (Table S7, Figure 2A, B). However, they were more likely to interact with their mate at feeders compared to monogamous and primary females (Table S7, Figure 2C). Of eight polygynous males for which pre-breeding interactions were available for both females, six interacted more with the primary female (measured as the proportion of days with at least one interaction), while two interacted more with the secondary female (cases α and β; Table S3, Figure S1B).

Polygynous and monogamous males did not differ in the number of females they interacted with outside their pair bonds (Table S8), but the proportion of these females that disappeared before egg laying was higher for polygynous males (25.0 ± 32.1 % for polygynous vs. 13.2 ± 19.5 % for monogamous males; Table S8). Secondary females interacted with more males outside the pair bond than primary or monogamous females (median of 6 vs. 1; Table S8) and the proportion of these males that disappeared before egg laying was higher for secondary females (21.0 ± 27.8 % for secondary females vs. 14.5 ± 17.6 % for primary females and 10.4 ± 22.8 % for monogamous females; Table S8).

Traits of males and females involved in polygyny (origin vi)

Polygynous and monogamous males did not differ in tarsus length (Table 2), but the proportion of yearlings was lower among polygynous males (23%, $n = 31$) than among monogamous males (48%, $n = 1162$; Table 2). Presence at the study site at the start of the breeding season did not differ for polygynous and monogamous males (Table 2).

Monogamous, primary and secondary females did not differ in tarsus length (Table 2). The proportion of yearlings did not differ significantly between females of different mating status, but secondary females were more often yearlings than primary females (62% vs. 36% yearlings; Table 2). Presence on the study site at the start of the breeding season was also similar for monogamous, primary and secondary females (Table 2).
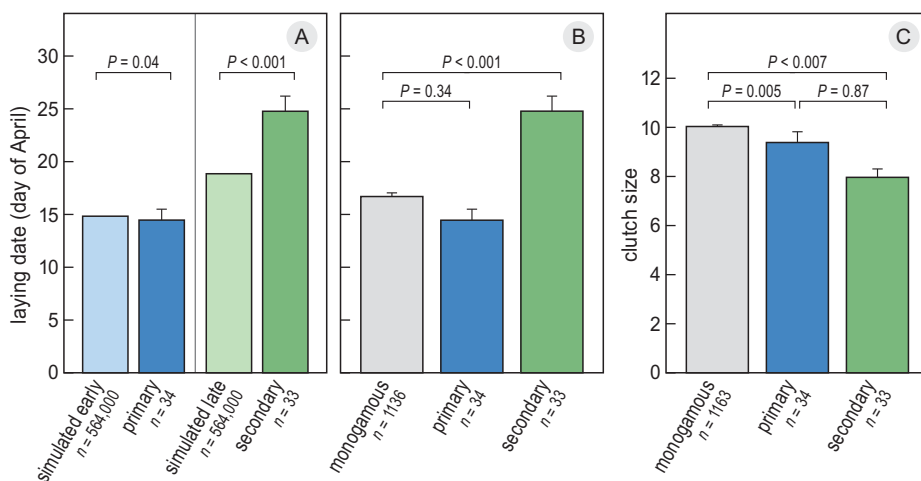

Figure 1. Laying date and clutch size for nests of monogamous and polygynous males. (A) Laying dates of primary (blue) and secondary females (green) compared to, respectively, early simulated breeding attempts (based on random pairings of two first attempts of monogamous females; light blue) and late simulated breeding attempts (light green). *P*-values are from models presented in Table S6, which correct for effects of female age. (B) Laying dates of monogamous (light grey), primary (blue) and secondary females (green). *P*-values are from a model presented in Table S6, which corrects for effects of female age. (C) Clutch size for monogamous (light grey), primary (blue) and secondary females (green). *P*-values are from the model presented in Table S11, which corrects for effects of laying date and habitat quality. Bars and their whiskers show means and standard errors.
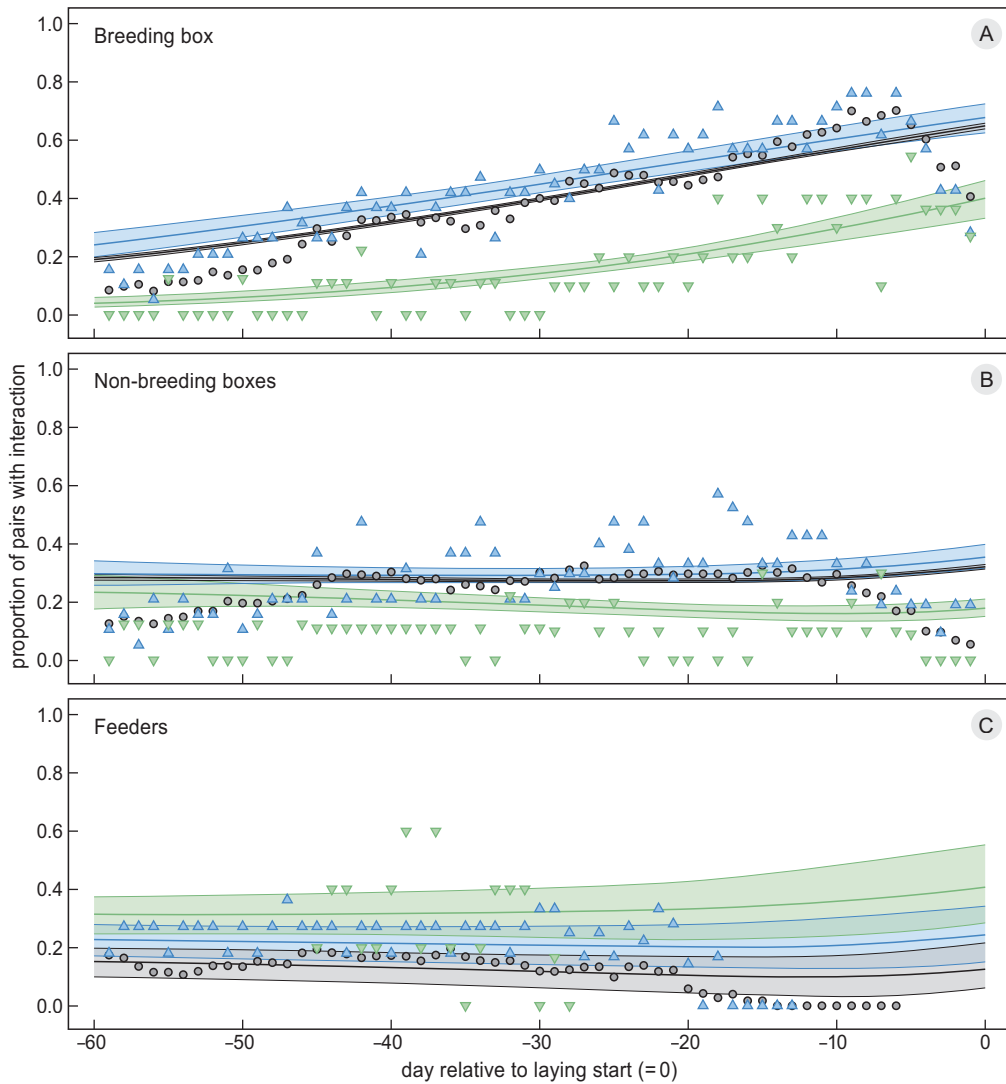
Figure 2. Interactions during the pre-breeding period (period of 60 days before egg laying started) between monogamous males and their mates (black), between polygynous males and their primary females (blue) and between polygynous males and their secondary females (green) at (A) the breeding box, (B) other nestboxes, and (C) feeders. Lines and shading indicate the model fit and its 95% confidence intervals (Table S7). Symbols show the proportion of pairs that interacted (not shown when based on less than five pairs). Sample sizes: (A, B) monogamous: $n = 26,970$ pair-day combinations (368 to 510 pairs per day), primary: $n = 1195$ pair-day combinations (19 to 21 pairs per day), secondary: $n = 559$ pair-day combinations (8 to 11 pairs per day). (C) monogamous: $n = 13,682$ pair-day combinations (1 to 364 pairs per day), primary: $n = 496$ pair-day combinations (1 to 12 pairs per day), secondary: $n = 182$ pair-day combinations (1 to 6 pairs per day).

Polygyny and parental care patterns (outcome i)
Controlling for variation in brood size, females mated to polygynous males visited the nest at similar rates during the nestling period as monogamous females (Figure 3, Table S9). If anything, females mated to polygynous males, especially secondary females, worked somewhat harder than monogamous females (Figure 3H, Table S9).

Both primary and secondary nests were visited less often by the male during the nestling period than nests of monogamous males (Figure 3, Table S9). Across both nests, polygynous males invested less in nestling feeding than monogamous males (Figure 4A–C, Table S9). This was not because polygynous males fed at lower rates: on days when males fed at least once, inter-visit intervals and the total number of feeds per

day were similar for polygynous and monogamous males (Figure 4D–F, Tables S9–10). However, polygynous males more often did not feed at all (on 22.1 ± 32.0 % of days during the nestling period, compared to 8.3 ± 25.8 % of days for monogamous males; Figure 4G, Table S10).

For 12 of 25 males with feeding data available from both nests, one of the nests failed before hatching or early in the nestling period. The other 13 males could have fed at both nests on a total of 143 days (male-day combinations with nestlings in both nests), but did so only on 31 days (22%). On 35 days they visited neither

Table 2. Correlates of polygyny. Comparison of tarsus length (in mm), age (yearling or older), presence at study site (at least 60 days before first laying in the population), and between-season local survival (yes/no) between monogamous and polygynous males, and between monogamous, primary and secondary females. Models are generalized linear mixed-effect models (9a–h in Table S2) with random intercepts for year and breeder's identity and with categorical error structure (estimates on logit-scale), except for tarsus length (Gaussian error structure).

		Estimate	95% CI	P (MCMC)
Males				
Tarsus length[1,2]	Intercept	17.1		
	Polygynous vs. monogamous	0.2	–1.5 to 1.9	0.83
Age (yearling or older)[1,3]	Intercept	0.23		
	Polygynous vs. monogamous	3.05	1.34 to 4.87	< 0.001
Presence at study site[4]	Intercept	11.40		
	Polygynous vs. monogamous	–2.65	–11.28 to 6.09	0.49
Survival[1,5]	Intercept	–0.55		
	Polygynous vs. monogamous	–1.42	–3.09 to 0.68	0.14
	Male age (older vs. yearling)	–1.28	–2.17 to –0.41	< 0.001
Females				
Tarsus length[6,7]	Intercept	16.6		
	Primary vs. monogamous	–0.1	–1.4 to 1.4	0.92
	Secondary vs. monogamous	0.0	–1.3 to 1.4	0.99
	Secondary vs. primary[8]	*0.0*	*–1.7 to 2.0*	*0.98*
Age (yearling or older)[6,9]	Intercept	0.07		
	Primary vs. monogamous	1.54	–0.28 to 3.04	0.07
	Secondary vs. monogamous	–0.98	–2.60 to 0.66	0.25
	Secondary vs. primary[8]	*–2.52*	*–4.86 to –0.41*	*0.03*
Presence at study site[10]	Intercept	–1.82		
	Primary vs. monogamous	–3.78	–11.51 to 2.94	0.27
	Secondary vs. monogamous	–4.78	–15.39 to 4.59	0.33
	Secondary vs. primary[8]	*–0.10*	*–11.80 to 9.68*	*0.26*
Survival[6,11]	Intercept	–1.24		
	Primary vs. monogamous	–2.36	–4.25 to –0.33	0.01
	Secondary vs. monogamous	–3.58	–5.84 to –1.38	< 0.001
	Secondary vs. primary[8]	*–1.29*	*–4.45 to 1.44*	*0.39*
	Female age (older vs. yearling)	–0.43	–1.25 to 0.36	0.28

[1]n = 1162 breeding males (687 individuals), 35 of which are polygynous, 551 of which are yearlings and 542 of which are surviving. [2]Posterior mean (95% CI) for random effects and residual variances: year: 0.02 (0.00 to 0.08), male identity: 0.20 (0.17 to 0.23), residual: <0.001. [3]Posterior mean (95% CI) for random effects variances: year: 0.40 (0.07 to 0.87), male identity: 0.06 (0.00 to 0.22). [4]n = 699 breeding males (422 individuals), 28 of which are polygynous. Posterior mean (95% CI) for random effects variances: year: 77.1 (8.8 to 212.4), male identity: 37.2 (2.7 to 98.3). [5]Posterior mean (95% CI) for random effects variances: year: 2.5 (0.72 to 5.3), male identity: 1.5 (0.46 to 2.7). [6]n = 1,201 breeding females (766 individuals), 34 of which are primary and 33 secondary females, 605 of which are yearlings and 491 of which are surviving. [7]Posterior mean (95% CI) for random effects and residual variances: year: 0.03 (0.00 to 0.10), female identity: 0.02 (0.00 to 0.06), residual: <0.001. [8]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown). [9]Posterior mean (95% CI) for random effects variances: year: 0.37 (0.06 to 0.82), female identity: 0.09 (0.00 to 0.31). [10]n = 568 breeding females (351 individuals), of which 24 are primary and 10 secondary females. Posterior mean (95% CI) for random effects variances: year: 129.2 (8.2 to 356.2), female identity: 46.6 (8.0 to 109.9). [11]Posterior mean (95% CI) for random effects variances: year: 1.7 (0.44 to 3.5), female identity: 1.1 (0.00 to 2.1).

nest, on 62 days only the primary nest and on 13 days only the secondary nest.

The larger the difference in hatch date between the primary and secondary nest the smaller the male's investment at the secondary nest (effect of days difference in hatch date on proportion of feeds at secondary nest on logit-scale: –0.81, 95% CI: –1.74 to –0.01, P = 0.04, n = 13, model 11). Nine of the 13 males visited the secondary nest less than 10 times in total (proportion of feeds provided at secondary nest: 0 to 7%, mean 1 ± 2%; Figure S1C). One secondary female, with a

nest where the polygynous male did not feed, nevertheless had male help: a male breeding nearby took over after his own breeding attempt failed (Figure S8, case ζ). Only 4 of the 13 males contributed substantially at both nests (cases α, β, δ and η: proportion of feeds provided at secondary nests 15 to 85%, mean 50 ± 29%; Figures 5, S1C, S3, S4, S6). In case η the male switched to feeding exclusively at the secondary nest, although the primary nest was still active and eventually fledged successfully. This occurred after the secondary female disappeared (Figure 5A).

Figure 3. Patterns of parental care for males (left) and females (right) of different mating status. Number of feeding visits per nestling per day (A–B) at nests of monogamous parents (light grey), (C–D) at primary nests (blue), and (E–F) at secondary nests (green). Horizontal bars inside boxes indicate medians, boxes indicate inter-quartile ranges (IQR) and whiskers indicate the extreme values within the interval of 1.5 times the IQR. Numbers below boxplots indicate sample sizes. Panels G and H show the model fit (solid line) with its 95% confidence intervals (shaded areas; Table S9).

Polygyny and reproductive success (outcome ii)
Overall, primary and secondary females produced smaller clutches than monogamous females (accounting for effects of laying date and habitat quality; Figure 1C, Table S11). Nests of monogamous and polygynous males had similar hatching success, nestling weight and recruitment rate (Table S12). However, fledging success was reduced for both primary and secondary

nests compared to nests of monogamous pairs (Figure 6A, Table S13), which led to substantially lower fledging success for polygynous males (both nests combined: 43.6 ± 27.0%) compared to monogamous males (68.7 ± 33.7%; Table S13). This reduced fledging success remained even after controlling for habitat quality (number and average diameter of oak trees) and male feeding effort (Table S13). Secondary nests, but not

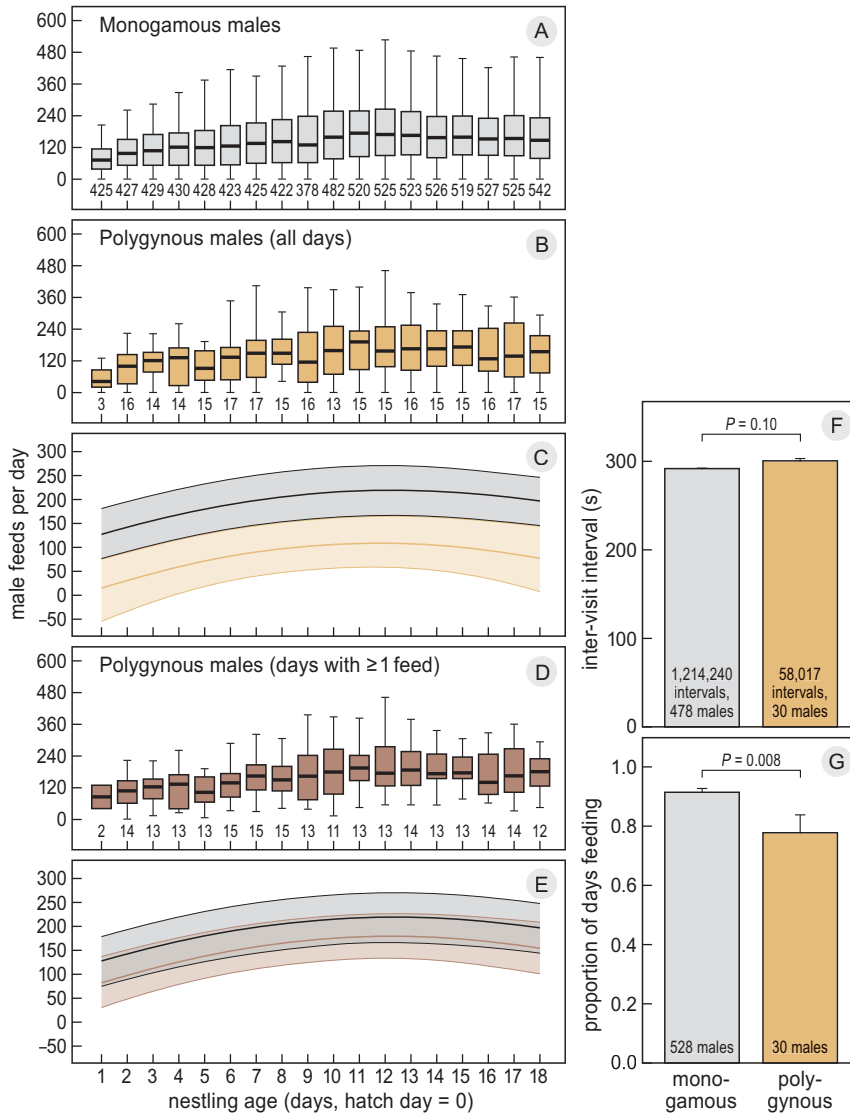**Figure 4.** Patterns of parental care for males of different mating status. (A, B, D) The total number of feeding visits per day for monogamous (A, light grey) and polygynous males (B, D). In B, all days of the nestling period are included (orange). In D, only days on which a male visited at least once are included (brown). Horizontal bars inside boxes indicate medians, boxes indicate inter-quartile ranges (IQR) and whiskers indicate the extreme values within the interval of 1.5 times the IQR. Numbers below boxplots indicate sample sizes. Panels C and E show the model fit (solid line) with its 95% confidence intervals (shaded areas, Table S9). (F) The duration of inter-visit intervals (in seconds; only for visits on the same day). (G) Proportion of days where a male visited a nest at least once. *P*-values are from models presented in Table S10, which correct for effects of hatch date, brood size and, for panel F, nestling age. Bars and whiskers show means and standard errors. Numbers inside bars indicate sample sizes.
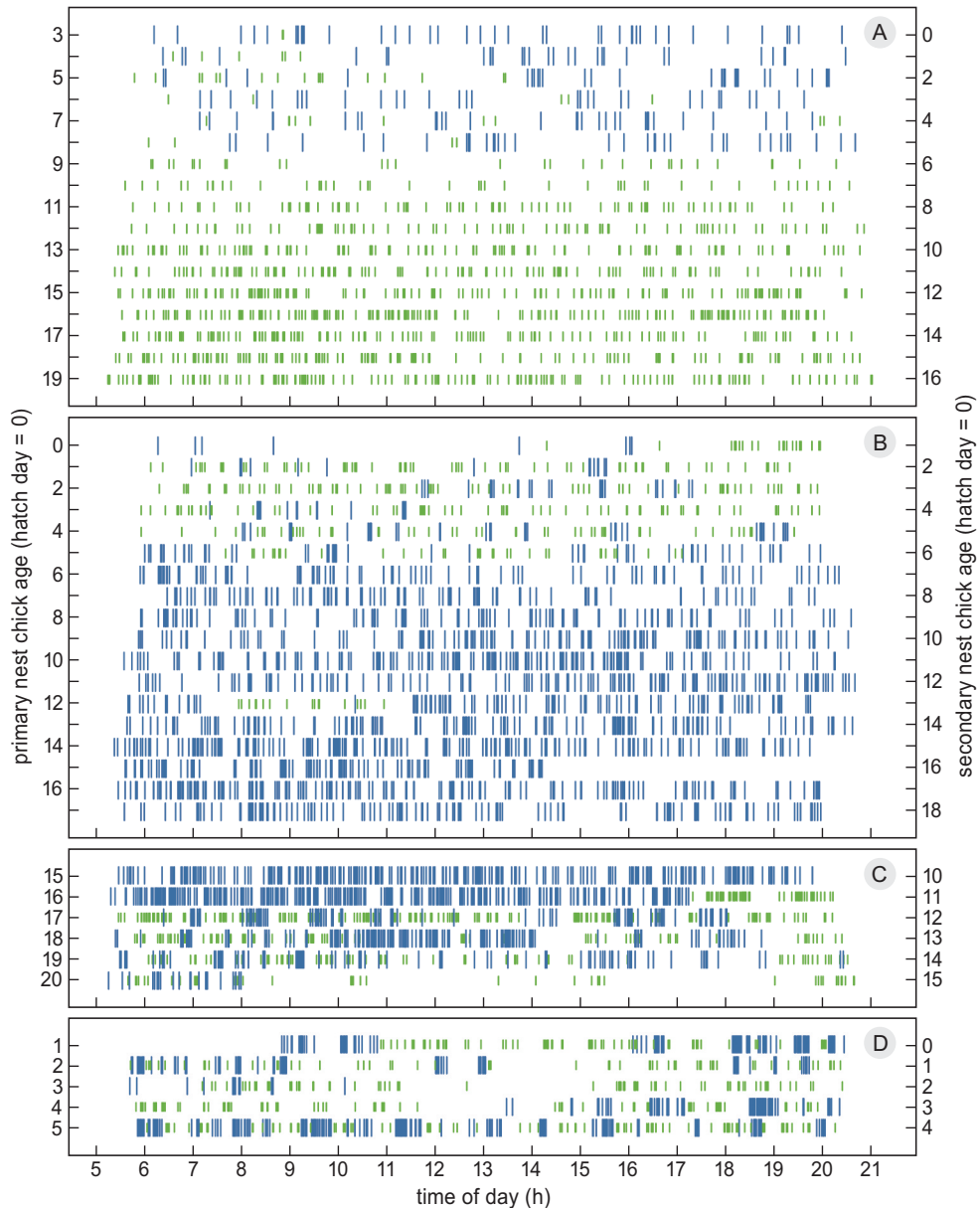
Figure 5. Actograms showing daily patterns of male nest visits during the nestling period at both nests of the four polygynous males that regularly visited both nests. Only periods when both nests of a polygynous male contained nestlings and data are available for both nests are presented. Each line represents a day, where time of day is indicated at the bottom and nestling age (hatch day = 0) is indicated on the left for the primary brood (blue) and on the right for the secondary brood (green). Male visits are indicated with vertical bars, visits to the primary brood by longer blue bars, visits to the secondary brood by shorter green bars. All nests fledged at least five young. (A) The male (case η in Table S3) switched 'priority' from the primary to the secondary nest when the secondary brood was six days old. The secondary female received a transponder when her young were nine days old. She never returned to the nest after capture and disappeared a couple of days later (last recorded at another site when her young were 14 days old). (B) The male (case α) initially visited the nest of the secondary female more often, but later switched almost exclusively to the nest of the primary female. (C) The male (case β) preferentially visited the primary nest until the young fledged, but increased his investment at the secondary nest towards the end of the nestling period of the primary nest. (D) The male (case δ) intermingled visits at both nests.

primary nests, tended to have a higher risk of complete failure after hatching compared to nests of monogamous males (Figure 6B, Table S13). When only nests with at least one fledgling were considered, fledging success was similar for all nest categories (Figure 6C, Table S13).

Paternity loss was similar between primary and monogamous nests, but more common at secondary nests than at monogamous nests (Figure 6D–E, Table S14). Among nests with at least one extra-pair young, nests of secondary females also had more extra-pair young (Figure 6F, Table S14). Overall, young in nests of

polygynous males were more likely sired by extra-pair males than young in nests of monogamous males (Table S14), but there was no difference when considering only males with paternity loss (accounting for the total number of young; Table S14). The sires of the extra-pair young in secondary nests were more often non-breeding males (i.e. males not breeding in a nestbox in the same year; 15/23 sires, 65%) than those in monogamous nests (100/437 sires, 23%; Fisher's exact test: $P < 0.001$). Note that we excluded monogamous nests containing extra-pair young sired by both breeding and non-breeding males, but inclusion in

Figure 6. Measures of reproductive success for females and males of different mating status. (A) Proportion of young fledged for all nests. (B) Proportion of failed nests (zero fledglings). (C) Proportion of young fledged for nests with at least one fledgling. (D) Proportion of extra-pair young (EPY). (E) Proportion of nests with extra-pair young. (F) Proportion of extra-pair young for nests with at least one extra-pair young. (G) The total number of fledglings sired (within- and extra-pair) by monogamous and polygynous males. P-values in (A–C, G) are from models presented in Table S13 which correct for effects of hatch date and (panel G) male age. P-values in (D–F) are from models presented in Table S14, which correct for effects of male age and hatch date. Bars and whiskers show means and standard errors. Numbers inside bars indicate sample sizes.

either group did not affect the conclusion. In two nests, young were sired by a male that had been identified as the female's previous mate that had disappeared. Paternity gain was similar for polygynous and monogamous males (Table S14).

As a result of reduced fledging success and increased paternity loss, polygynous males did not sire significantly more fledglings than monogamous males (Figure 6G, Table S13).

Polygyny and survival (outcome iii)

The probability of local survival did not differ significantly between polygynous and monogamous males (Figure 7A, Table 2), but primary and secondary females had a lower local survival probability compared to monogamous females (19.4 vs. 42.2 %; Figure 7B, Table 2).
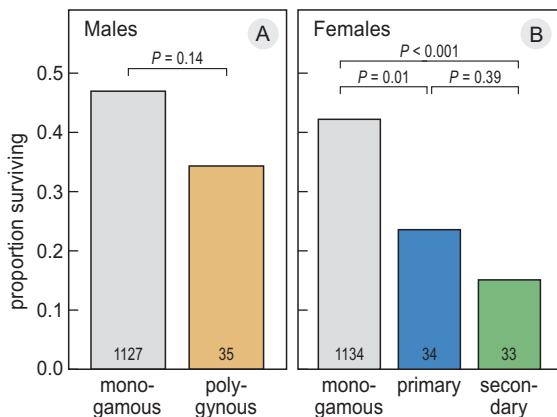

Figure 7. Between-year local survival for (A) males and (B) females of different mating status. Survival is defined as an individual registered after 15 March in the subsequent year. *P*-values are from models presented in Table 2, which correct for effects of age on survival. Bars and whiskers show means and standard errors. Numbers inside bars indicate sample sizes.

DISCUSSION

Classification of primary and secondary females

In predominantly monogamous species polygyny typically arises when females mate with already mated males (Bensch 1997, Santoro 2020). Mating order thus distinguishes primary and secondary females. In the Blue Tit this is the case for successive and replacement polygyny, which account for most cases of polygyny (Kempenaers 1994, this study). In this and many other

studies of polygyny (e.g. Bruun *et al.* 1997, Pribil 2000, Moreno *et al.* 2002) mates of a polygynous male are classified as primary or secondary females based on which female started laying earlier, respectively later, whereby laying order is assumed to reflect mating order (Smith *et al.* 1994). To evaluate this assumption, we assessed mating order based on the first pre-breeding interaction at a nestbox and found that it matched laying order in 6 out of 8 cases. Of the two remaining cases, one (case β) was a case of parallel polygyny where the male started interacting with both females around the same time. In the other case (α) the classification of females based on order of laying date was not correct.

The definition of female status is not so clear for cases of parallel polygyny: polygyny does not arise because a female mates with an already mated male, but instead both females maintain long-lasting bonds with the male (case ε, year-round polygyny sensu Kempenaers 1994) or the male establishes two bonds simultaneously (cases β and γ). In all other cases, mating order distinguishes the two females of a polygynous male, but it is unclear how this relates to the timing of the two nesting attempts later during the breeding season and to patterns of male care (Lamers *et al.* 2020). We found that order of laying correctly reflected intensity of male pre-breeding interactions with his two females in seven of nine cases. In the two cases where this was not true (α and β), the interactions did reflect mating order. Order of laying further correctly predicted male investment at his two nests in 9 of 13 cases (excluding 12 cases where one of the broods failed before hatching or early in the nestling period; Figure S1C). Note that in the four cases where this was not true (α, β, δ and η; Figure 5), males divided their care between the primary and the secondary brood. Only one secondary brood received considerably more feeding visits than the primary brood (case η), most likely because the secondary female abandoned the brood (Figure 5A). Males also switched to feeding at the secondary nest when the primary female's nest failed. In summary, our results suggest that classification of females based on the start of laying is both reliable and biologically meaningful whenever the difference in laying date between the two females is sufficiently large (≥1 week).

Types of polygyny and differences to another Blue Tit population

Successive polygyny was more common in a Belgian population (Kempenaers 1994) than in our population. This may be due to methodological limitations of our

study: often, key individuals did not have a transponder, so we could not assign the origin of polygyny. However, successive polygyny may be truly more common in the Belgian population. The frequency of polygyny in that population was substantially higher (20% of males) than in our population (3% of males) and fluctuated less between years (Kempenaers 1994). The study plot in Belgium was surrounded by poor quality habitat (e.g. gardens and urban habitat; Kempenaers 1994), whereas our study site is part of a larger forest (albeit without nestboxes and with lower oak density). In the former, a larger population of female floaters attempting to settle in high-quality breeding habitat may cause higher levels of (successive) polygyny (Kempenaers 1994). In contrast, in our population females may rarely become floaters, but instead settle in the surrounding forest (see Dhondt *et al.* 1983 for a similar argument). Previous studies have shown that a female-biased sex ratio in small, remnant populations can lead to increased rates of polygyny (Kus *et al.* 2017). We suggest that habitat fragmentation may increase rates of polygyny, because increased settlement as secondary female occurs when suitable breeding habitat is patchy.

Polygyny and territory quality

In line with the idea that secondary females actively chose high quality sites for breeding, polygyny at the Belgian site tended to occur at attractive (behaviourally preferred) locations (Kempenaers 1995). We found no such relationship of polygyny with territory quality in our population, suggesting that mechanisms leading to polygyny may differ between the populations or that habitat quality is less heterogeneous in our population. If anything, habitat quality was somewhat lower in territories of polygynous males, because the diameter of oaks was slightly (c. 3cm) smaller while density of oaks was similar. Secondary females did not target areas that were particularly preferred by other females: neighbourhood distances at locations of settlement of secondary females were similar to those in the rest of the study site at the time when secondary females settled. This also shows that secondary females were not targeting lower density areas, e.g. to minimize interference by other females. Interference by females other than the primary female may not be important. After settling, the breeding distance between secondary females and neighbours other than the primary female was similar to the breeding distance between neighbouring monogamous females. Thus, secondary females did not 'squeeze into' an existing neighbourhood. Instead, they occupied a nestbox close to the nest of the primary female (on average 18 m closer than a 'typical' neighbourhood distance; see Canal *et al.* 2020 for a similar result), and hence settled into the existing territory of an already mated male.

Breeding phenology and clutch size

While the laying date of primary females did not differ from that of monogamous females, secondary females started laying approximately a week later (see also Canal *et al.* 2020). However, they still bred earlier than females that produced a replacement clutch. This suggests that secondary females did not have an undiscovered failed nesting attempt (e.g. in a natural cavity). We show evidence that several secondary females lost their initial social partner earlier in the season. An explanation for their late laying date then is that they needed time to find a new mate or breeding site. Furthermore, it has been described previously in Blue Tits that aggression of the primary female towards intruding females declines as the primary female's breeding progresses (Kempenaers 1995). Female-female aggression may thus delay establishment and hence start of laying of secondary females.

The difference in timing between the primary and secondary brood decreased as breeding progressed, because secondary females laid smaller clutches than the primary female of their mate. In contrast to a previous study (Kempenaers 1995), we found that secondary females laid smaller clutches than expected based on their laying date. This suggests that secondary females might use clutch size reduction strategically to accelerate breeding compared to the primary female, thereby increasing the likelihood of obtaining paternal care (Kempenaers 1995). However, primary females also laid smaller clutches than expected based on their laying date and the effect was not explained by differences in habitat quality (see Czapka & Johnson 2000 for a similar result in House Wrens *Troglodytes aedon*). In the European Starling, males were more likely to attract a second female when the clutch size of the primary female was experimentally reduced, because males invested less in incubating these clutches and spent more time courting additional females (Komdeur *et al.* 2002). In the Blue Tit, males do not incubate, but they feed their incubating mate. However, male investment in incubation feeding is independent of clutch size (Bambini *et al.* 2019). Also, males frequently associate with the secondary female before clutch completion of the primary female (Figures 2, S2–8). It is therefore unlikely that small primary clutches influenced the probability that a male became polygynous. Both primary and secondary females may produce smaller

clutches in anticipation of reduced male help in the polygynous mating situation, while secondary females may produce smaller clutches than the primary female of their mate, because they breed later and can expect to receive a smaller share of paternal care.

Total amount and distribution of parental care by polygynous males

On a given day, polygynous males overall made fewer nest visits than monogamous males, despite having two broods to care for (Figure 4). This pattern did not change when accounting for male age (result not shown). Polygynous males may thus have been able to invest more into self-maintenance and survival. However, in contrast to the Belgian population (Kempenaers 1994), polygynous males in our population did not survive better than monogamous males (Figure 7). Also, polygynous males did not consistently invest less in care. During periods when polygynous males provided care, their inter-visit intervals were similar to those of monogamous males (Figure 4F). However, polygynous males more often did not visit at all on a particular day during the nestling period.

Polygynous males rarely divided parental care between their two nests. This is in line with previous studies on Blue Tits and other species showing that male help at secondary nests was often absent or strongly reduced (Dyrcz 1986, Lifjeld & Slagsvold 1989, Johnson *et al.* 1993, Pinxten & Eens 1994, Kempenaers 1995, Rodrigues 1996, Sandell *et al.* 1996, Sejberg *et al.* 2000, Forstmeier *et al.* 2001, Moreno *et al.* 2002). However, in these studies investment of polygynous males was assessed over much shorter periods (0.5–5 hours over a period of 1–11 days). Here, we show how males switched between nests during the entire (or most of the) nestling phase. Of 13 polygynous males that could have divided their care, 9 males almost exclusively visited the primary brood (>90% of visits). In three of the four cases where males did provide substantially at both nests, the male appeared to focus on one of the nests on most days (Figure 5). Days where males switched frequently between the two nests occurred during a few days (up to five) when they shifted their exclusive focus from one nest to the other. It is not clear why feeding at two nests on the same day is so rare. It is unlikely that switching is costly in terms of finding food or travel distance, because the two nests were close together. Recent studies suggest that coordination of visits with the partner can affect offspring fitness (Spoon *et al.* 2006, Raihani *et al.* 2010, Mariette & Griffith 2015). Perhaps coordination with the partner is more difficult when switching between nests.

A previous study (Kempenaers 1995) showed that the amount of paternal care obtained by secondary females depended on the difference in hatching date between the primary and secondary clutch. Here, we found a similar pattern. Further study is needed to determine whether male division of care can be explained by the relative number of pre-breeding interactions between the male and his two females. A polygynous male may base his paternal investment on the relative amount of time spent, the intensity of interactions or the number of copulations with each of the two females. This would indirectly link the low levels of male care with the higher level of extra-pair paternity observed at secondary nests.

Polygyny and paternity

Polygynous males generally seem more susceptible to cuckoldry than monogamous males (reviewed in Vedder *et al.* 2011, but see Sousa & Westneat 2013). Most studies found that this is due to a similar level of paternity loss in the primary and the secondary brood (Dunn & Robertson 1993, Pilastro *et al.* 2002, Poirier *et al.* 2004, Vedder *et al.* 2011). One study found higher paternity loss only in primary nests (Bollinger & Gavin 1991), while another study reported higher loss only in secondary nests (Soukup & Thompson 1997). We found that polygynous males suffered higher paternity loss than monogamous males, because their secondary nests were more likely to contain extra-pair young and contained more extra-pair young (if any). We found no differences between yearling and older polygynous males ($P > 0.2$ for the effect of the interaction between mating status and male age on paternity loss), suggesting that the effect was not driven by higher losses for yearling males alone. However, our sample of yearling males ($n = 7$) is small. These results contrast with three previous studies that examined the link between polygyny and extra-pair paternity in Blue Tits. In a Belgian population paternity loss was less common for polygynous than for monogamous males (Kempenaers *et al.* 1992). In a population in Austria, primary and secondary nests did not differ in patterns of paternity, but adult polygynous males lost less paternity than either monogamous or yearling polygynous males (Schlicht & Kempenaers 2013). Finally, in a Dutch population paternity loss was higher for yearling polygynous males and consistent between primary and secondary nests (Vedder *et al.* 2011). In all three populations, polygyny occurred more frequently than in our population (3% of males vs. 20%, 8% and 15%, respectively; Kempenaers 1994, Vedder *et al.* 2011, Schlicht & Kempenaers 2013).

In two cases of replacement polygyny, our results show that paternity loss in the secondary nest could be attributed to the male that had been identified as the secondary female's initial (lost) mate. Polygynous males may thus suffer increased paternity loss in their secondary nests, if secondary females have copulated with another male before establishment of the pair bond with the polygynous male. Indeed, in monogamous nests extra-pair sires are usually males breeding nearby in the study site, whereas in secondary nests the majority of the extra-pair sires were non-breeding males.

Why do females become secondary females?
As is the case in many species (Slagsvold & Lifjeld 1994), females settling as secondary females in our population received less male help in raising nestlings than monogamous females (Figure 3). Their young had a reduced likelihood of fledging (Figure 6), even when accounting for male help and habitat quality. Furthermore, secondary females were less likely to survive (i.e. be observed in the next season) than monogamous females (Figure 7). This raises the question of why a female would settle as a secondary female. First, the apparent disadvantages of this mating situation may not (only) be a consequence of polygyny. Instead, these females may be of lower quality and hence would also have lower reproductive success and survival in a monogamous mating, as well as being more likely to become secondary females (Forstmeier *et al.* 2001, Grønstøl *et al.* 2003). Nevertheless, low quality females should still do better by settling with an unmated male, (1) to avoid aggression from a primary female (Slagsvold & Lifjeld 1994, Kempenaers 1995) and (2) to increase the probability of receiving male help in raising the brood. Second, an already mated male might still be a better partner that provides more care than an unmated male (Bensch 1997). However, given that males rarely divided care between the two nests, this is unlikely to be relevant in our population. Third, a particular mated male may produce offspring genotypes of higher fitness together with the female than a particular unmated male (Weatherhead & Robertson 1979). This seems unlikely, because genetic benefits are expected to be small (Akçay & Roughgarden 2007), and will be reduced further when some offspring are sired by extra-pair males. Indeed, secondary females in our population were more likely to have extra-pair young than monogamous females (Figure 6). Fourth, superior quality of the mated male's territory may compensate for reductions in paternal care (polygyny threshold model; Verner 1964, Orians 1969, Witten-

berger 1976). We found that, if anything, the opposite is the case. Secondary females settled in areas with similar numbers of oak trees, but where oak diameter is slightly smaller. They also bred at higher local density (closer proximity to neighbouring female). In conclusion, females in our population should prefer to settle with an unmated male rather than become a secondary female, if they have the choice.

The role of social turnover and familiarity
Several lines of evidence suggest that secondary females in our population often settled with a familiar male. (1) Secondary females often interacted with the future polygynous male at feeders (Figure 2). (2) Secondary females were often present in the neighbourhood before associating with the polygynous male. (3) One secondary female had been monogamously paired to the polygynous male in a previous season (Figure S7). Secondary females were observed with other males, but the probability that these males disappeared from the study site before breeding commenced was higher than for other females (Table S8). Interacting with multiple males in the pre-breeding period (either at nest sites or during foraging) may facilitate faster remating after mate loss. In the majority of cases (six out of nine where we could trace its origin), social polygyny arose after the disappearance (presumably death) of a paired male, whereby the widow then bred with an already mated instead of an unmated male.

Social associations with other males might also be important for obtaining male help during the nestling period. Indeed, Figure S8 shows an example of a male that had interacted with a female in the pre-breeding period, while both were mated to other partners, and fed the female's offspring after his breeding attempt failed, despite not being the father of any of those offspring (see also Kempenaers 1993). In general, familiarity with a potential mate may facilitate coordination of activities or division of labour among partners, which is necessary during pair bond formation, nest site selection, territory defence, copulation, incubation feeding or nestling care (Stamps *et al.* 2002, Spoon *et al.* 2006, van de Pol *et al.* 2006, Adkins-Regan & Tomaszycki 2007, Hall & Magrath 2007, Raihani *et al.* 2010, Mariette & Griffith 2012). A preference for familiar individuals during mate choice has been shown in a number of species (Cheetham *et al.* 2008) and may even override preferences for sexually selected ornaments (Senar *et al.* 2013). Overall, our data indicate that individuals that end up breeding together typically start to associate weeks before egg laying starts (Figure 2; see also Beck *et al.* 2020).

Thus, when the season has already progressed (e.g. after mate loss) females may prefer to mate with a familiar male or with a male at a familiar site, even if this male is already paired and even when unmated, unfamiliar males are present in the area. We suggest that polygyny may arise due to a combination of benefits of familiarity to site and potential mates and time-constraints to explore other options. In addition, secondary females may be making the best of a bad situation, because if unmated males are absent the alternative may be that they do not breed at all (Kempenaers 1994).

Social associations and site familiarity may also promote the formation of polygyny for males. Primary females were more likely to have bred together with their mate in the previous year than monogamous females (controlling for breeding experience). Thus, polygynous males often bred with a familiar mate in a familiar area (in the same territory; see also Valcu & Kempenaers 2008), and probably needed less time for territory establishment and pairing. This may have enabled these males to familiarize with additional females, eventually facilitating social polygyny. During the pre-breeding period the probability that a social partner disappeared was higher for secondary females, but also for polygynous males (Table S8). The social turnover that results when individuals disappear (either due to death or to competitive exclusion) thus appears to play a general role in the formation of polygyny. In case γ (Figure S5), polygyny probably arose after the disappearance of a female, because the vacancy was filled by two females simultaneously.

While many of these findings are based on small sample sizes or have anecdotal character, taken together they point to a role of social turnover and familiarity in the formation of polygyny.

Disadvantages of polygyny for primary females

As in many other species (Slagsvold & Lifjeld 1994, Ligon 1999), polygyny also appears disadvantageous for primary females: they received less male help than monogamous females (Figure 3), fledging success of their nests was lower (Figure 6), even when taking male help and habitat quality into account, and their probability of surviving until the next season was lower than that of monogamous females (Figure 7; see Lamers *et al.* 2020 for a similar result). We cannot exclude that this is at least partly because primary females also represent a subset of lower-quality females. However, this seems unlikely, because primary females resembled monogamous females until laying started. Primary and monogamous females did not

differ in the rate of interactions with their mate before breeding started (Figure 2). Primary females were slightly more likely to interact with their mate at the breeding box than monogamous females, while secondary females were far less likely to have those interactions (Figure 2). Furthermore, laying date and patterns of extra-pair paternity did not differ between primary and monogamous females (Figures 1, 6). Before the settlement of a secondary female, primary and monogamous females also bred at a similar distance to their neighbours.

Primary females produced smaller clutches than monogamous females, similar to secondary females. The amount of male care they received lay between that received by secondary and monogamous females (Figure 3). Fledging success and the probability of local survival were lower and did not differ between primary and secondary females (Figures 6–7). Thus, primary females resembled monogamous females in traits expressed early in the season, before and during the formation of polygyny, but their situation deteriorated after the settlement of the secondary female.

Do polygynous males benefit from polygyny?

Males are generally thought to benefit from polygyny, because mating with multiple females can substantially increase their reproductive success (e.g. Orians 1969, Jungwirth & Johnstone 2019). In a Belgian population, males actively attracted secondary females (Kempenaers 1995) and polygyny lead to increased reproductive success for males (Kempenaers 1994). In two other Blue Tit populations, polygyny also strongly and positively contributed to male reproductive success (Vedder *et al.* 2011, Schlicht & Kempenaers 2013), a common finding also in other species (e.g. Rodrigues 1996, Smith & Sandell 1998, Czapka & Johnson 2000, Ferretti & Winkler 2009, Newell *et al.* 2013).

In contrast, in our population, polygynous males did not obtain higher reproductive success than monogamous males in terms of number of fledglings sired (Figure 6G). Primary and secondary females laid smaller clutches than monogamous females (Figure 1C), secondary broods had an increased probability to contain extra-pair young and, if so, they contained more extra-pair young than broods of monogamous males (Figure 6), and fledging success of both primary and secondary broods was lower than that of broods of monogamous males (Figure 6). Polygynous males lost most of the additional offspring due to low fledging success at both primary and secondary nests, but they fledged 1.6 young more than monogamous males (95% CI: 0.5–2.7, $P = 0.01$, model analogous to Table S13).

This 'profit' was then lost due to extra-pair paternity in secondary nests. Reduced fledging success was not explained by the lower feeding rates experienced by nestlings in primary and secondary nests. This suggests that parents might have provided smaller or lower-quality food items at primary and secondary nests. Females that bred in a polygynous situation might also have been more likely to abandon the breeding attempt. Reduced fledging success of secondary nests, with a trend for a higher rate of brood failure after hatching, was reported in the Belgian population (Kempenaers 1994). Similarly, higher nest desertion of both primary and secondary females was found in the European Starling (Eens & Pinxten 1995). In our population, complete failures after hatching explained reduced fledging success in nests of polygynous males (Figure 6), suggesting that female abandonment may play a role.

Reduced fledging success of nests raised by polygynous males, in particular secondary nests, is a common finding (Ligon 1999, Huk & Winkel 2006) as is an increased rate of paternity loss (Vedder *et al.* 2011) and reduced clutch size (Slagsvold & Lifjeld 1994, Czapka & Johnson 2000, Komdeur *et al.* 2002). Indeed, the combination of these effects caused polygynous males to have lower reproductive success than monogamous males in a population of Tree Swallows *Tachycineta bicolor* (Dunn & Robertson 1993) and similar success in a population of Rock Sparrows *Petronia petronia* (Pilastro *et al.* 2002). In most studies polygynous males nevertheless sire considerably more fledglings than monogamous males (Cordero *et al.* 2003, Poirier *et al.* 2004, Hamao & Saito 2005, Vedder *et al.* 2011). However, this does not consider the quality of those fledglings. Reproductive success of monogamous and polygynous males may be similar when measured at the recruitment stage (Lubjuhn *et al.* 2000).

Conclusions

Many hypotheses have been proposed for why females end up mating with already mated males (reviewed by Ligon 1999). Our study suggests that in facultatively polygynous species such as the Blue Tit, polygyny mainly arises due to constraints. Females typically mated with males that were available within their familiar area and social environment. Whether females prefer a familiar breeding site and mate or make the best of a bad situation given time constraints remains to be seen, but if the former, polygyny may arise as a by-product without actually being adaptive (mal-adapted female model; Searcy & Yasukawa 1989). The costs and benefits classically invoked for secondary females may then have limited bearing on determining the mating situation. This may also be true when two females settle at the same time with the same male (parallel polygyny), because neither of them 'decides' to settle with an already mated male.

The results of our study also suggest that social turnover plays an important role in the formation of polygyny. While many researchers are aware that replacement polygyny occurs, this is often treated as an exceptional occurrence with little impact on selective processes (e.g. Ford 1983). However, high fluidity in mating constellations is probably common in many systems (Grinkov *et al.* 2018). The formation of polygyny is often not documented in detail, but whenever males attempt to settle and then vanish before breeding, mate loss may be involved in the origin of polygyny. This scenario is potentially relevant in many polygynous systems, especially in short-lived species.

Males are generally thought to benefit from polygyny and most studies suggest they do. In our study a male's 'decision' to become polygynous seemed to have little adaptive value. Similar to females, males may follow behavioural predispositions that sometimes lead to polygyny. This may explain why in many facultative polygynous species polygyny is neither increasing in frequency nor completely eliminated. Anthropogenic effects on mortality, sex ratio or habitat continuity may then affect the occurrence of polygyny, either as a by-product of behavioural predispositions selected in another context or due to a change in the costs and benefits of polygyny.

We conclude that site attachment and social associations are an important driver for reproductive decisions in the Blue Tit and in combination with social turn-over can explain the occurrence of polygyny without invoking adaptive benefits and selection for a particular mating strategy.

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SAMENVATTING

Klassieke verklaringen voor polygynie (het hebben van meerdere vrouwtjes) hebben betrekking op habitat, genetische factoren en vaderlijke zorg, maar er is weinig aandacht voor de sociale dynamiek. We hebben facultatieve sociale polygynie bestudeerd in een populatie Pimpelmezen *Cyanistes caeruleus* met een klein percentage polygynie (3% van de mannetjes over een periode van 12 jaar). Het voorkomen van polygynie werd het best voorspeld door sociale veranderingen na het verdwijnen van een of meer individuen. Habitatkwaliteit en individuele fenotypische eigenschappen waren onbelangrijk. Vrouwtjes vestigden zich als secundaire vrouwtjes met een mannetje en in een gebied waarmee ze eerder waren verbonden, wat wijst op een rol van bekendheid bij de vorming van polygynie. Vrouwtjes die gepaard waren met polygyne mannetjes kregen minder hulp bij het voeren van de jongen. Minder vaderlijke zorg is een potentiële kostenpost, omdat deze vrouwtjes minder goed overleefden dan vrouwtjes die gepaard waren met monogame mannetjes. Ondanks het feit dat polygyne mannetjes hun zorg zelden over beide nesten verdeelden, kregen zowel primaire als secundaire nesten minder ouderzorg. De kans dat een mannetje op een willekeurige dag helemaal niet in ouderzorg investeerde was groter voor polygyne dan voor monogame mannetjes. Daardoor investeerden polygyne mannetjes in totaal minder in ouderzorg dan monogame mannetjes. Polygyne mannetjes wisselden zelden hun bezoeken aan beide nesten af, wat duidt op een mogelijke kostenpost van het wisselen tussen voederlocaties. Zowel primaire als secundaire nesten hadden minder succes (kleiner percentage uitgevlogen jongen), zelfs als met variatie in habitatkwaliteit en vaderlijke zorg in de analyse rekening wordt gehouden. Het kleinere succes is vooral te wijten aan een groter percentage nesten dat faalt. Buitenechtelijke jongen kwamen meer voor bij secundaire nesten, vermoedelijk omdat het secundaire vrouwtje ook copuleerde met een vorige partner die was verdwenen. Als gevolg van het grotere vaderschapsverlies en het verminderde uitvliegsucces, brachten polygyne mannetjes in een seizoen niet meer jongen voort dan monogame mannetjes. Het voordeel van sociale polygynie voor mannetjes lijkt dus beperkt. In onze populatie ontstaat sociale polygynie waarschijnlijk vooral als een bijproduct van sterfte van mannetjes tijdens het broedseizoen. Weduwvrouwtjes gaan zich dan als secundaire partner vestigen met een bekende man of in een bekend gebied, waardoor ze het beste maken van een slechte situatie.

Supplementary Material is available online
www.ardeajournal.nl/supplement/s109–91–118.pdf

SUPPLEMENTARY MATERIAL

Table S1. Microsatellite loci for Blue Tits. Primer sequences include information on fluorescence labels used. C refers to the primer concentration in multiplex primer mix. Size range and number of alleles refer to 2018 data ($n = 1696$; Phtr3 from 2017, $n = 1905$).

Locus	Accession no.	published in	Primer sequences (5' – 3')	C (µM)	Multi-plex Mix	Size range (bp)	number of alleles
ADCYAP1_bm	FJ464427	Steinmeyer *et al.* (2009, supplement)	VIC-GATGTGAGTAACCAGCCACT ATAACACAGGAGCGGTGA	0.2	2[1]	160 – 172	10
ClkpolyQ	AY338423-28	Johnsen *et al.* (2007)	6FAM-TTTTCTCAAGGTCAGCAGCTTGT CTGTAGGAACTGTTGYGGKTGCTG	0.36	4[2]	266 – 283	7
Mcµ4	U82388	Double *et al.* (1997)	PET-ATAAGATGACTAAGGTCTCTGGTG TAGCAATTGTCTATCATGGTTTG	1.1	2[1]	156 – 194	19
PAT MP 2-43	AM056063	Otter *et al.* (1998)	6FAM- ACAGGTAGTCAGAAATGGAAAG GTATCCAGAGTCTTTGCTGATG	0.24	4[2]	125 – 155	8
Pca3	AJ279805	Dawson *et al.* (2000)	PET-GGTGTTTGTGAGCCGGGG TGTTACAACCAAAGCGGTCATTTG	0.8	1[3]	154 – 234	43
Pca4	AJ279806	Dawson *et al.* (2000)	NED-AATGTCTTACAGGCAAAGTCCCCA AACTTGAAGCTTCTGGCCTGAATG	0.42	4[2]	149 – 201	18
Pca7	AJ279809	Dawson *et al.* (2000)	6FAM-TGAGCATCGTAGCCCAGCAG GGTTCAGGACACCTGCACAATG	0.25	1[3]	105 – 141	18
Pca8	AJ279810	Dawson *et al.* (2000)	NED-ACTTCTGAAACAAAGATGAAATCA TGCCATCAGTGTCAAACCTG	0.48	1[3]	255 – 401	73
Pca9	AJ279811	Dawson *et al.* (2000)	VIC-ACCCACTGTCCAGAGCAGGG AGGACTGCAGCAGTTTGTGGG	0.3	3[4]	111 – 135	13
Phtr3[5]	AM056070	Fridolfsson *et al.* (1997)	NED-ATTTGCATCCAGTCTTCAGTAATT CTCAAAGAAGTGCATAGAGATTTCAT	1.4	2[1,5]	118 – 148 [5]	16[5]
PK11	AF041465	Tanner *et al.* (1995)	PET-CTTTAAGAATTCAAATACAGAGTAGG GTTTTCTCCTTTCTACACTGAGG	0.54	4[2]	63 – 97	14
PK12	AF041466	Tanner *et al.* (1995)	VIC-CCTCCTGCAGTTGCCTCCCG CGTGGCCATGTTTATAGCCTGGCACTAAGAAC	1.14	4[2]	168 – 226	27
PmaTAGAn71[5]	AY260537	Saladin *et al.* (2003)	NED-TCAGCCTCCAAGGAAAACAG GCATAAGCAACACCATGCAG	0.3	2[1,5]	190 – 310 [5]	29[5]
POCC1	U59113	Bensch *et al.* (1997)	6FAM- TTCTGTGCTGCAATCACACA GCTTCCAGCACCACTTCAAT	0.8	3[4]	219 – 255	25
POCC6	U59117	Bensch *et al.* (1997)	VIC-TCACCCTCAAAAACACACACA ACTTCTCTCTGAAAAGGGGAGC	0.25	1[3]	195 – 253	28
P2/P8	AF006659-62	Griffiths *et al.* (1998)	6FAM-CTCCCAAGGATGAGRAAYTG TCTGCATCGCTAAATCCTTT	0.3	2[1]	319, 383	2

[1]Cycling conditions for mix 2: 5 min initial denaturation at 95˚C; 27 cycles of 30 s denaturation at 94˚C, 90 s annealing at 56˚C, and 1 min extension at 72˚C; followed by a 30 min completing final extension at 60˚C.

[2]Cycling conditions for mix 4: 5 min initial denaturation at 95˚C; 23 cycles of 30 s denaturation at 94˚C, 90 s annealing at 58˚C, and 1 min extension at 72˚C; followed by a 30 min completing final extension at 60˚C.

[3]Cycling conditions for mix 1: 5 min initial denaturation at 95˚C; 15 cycles of 30 s denaturation at 94˚C, 90 s touch down annealing at 60˚C decreasing by 0.3˚C per cycle, and 1 min extension at 72˚C; 11 cycles of 30 s denaturation at 94˚C, 90 s annealing at 53˚C, and 1 min extension at 72˚C; followed by a 30 min completing final extension at 60˚C.

[4]Cycling conditions for mix 3: 5 min initial denaturation at 95˚C; 14 cycles of 30 s denaturation at 94˚C, 90 s annealing at 56˚C, and 1 min extension at 72˚C; 11 cycles of 30 s denaturation at 94˚C, 90 s annealing at 57˚C, and 1 min extension at 72˚C; followed by a 30 min completing final extension at 60˚C.

[5]Phtr3 was replaced by PmaTAGAn71 from 2018 onwards.

Table S2. Summary of statistical models and their structure. 'mono' = monogamous, 'poly' = polygynous, 'prim' = primary, 'sec' = secondary. 'Step' refers to the steps of analysis described at the end of the introduction. Results refers to the Table where results are presented unless they are described in the text.

Step	Model no.	Dependent variable	Explanatory variable(s) of interest	Covariate(s)	Random structure	Error structure[1]	Results
origin i	1a	proportion of poly ♂♂ among breeding ♂♂	no. of breeding ♂♂	–	–	B	in text
origin i	1b	experienced ♀♀: rebreeding with former mate (Y/N)	mating status (mono/prim)	–	intercept: ♀ identity	C	in text[2]
origin iii	2a	neighbour distance before settlement of sec ♀♀	neighbour category (1/2)	–	intercept: year	G	S4
origin iii	2b	neighbour distance before settlement of sec ♀♀	neighbour category (1/2)	–	intercepts: year, identity of the two neighbouring boxes	G	S4
origin iii	2c	neighbour distance after settlement of sec ♀♀	neighbour category (1/2/3/4)	–	intercept: year	G	S4
origin iii	3a	no. of oaks within 75 m	mating status (mono/prim/sec)	–	intercept: year	G	S5
origin iii	3b	average diameter of oaks within 75 m	mating status (mono/prim/sec)	–	intercept: year	G	S5
origin iv	4a	laying date	mating status (mono/prim/sec)	♀ age (categorical)	intercept: year, ♀ identity	G	S6
origin iv	4b	laying date	sec vs. replacement	♀ age (categorical)	intercepts: year, ♀ identity	G	S6
origin iv	4c	laying date	prim vs. simulated early	♀ age (categorical)	intercepts: year, ♀ identity	G	S6
origin iv	4d	laying date	sec vs. simulated late	♀ age (categorical)	intercepts: year, ♀ identity	G	S6
origin iv	4e	Δ laying date	Δ sec-prim vs. Δ simulated late-early	–	intercept: year	P	S6
origin iv	5a	Δ clutch size (prim-sec)	difference to 0	–	intercept: year	G	in text[3]
origin iv	5b	Δ incubation duration (prim-sec)	difference to 0	–	intercept: year	G	in text[4]
origin iv	6	clutch size	mating status (mono/prim/sec)	laying date, number and average diameter of oak trees within 75 m	intercepts: year, ♀ identity	G	S11
origin v	7	interaction (y/n) between pair members on a day of the pre-breeding period	mating status (mono/prim/sec) x location (breeding box/other nestbox/feeder)	days to laying date	intercepts: year, ♂ identity, ♀ identity, slopes for days to laying date: ♂ identity, ♀ identity	C	S7
origin v	8a	♂♂: no. of interacting ♀♀ (mates excluded) of the pre-breeding period	mating status (mono/poly)	no. of days data are available	intercepts: year, ♂ identity	P	S8
origin v	8b	♂♂: proportion of interacting ♀♀ (mates excluded) of the pre-breeding period lost before laying date	mating status (mono/poly)	no. of days data are available	intercepts: year, ♂ identity	B	S8
origin v	8c	♀♀: no. of interacting ♂♂ (mates excluded) of the pre-breeding period	mating status (mono/prim/sec)	no. of days data are available	intercepts: year, ♀ identity	P	S8
origin v	8d	♀♀: proportion of interacting ♂♂ (mates excluded) of the pre-breeding period lost before laying date	mating status (mono/prim/sec)	no. of days data are available	intercepts: year, ♀ identity	B	S8
origin vi	9a	♂♂: tarsus length	mating status (mono/poly)	–	intercepts: year, ♂ identity	G	2
origin vi	9b	♂♂: age (categorical)	mating status (mono/poly)	–	intercepts: year, ♂ identity	C	2
origin vi	9c	♂♂: presence at study site at start of pre-breeding period (y/n)	mating status (mono/poly)	–	intercepts: year, ♂ identity	C	2

Table S2. Continued.

Step	Model no.	Dependent variable	Explanatory variable(s) of interest	Covariate(s)	Random structure	Error structure[1]	Results
outcome iii	9d	♂♂: local survival to next breeding season (y/n)	mating status (mono/poly)	–	intercepts: year, ♂ identity	C	2
origin vi	9e	♀♀: tarsus length	mating status (mono/prim/sec)	–	intercepts: year, ♀ identity	G	2
origin vi	9f	♀♀: age (categorical)	mating status (mono/prim/sec)	–	intercepts: year, ♀ identity	C	2
origin vi	9g	♀♀: presence at study site at start of pre-breeding period (y/n)	mating status (mono/prim/sec)	–	intercepts: year, ♀ identity	C	2
outcome iii	9h	♀♀: local survival to next breeding season (y/n)	mating status (mono/prim/sec)	–	intercepts: year, ♀ identity	C	2
outcome i	10a	no. of feeds per nestling per day performed by ♀ (square-root-transformed)	mating status (mono/prim/sec)	nestling age (log-transformed), relative hatch date	intercepts: year, ♂ identity, ♀ identity, slope for nestling age (log-transformed): ♀ identity	G	S9
outcome i	10b	no. of feeds per nestling per day performed by ♂ (square-root-transformed)	mating status (mono/prim/sec)	nestling age (log-transformed), relative hatch date	intercepts: year, ♂ identity, ♀ identity, slope for nestling age (log-transformed): ♂ identity	G	S9
outcome i	10c	total no. of feeds per day performed by ♂ (square-root-transformed, all days included)	mating status (mono/poly)	nestling age (log-transformed), relative hatch date (both from nest with higher no. of ♂ feeds on given day)	intercepts: year, ♂ identity, ♀ identity (of nest with higher no. of ♂ feeds on given day), slope for nestling age (log-transformed): ♂ identity	G	S9
outcome i	10d	total no. of feeds per day performed by ♂ (square-root-transformed, days without feeds excluded)	mating status (mono/poly)	nestling age (log-transformed), relative hatch date (both from nest with higher no. of ♂ feeds on given day)	intercepts: year, ♂ identity, ♀ identity (of nest with higher no. of ♂ feeds on given day), slope for nestling age (log-transformed): ♂ identity	G	S9
outcome i	11	total no. of ♂ feeds at sec nest / total no. of ♂ feeds at prim+sec nest	Δ hatch date (sec-prim)	–	intercept: year	B	in text[5]
outcome i	12a	inter-visit interval between two successive ♂ feeds	mating status (mono/poly)	nestling number, nestling age (log-transformed), relative hatch date (all from nest visited at end of inter-visit interval)	intercepts: year, ♂ identity, ♀ identity (of nest visited at end of inter-visit interval), slope for nestling age (log-transformed): ♂ identity	P	S10
outcome i	12b	proportion of days with total no. of ♂ feeds ≥1	mating status (mono/poly)	nestling number, relative hatch date (both from nest visited more often by ♂)	intercepts: year, ♂ identity, ♀ identity (of nest visited more often by ♂)	B	S10
outcome ii	13a	♂♂: offspring probability of hatching	mating status (mono/poly)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S12
outcome ii	13b	♂♂: average nestling weight (g)	mating status (mono/poly)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	G	S12
outcome ii	13c	♂♂: offspring probability of recruitment	mating status (mono/poly)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S12
outcome ii	13d	♀♀: offspring probability of hatching	mating status (mono/prim/sec)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S12
outcome ii	13e	♀♀: average nestling weight (g)	mating status (mono/prim/sec)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	G	S12

Table S2. Continued.

Step	Model no.	Dependent variable	Explanatory variable(s) of interest	Covariate(s)	Random structure	Error structure[1]	Results
outcome ii	13f	♀♀: offspring probability of recruitment	mating status (mono/prim/sec)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S12
outcome ii	14a	♂♂: fledgling no. ≥1 (y/n)	mating status (mono/poly)	–	intercepts: year, ♂ identity	C	S13
outcome ii	14b	♂♂: offspring probability of fledging	mating status (mono/poly)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S13
outcome ii	14c	♂♂: offspring probability of fledging	mating status (mono/poly)	♂ feeding effort, oak number, average oak tree tree diameter, relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S13
outcome ii	14d	♂♂: offspring probability of fledging (nests with ≥1 fledglings)	mating status (mono/poly)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S13
outcome ii	14e	♂♂: total no. of fledglings sired	mating status (mono/poly)	♂ age (categorical), relative hatch date (average for poly ♂♂)	intercepts: year, ♂ identity	G	S13
outcome ii	14f	♀♀: fledgling no. ≥1 (y/n)	mating status (mono/prim/sec)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S13
outcome ii	14g	♀♀: offspring probability of fledging	mating status (mono/prim/sec)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S13
outcome ii	14h	♀♀: offspring probability of fledging	mating status (mono/prim/sec)	relative hatch date, ♂ feeding effort, oak tree number, average oak tree diameter, relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S13
outcome ii	14i	♀♀: offspring probability of fledging (nests with ≥1 fledglings)	mating status (mono/prim/sec)	relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S13
outcome ii	15a	♂♂: probability of young being EPY (all ♂♂)	mating status (mono/poly)	♂ age (categorical), relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S14
outcome ii	15b	♂♂: probability of young being EPY (only ♂♂ with paternity loss)	mating status (mono/poly)	♂ age (categorical), relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S14
outcome ii	15c	♂♂: probability of siring ≥1 EPY	mating status (mono/poly)	♂ age (categorical), relative hatch date	intercepts: year, ♂ identity	C	S14
outcome ii	15d	♂♂: no. of EPY sired (all ♂♂)	mating status (mono/poly)	♂ age (categorical), relative hatch date	intercepts: year, ♂ identity	P	S14
outcome ii	15e	♂♂: no. of EPY sired (only ♂♂ with paternity gain)	mating status (mono/poly)	♂ age (categorical), relative hatch date	intercepts: year, ♂ identity	P	S14
outcome ii	15f	♀♀: probability that nest contains ≥ 1 EPY	mating status (mono/prim/sec)	♂ age (categorical), relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S14
outcome ii	15g	♀♀: probability of young being EPY (all nests)	mating status (mono/prim/sec)	♂ age (categorical), relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S14
outcome ii	15h	♀♀: probability of young being EPY (only nests that contain EPY)	mating status (mono/prim/sec)	♂ age (categorical), relative hatch date	intercepts: year, ♂ identity, ♀ identity	C	S14

[1]G: Gaussian error structure, identity-link. C: categorical error structure (binary data), logit-link. B: binomial error structure (proportion data, family 'multinomial2'), logit-link. P: Poisson error structure, log-link.
[2]Posterior mean (95% CI) for variance of female identity random effect: 0.36 (0.00 to 1.3).
[3]Posterior mean (95% CI) for variance of random effect year: 0.77 (0.00 to 3.1) and residual variance: 11.0 (6.1 to 16.9).
[4]Posterior mean (95% CI) for variance of random effect year: 4.1 (0.00 to 13.8) and residual variance: 9.3 (3.6 to 16.4).
[5]Posterior mean (95% CI) for variance of random effect year: 17.4 (0.00 to 55.7) and residual variance: 36.2 (5.8 to 92.01).

Table S3. Classification of primary and secondary breeding attempts for 17 polygynous males (cases). The primary attempt (labelled **1**) is by definition the one with the earlier laying date (**2** refers to the secondary attempt). '–' denotes unavailable information. Cases for which a detailed figure is provided in the supplement are underlined. Underlined cases in the column for male feeds indicate the four cases illustrated in Figure 5 where the males invested substantially (but not necessarily similarly) at both nests during nestling feeding.

Case	Days difference between 2 and 1 in date of				Type of polygyny	Female with earlier interaction	Female with higher rate of interactions	Nest with more male feeds	Primary female at nest
	Laying	Clutch completion	Hatching	Fledging					
α	1	0	–1	–1	replacement	2	2	1	2
β	3	3	5	6	parallel	2	2	1	1 or 2
γ	3	6	4	–	parallel	–	–[1]	1	1
δ	6	6	1	–1	successive	1	1	1	1
ε	1	3	–	–	parallel	1	1	–	1
ζ	10	6	3	2	replacement	1	1	1	1
η	2	2	3	4	–	–	–	2	1 or 2
θ	15	9	13	13	–	1	1	–	1
ι	2	–2	–2	–1	replacement	1	1	–	1
κ	1	1	0	–	–	–	–	1	1
λ	11	12	7	5	–	–	–	1	1
μ	3	–1	0	–	–	–	–	1	1
ν	2	2	4	–	replacement	–	–	1	1
ξ	17	15	13	12	–	–	–	1	1
o	10	3	–[2]	–	replacement	1	1	–	1
π	26	25	15	12	–	–	–	1	1
ρ	5	3	4	3	–	–	–	1	1

[1]Data of primary female are incomplete. Qualitative classification of polygyny is possible, but not the quantitative assessment of pre-breeding interactions.

[2]Both nests hatched, but exact hatch date is unavailable for one of them.

Table S4. Distance between neighbouring boxes (in meters) before and after settlement of secondary females. Neighbour category 1: nests of two monogamous males, category 2: primary nest of a polygynous male and the nest of another (monogamous or polygynous) male, category 3: secondary nest of a polygynous male and the nest of another (monogamous or polygynous) male, category 4: primary and secondary nest of the same polygynous male. Shown are results from linear mixed-effect models with year as random intercept (model 2a–c in Table S2). In a second version the identity of the two neighbouring boxes was included as random intercepts to account for consistent between-year variation in local breeding density. After settlement, results for both versions were similar and only the first version is shown. Before settlement: n = 3157 neighbourhoods, 181 of which are of category 2. After settlement: n = 3251 neighbourhoods, 147 of which are of category 2, 131 of category 3 and 35 of category 4.

	Estimate	95% CI	P (MCMC)
Before settlement of secondary females[1]			
Intercept (category 1)	72.6		
Category 2 vs. 1	4.8	1.2 to 8.8	0.01
Before settlement of secondary females, accounting for consistent between-year variation in local breeding density[2]			
Intercept (category 1)	71.6		
Category 2 vs. 1	3.5	–0.5 to 7.7	0.10
After settlement of secondary females[3]			
Intercept (category 1)	72.2		
Category 2 vs. 1	0.01	–4.5 to 4.3	0.99
Category 3 vs. 1	–3.5	–8.3 to 0.8	0.14
Category 3 vs. 2[4]	*–3.4*	*–8.9 to 2.4*	*0.26*
Category 4 vs. 1	–14.8	–23.4 to –6.4	< 0.001
Category 4 vs. 2[4]	*–14.7*	*–23.2 to –4.4*	*0.002*
Category 4 vs. 3[4]	*–11.4*	*–20.3 to –1.7*	*0.02*

[1]Posterior mean (95% CI) for random effects and residual variances: year: 134.8 (49.6 to 274.8), residual: 692.5 (659.3 to 727.3).
[2]Posterior mean (95% CI) for random effects and residual variances: year: 116.6 (33.8 to 231.5), box 1 identity: 85.9 (59.6 to 113.7).
box 2 identity: 54.0 (34.0 to 75.2), residual: 562.2 (529.6 to 591.6).
[3]Posterior mean (95% CI) for random effects and residual variances: year: 138.5 (44.4 to 293.3), residual: 666.7 (633.7 to 698.1).
[4]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown).

Table S5. Measures of habitat quality (number of oak trees and their average diameter within 75 m of a nestbox) for females of different mating status. Shown are results from linear mixed-effect models with year as random intercept (model 3a–b). n = 1207 breeding attempts, of which 35 are primary and 35 are secondary nests.

	Estimate	95% CI	P (MCMC)
Number of oaks[1]			
Intercept	295.0		
Primary vs. monogamous	–6.4	–66.3 to 52.5	0.82
Secondary vs. monogamous	–18.2	–76.8 to 41.1	0.52
Secondary vs. primary[2]	*–11.7*	*–89.9 to 77.4*	*0.78*
Average diameter of oak trees (cm)[3]			
Intercept	70.5		
Primary vs. monogamous	–3.4	–6.1 to –0.8	0.01
Secondary vs. monogamous	–2.9	–6.1 to –0.4	0.04
Secondary vs. primary[1]	*0.5*	*–3.8 to 4.1*	*0.80*

[1]Posterior mean (95% CI) for random effects and residual variances: year: 25.3 (0.00 to 116.4), residual: 30,891 (28,569 to 33,526).
[2]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown).
[3]Posterior mean (95% CI) for random effects and residual variances: year: 0.11 (0.00 to 0.45), residual: 70.8 (65.5 to 76.5).

Table S6. Differences in laying date (in days) between primary and secondary females and monogamous females, replacement breeding attempts and simulated early and late attempts (based on random pairings of monogamous attempts, see Methods). Shown are results from linear mixed-effect models with year and female identity as random intercepts, except for the last model which has Poisson error structure (estimates on log-scale) and only year as random intercept (model 4a–e). $n = 1136$ monogamous attempts, 30 replacement attempts, 34 primary and 33 secondary breeding attempts (from 35 events of polygyny; one primary and two secondary females are excluded because age information is not available), 564,000 simulated pairings.

	Estimate	95% CI	P (MCMC)
Primary and secondary vs. monogamous ($n = 1203$)[1]			
Intercept	1.6		
Primary vs. monogamy	–0.7	–2.1 to 0.7	0.34
Secondary vs. monogamy	8.5	7.0 to 9.8	<0.001
Female age (adult vs. yearling)	–1.6	–2.1 to –1.2	<0.001
Secondary vs. replacement ($n = 63$)[2]			
Intercept	19.4		
Secondary vs. replacement	–15.2	–19.6 to –9.8	<0.001
Female age (adult vs. yearling)	2.6	–2.2 to 7.7	0.29
Primary vs. simulated early attempts ($n = 564,034$)[3]			
Intercept	0.8		
Primary vs. simulated early	0.5	0.04 to 1.0	0.04
Female age (adult vs. yearling)	–1.4	–1.4 to –1.4	(<0.001)[4]
Secondary vs. simulated late attempts ($n = 564,033$)[5]			
Intercept	2.0		
Secondary vs. simulated late	8.0	7.1 to 8.8	<0.001
Female age (adult vs. yearling)	–1.9	–1.9 to –1.9	(<0.001)[4]
Difference in laying date between primary and secondary vs. simulated early and late attempts ($n = 564,035$)[6]			
Intercept	1.02		
Polygyny vs. simulated	0.98	0.72 to 1.23	<0.001

[1]Posterior mean (95% CI) for random effects and residual variances: year: 0.23 (0.00 to 0.61), female identity: 7.9 (5.7 to 10.0), residual: 12.3 (10.7 to 14.0).
[2]Posterior mean (95% CI) for random effects and residual variances: year: 0.54 (0.00 to 1.3), female identity: 2.4 (0.00 to 4.8), residual: 56.5 (31.9 to 115.8).
[3]Posterior mean (95% CI) for random effects and residual variances: year: 1.6 (0.52 to 3.3), female identity: 11.8 (10.6 to 13.0), residual: 1.4 (1.4 to 1.4).
[4]The effect of female age is pseudo-replicated due to the simulation.
[5]Posterior mean (95% CI) for random effects and residual variances: year: 2.2 (0.70 to 4.5), female identity: 21.6 (19.3 to 23.7), residual: 2.3 (2.3 to 2.3).
[6]Posterior mean (95% CI) for random effects and residual variances: year: 0.16 (0.05 to 0.31), residual: 0.55 (0.54 to 0.55).

Table S7. Interactions among pair members during the pre-breeding period (60 days prior to egg laying, see Methods). Time to first egg is the number of days until laying start. Shown are results from a generalized linear mixed-effect model with categorical error structure (estimates on logit-scale) and with year, male identity and female identity as random intercept and random slopes of time to first egg for male and female identity[1] (model 7). n = 74,419 interaction-days from 526 breeding attempts, of which 20 are primary and 9 are secondary nests.

	Estimate	95% CI	P (MCMC)
Intercept	1.61		
Time to first egg (days)	0.12	0.11 to 0.15	<0.001
Other nestboxes vs. breeding box	–2.12	–2.22 to –2.04	<0.001
Feeder vs. breeding box	–3.08	–3.22 to –2.95	<0.001
Primary vs. monogamous	0.68	0.12 to 1.19	0.01
Secondary vs. monogamous	–1.72	–2.83 to –0.74	<0.001
Secondary vs. primary[2]	*–2.43*	*–3.52 to –1.28*	*<0.001*
Other boxes × primary	0.29	–0.15 to 0.75	0.21
Other boxes × secondary	0.30	–0.50 to 1.15	0.49
Feeder × primary	–0.59	–1.25 to 0.11	0.09
Feeder × secondary	3.79	2.79 to 4.83	<0.001

[1]Posterior mean (95% CI) for random effects variances: year: 0.43 (0.08 to 1.1), male identity: 0.79 (0.58 to 0.99), female identity: 0.73 (0.55 to 0.90), slope for days to laying start – male identity: 0.00 (0.00 to 0.001), slope for days to laying start – female identity: 0.002 (0.001 to 0.002).
[2]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown).

Table S8. Interactions among males and females not breeding together during the pre-breeding period (60 days prior to egg laying, see Methods). Shown are the results of generalized linear mixed-effect models with either the number of interacting individuals (for breeding males and females) as the dependent variable (Poisson error, estimates on log-scale), or the proportion of those interacting individuals that disappeared before laying started (binomial error, estimates on logit-scale). The number of days for which data are available varies depending on when individuals received a transponder (range 21 to 60 days). All models include year and breeder identity as random intercepts (model 8a–d).

	Estimate	95% CI	P (MCMC)
BREEDING MALES[1]			
Number of interacting females (mates excluded)[2]			
Intercept	–2.30		
Polygynous vs. monogamous	–0.34	–0.97 to 0.26	0.30
Number of days data are available	0.05	0.03 to 0.07	<0.001
Proportion of interacting females lost (mates excluded)[3]			
Intercept	–2.70		
polygynous vs. monogamous	0.64	0.27 to 1.07	<0.001
number of days data are available	0.01	–0.02 to 0.04	0.50
BREEDING FEMALES[4]			
Number of interacting males (mates excluded)[5]			
Intercept	–1.97		
Primary vs. monogamous	–0.02	–0.82 to 0.83	0.98
Secondary vs. monogamous	1.30	0.26 to 2.17	0.01
Secondary vs. primary[6]	*1.30*	*0.06 to 2.64*	*0.05*
Number of days data are available	0.02	0.002 to 0.04	0.01
Proportion of interacting males lost (mates excluded)[7]			
Intercept	–2.12		
Primary vs. monogamous	0.54	–0.14 to 1.29	0.14
Secondary vs. monogamous	1.09	0.41 to 1.84	0.003
Secondary vs. primary[6]	*0.68*	*–0.42 to 1.68*	*0.20*
Number of days data are available	–0.009	–0.03 to 0.01	0.40

[1]n = 560 breeding males (346 individuals), of which 24 are polygynous.
[2]Posterior mean (95% CI) for random effects and residual variances: year: 6.4 (1.5 to 15.3), male identity: 1.5 (1.1 to 1.9), residual: 0.48 (0.33 to 0.64).
[3]Posterior mean (95% CI) for random effects variances: year: 1.9 (0.23 to 5.3), male identity: 0.01 (0.00 to 0.04).
[4]n = 579 breeding females (380 individuals), of which 23 are primary and 11 are secondary females.
[5]Posterior mean (95% CI) for random effects and residual variances: year: 5.9 (1.2 to 13.7), female identity: 2.0 (1.3 to 2.6), residual: 1.4 (0.97 to 1.9).
[6]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown).
[7]Posterior mean (95% CI) for random effects variances: year: 1.3 (0.17 to 3.4), female identity: 0.02 (0.00 to 0.07).

Table S9. Comparison of the number of feeding visits for females and males of different mating status. Shown are results from linear mixed-effect models with the number of feeds per nestling per day or the total number of feeds per day as the dependent variable (all square-root-transformed). Male feeds at primary and secondary nests are treated separately for 'feeds per nestling', but pooled for 'total feeds'. Models include year, male identity and female identity as random intercepts and the random slope of log-transformed nestling age (for female or male identity, as appropriate; model 10a–d).

	Estimate	95% CI	P (MCMC)
Female feeds per nestling per day[1]			
Intercept	2.02		
Primary vs. monogamous	0.14	–0.11 to 0.40	0.28
Secondary vs. monogamous	0.50	0.08 to 0.92	0.01
Secondary vs. primary[2]	*0.35*	*–0.07 to 0.85*	*0.13*
Hatch date[3]	–0.02	–0.03 to –0.01	0.01
Nestling age[4]	0.85	0.80 to 0.90	<0.001
Male feeds per nestling per day[5]			
Intercept	3.16		
Primary vs. monogamous	–0.54	–0.84 to –0.28	<0.001
Secondary vs. monogamous	–3.22	–3.68 to –2.83	<0.001
Secondary vs. primary[2]	–2.69	–3.22 to –2.21	<0.001
Hatch date[3]	–0.05	–0.06 to –0.03	<0.001
Nestling age[4]	0.48	0.43 to 0.53	<0.001
Total male feeds per day[6]			
Intercept	8.96		
Polygynous vs. monogamous	–1.72	–2.59 to –0.78	<0.001
Hatch date[3]	–0.19	–0.24 to –0.15	<0.001
Nestling age[4]	1.22	1.09 to 1.36	<0.001
Total male feeds per day (days without feeds excluded)[7]			
Intercept	9.39		
Polygynous vs. monogamous	0.25	–0.56 to 0.96	0.49
Hatch date[3]	–0.09	–0.12 to –0.06	<0.001
Nestling age[4]	1.49	1.38 to 1.60	<0.001

[1]n = 8631 feeding days from 570 annual female breeders (407 individuals), of which 24 are primary and 24 are secondary females. Posterior mean (95% CI) for random effects and residual variances: year: 0.65 (0.13 to 1.6), male identity: 0.78 (0.62 to 0.94), female identity: 0.56 (0.41 to 0.72), slope for nestling age (log-transformed) – female identity: 0.18 (0.14 to 0.21), residual: 0.69 (0.67 to 0.71).
[2]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown).
[3]Relative to annual mean.
[4]log days since hatching.
[5]n = 9112 feeding days from 559 annual male breeders (381 individuals), of which 31 are polygynous (feeding data at primary nest only: 7 males, at secondary nest only: 8 males, at both nests: 16 males). Posterior mean (95% CI) for random effects and residual variances: year: 1.2 (0.21 to 2.8), male identity: 1.9 (1.5 to 2.2), female identity: 2.2 (1.8 to 2.6), slope for nestling age (log-transformed) – male identity: 0.16 (0.13 to 0.19), residual: 0.67 (0.65 to 0.69).
[6]n = 8740 feeding days from 548 annual male breeders (375 individuals) of which 19 are polygynous. Posterior mean (95% CI) for random effects and residual variances: year: 7.4 (1.5 to 17.1), male identity: 12.5 (10.0 to 15.3), female identity: 13.9 (11.6 to 16.8), slope for nestling age (log-transformed) – male identity: 1.3 (1.0 to 1.6), residual: 4.9 (4.7 to 5.0).
[7]n = 7945 feeding days from 510 annual male breeders (349 individuals) of which 19 are polygynous. Posterior mean (95% CI) for random effects and residual variances: year: 4.5 (0.92 to 10.3), male identity: 3.2 (2.4 to 4.1), female identity: 4.5 (3.6 to 5.4), slope for nestling age (log-transformed) – male identity: 0.80 (0.64 to 0.96), residual: 3.6 (3.5 to 3.7).

Table S10. Patterns of feeding visits to nestboxes by males of different mating status. For polygynous males, this is independent of whether they fed the brood of the primary or the secondary female. Shown are results from generalized linear mixed-effect models (see below, Methods and model 12a–b in Table S2 for details).

	Estimate	95% CI	P (MCMC)
Inter-visit interval[1]			
Intercept	6.04		
Polygynous vs. monogamous	–0.04	–0.08 to 0.01	0.10
Hatch date[2]	–0.001	–0.003 to 0.001	0.54
Nestling age[3]	–0.20	–0.22 to –0.18	<0.001
Nestling number	–0.06	–0.06 to –0.05	<0.001
Proportion of days male feeds (logit–scale)[4]			
Intercept	11.18		
Polygynous vs. monogamous	–6.05	–10.38 to –1.52	0.008
Hatch date[2]	–0.32	–0.59 to –0.08	0.009
Nestling number	0.13	–0.42 to 0.69	0.63

[1]Inter-visit intervals in s, only for visits on the same day. Poisson error structure (estimates on log-scale). Random intercepts: year, male identity, and female identity. Random slope: log-transformed nestling age (for male identity). n = 882,476 inter-visit intervals from 341 annual male breeders (242 individuals), of which 30 are polygynous. Posterior mean (95% CI) for random effects and residual variances: year: 0.44 (0.09 to 1.0), male identity: 0.47 (0.18 to 0.68), female identity: 0.18 (0.06 to 0.40), slope for nestling age (log-transformed) – male identity: 0.10 (0.08 to 0.12), residual: 1.1 (1.1 to 1.2).
[2]Relative to annual mean.
[3]log days since hatching.
[4]Binomial error structure (estimates on logit-scale). Random intercepts: year, male identity. n = 558 annual male breeders (381 individuals), of which 30 are polygynous. Posterior mean (95% CI) for random effects variances: year: 8.1 (0.39 to 22.4), male identity: 69.0 (34.0 to 109.4), female identity: 53.4 (25.7 to 88.4).

Table S11. Population-wide comparison of clutch size for females of different mating status. Shown are results from a linear mixed-effect model, accounting for laying date and territory quality (the number and mean diameter of oak trees within 75m of the nestbox), and with year and female identity as random intercepts[1] (model 6). n = 1230 clutches from 767 individual females, of which 34 are primary and 33 are secondary clutches.

	Estimate	95% CI	P (MCMC)
Intercept	9.7		
Primary vs. monogamous	–0.8	–1.4 to –0.3	0.005
Secondary vs. monogamous	–0.9	–1.4 to –0.3	0.007
Secondary vs. primary[2]	*–0.07*	*–0.9 to 0.7*	*0.87*
Laying date[3]	–0.1	–0.1 to –0.1	<0.001
Number of oak trees	0.0005	–0.0001 to 0.001	0.13
Oak tree diameter (mean)	0.004	–0.008 to 0.02	0.55

[1]Posterior mean (95% CI) for random effects and residual variances: year: 0.65 (0.20 to 1.3), female identity: 1.1 (0.78 to 1.4), residual: 1.8 (1.6 to 2.0).
[2]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown).
[3]Relative to annual mean.

Table S12. Comparison of measures of reproductive success for nests of different status. Monogamous nests are compared to primary and secondary nests separately or combined (polygynous), reflecting measures of female or male success. Shown are results from generalized linear mixed-effect models with year, male identity and female identity as random intercepts (see below for error structure; model 13a–f).

	Estimate	95% CI	P (MCMC)
MEASURES OF MALE SUCCESS			
Probability of hatching[1,2]			
Intercept	7.55		
Polygynous vs. monogamous	–0.70	–1.79 to 0.49	0.23
Hatch date[3]	–0.07	–0.15 to 0.002	0.07
Nestling weight[4,5]			
Intercept	10.23		
Polygynous vs. monogamous	0.13	–0.23 to 0.45	0.49
Hatch date[3]	0.03	0.002 to 0.04	0.02
Probability of recruitment[1,6]			
Intercept	–6.65		
Polygynous vs. monogamous	–0.60	–1.52 to 0.42	0.23
Hatch date[3]	–0.04	–0.10 to 0.01	0.11
MEASURES OF FEMALE (NEST–WISE) SUCCESS			
Probability of hatching[1,7]			
Intercept	7.45		
Primary vs. monogamous	–1.11	–2.44 to 0.35	0.12
Secondary vs. monogamous	–0.21	–1.90 to 1.40	0.80
Secondary vs. primary[8]	*0.81*	*–1.17 to 2.79*	*0.16*
Hatch date[3]	–0.08	–0.15 to 0.002	0.05
Nestling weight[4,9]			
Intercept	10.23		
Primary vs. monogamous	0.40	–0.07 to 0.91	0.10
Secondary vs. monogamous	–0.21	–0.77 to 0.30	0.41
Secondary vs. primary[8]	–0.61	–1.39 to 0.04	0.08
Hatch date[3]	0.03	0.01 to 0.05	0.01
Probability of recruitment[1,10]			
Intercept	–6.67		
Primary vs. monogamous	–0.48	–1.68 to 0.81	0.46
Secondary vs. monogamous	–0.87	–2.49 to 0.51	0.25
Secondary vs. primary[8]	–0.40	–2.37 to 1.39	0.69
Hatch date[3]	–0.04	–0.10 to 0.01	0.13

[1]Model with categorical error structure (estimates on logit-scale). n = 9857 young (from 1090 nests of 702 individual females, of which 23 are primary and 30 secondary females, and 653 individual males, of which 34 are polygynous), of which 9217 hatched and 560 recruited and 210 of which are from primary and 206 are from secondary nests.
[2]Posterior mean (95% CI) for random effects variances: year:2.5 (0.53 to 5.3), male identity: 0.66 (0.29 to 1.1), female identity: 1.8 (1.2 to 2.3).
[3]Relative to annual mean.
[4]Weight in g. Model with Gaussian error structure. n = 8351 young with weight data (mean ± SD = 10.2 ± 1.3 g, from 1006 nests of 647 individual females, of which 22 are primary and 24 are secondary females, and 620 individual males, of which 32 are polygynous), of which 169 are from primary and 146 are from secondary nests.
[5]Posterior mean (95% CI) for random effects and residual variances: year: 0.35 (0.11 to 0.74), male identity: 0.42 (0.35 to 0.50), female identity: 0.57 (0.49 to 0.67), residual: 0.77 (0.74 to 0.79).
[6]Posterior mean (95% CI) for random effects variances: year: 2.4 (0.58 to 5.2), male identity: 0.31 (0.07 to 0.56), female identity: 0.25 (0.04 to 0.50).
[7]Posterior mean (95% CI) for random effects variances: year: 2.3 (0.50 to 5.1), male identity: 0.65 (0.30 to 1.1), female identity: 1.8 (1.2 to 2.4).
[8]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown).
[9]Posterior mean (95% CI) for random effects and residual variances: year: 0.35 (0.10 to 0.67), male identity: 0.43 (0.35 to 0.51), female identity: 0.57 (0.48 to 0.66), residual: 0.77 (0.74 to 0.79).
[10]Posterior mean (95% CI) for random effects variances: year: 2.4 (0.51 to 5.4), male identity: 0.30 (0.06 to 0.53), female identity: 0.24 (0.00 to 0.44).

Table S13. Fledging success for nests of different status. Monogamous nests are compared to primary and secondary nests, separately or combined (polygynous), reflecting measures of female or male success. Shown are results from generalized linear mixed-effect models (see below, Methods and model 14a–i in Table S2 for details).

	Estimate	95% CI	P (MCMC)
MEASURES OF MALE SUCCESS			
Probability that male has ≥ 1 fledgling[1]			
Intercept	5.15		
Polygynous vs. monogamous	1.31	–1.40 to 4.24	0.38
Nestling probability of fledging (simple model)[2,3,4]			
Intercept	6.20		
Polygynous vs. monogamous	–3.09	–4.55 to –1.58	<0.001
Hatch date (relative to annual mean)	0.11	–0.005 to 0.22	0.05
Nestling probability of fledging (complex model)[2,5,6]			
Intercept	2.88		
Polygynous vs. monogamous	–2.94	–4.38 to –1.43	<0.001
Male feeding effort (difference to predicted)	0.005	–0.06 to 0.07	0.83
Oak tree number	–0.001	–0.004 to 0.002	0.35
Oak tree diameter (average)	0.06	–0.02 to 0.12	0.10
Hatch date (relative to annual mean)	0.03	–0.13 to 0.20	0.74
Nestling probability of fledging for nest(s) with ≥ 1 fledgling[2,7,8]			
Intercept	5.77		
Polygynous vs. monogamous	–0.78	–1.73 to 0.36	0.13
Hatch date (relative to annual mean)	–0.07	–0.14 to –0.003	0.05
Total number of fledglings sired[9]			
Intercept	5.33		
Polygynous vs. monogamous	0.50	–0.72 to 1.51	0.41
Male age (older vs. yearling)	1.32	0.92 to 1.74	<0.001
Hatch date (relative to annual mean)	–0.03	–0.08 to 0.03	0.36
MEASURES OF FEMALE (NEST–WISE) SUCCESS			
Probability that nest produces ≥ 1 fledgling[2,10]			
Intercept	8.31		
Primary vs. monogamous	–1.27	–5.07 to 2.59	0.48
Secondary vs. monogamous	–3.24	–6.98 to 0.24	0.06
Secondary vs. primary[11]	–2.05	–7.35 to 3.41	0.43
Hatch date (relative to annual mean)	0.14	–0.05 to 0.33	0.13
Nestling probability of fledging (simple model)[2,3,12]			
Intercept	6.20		
Primary vs. monogamous	–3.24	–4.82 to –1.57	<0.001
Secondary vs. monogamous	–2.44	–4.81 to –0.11	0.04
Secondary vs. primary[11]	0.71	–1.91 to 3.27	0.61
Hatch date (relative to annual mean)	0.11	–0.01 to 0.22	0.07
Nestling probability of fledging (complex model)[2,5,13]			
Intercept	2.84		
Primary vs. monogamous	–2.49	–4.19 to –0.66	0.002
Secondary vs. monogamous	–3.68	–6.00 to –1.67	0.002
Secondary vs. primary[11]	*–1.14*	*–3.45 to 1.28*	*0.34*
Male feeding effort (difference to predicted)	0.004	–0.06 to 0.07	0.87
Oak tree number	–0.001	–0.004 to 0.002	0.37
Oak tree diameter (average)	0.06	–0.007 to 0.12	0.06
Hatch date (relative to annual mean)	0.05	–0.11 to 0.22	0.53

Table S13. Continued.

	Estimate	95% CI	P (MCMC)
MEASURES OF FEMALE (NEST–WISE) SUCCESS			
Nestling probability of fledging for nests with ≥ 1 fledgling[2,7,14]			
Intercept	5.75		
Primary vs. monogamous	–1.00	–2.25 to 0.32	0.12
Secondary vs. monogamous	–0.45	–1.83 to 1.06	0.55
Secondary vs. primary[11]	0.51	–1.32 to 2.25	0.58
Hatch date (relative to annual mean)	–0.07	–0.14 to –0.01	0.02

[1]Model with categorical error structure (estimates on logit-scale) and year and male identity as random intercepts. n = 1098 annual male breeders (664 individuals), of which 34 are polygynous. Posterior mean (95% CI) for random effects variances: year: 1.5 (0.28 to 3.8), male identity: 0.26 (0.00 to 0.93).

[2]Model with categorical error structure (estimates on logit-scale) and year, male identity and female identity as random intercepts.

[3]n = 9857 young (from 1090 nests of 702 individual females, of which 23 are primary and 30 secondary females, and 653 individual males, of which 34 are polygynous), of which 9217 hatched, 8081 fledged, and 560 recruited and 210 of which are from primary and 206 are from secondary nests.

[4]Posterior mean (95% CI) for random effects variances: year: 2.6 (0.71 to 5.2), male identity: 4.2 (2.9 to 5.4), female identity: 8.8 (7.1 to 11.1).

[5]n = 2986 young with male feeding data (from 347 nests of 258 individual females, 21 of which are primary and 22 of which are secondary females, and 244 individual males, 29 of which are polygynous), of which 2691 fledged and 184 are from primary and 150 from secondary nests.

[6]Posterior mean (95% CI) for random effects variances: year:1.1 (0.12 to 2.8), male identity: 1.1 (0.17 to 2.1), female identity: 2.6 (1.4 to 4.0).

[7]n = 8966 young (from 996 nests of 643 individual females, of which 21 are primary and 25 secondary females, and 614 individual males, of which 32 are polygynous), of which 8081 fledged and 183 of which are from primary and 163 are from secondary nests.

[8]Posterior mean (95% CI) for random effects variances: year: 1.1 (0.09 to 2.8), male identity: 1.1 (0.19 to 2.1), female identity: 2.6 (1.3 to 3.9).

[9]Model with Gaussian error structure and year and male identity as random intercepts. n = 1094 annual male breeders (660 individuals), of which 34 are polygynous. Posterior mean (95% CI) for random effects and residual variances: year: 1.9 (0.54 to 4.01), male identity: 0.15 (0.00 to 0.51), residual: 10.7 (9.7 to 11.7).

[10]n = 1090 nests (from 653 individual males and 702 individual females), of which 24 are primary and 30 are secondary nests. Posterior mean (95% CI) for random effects variances: year: 2.5 (0.25 to 6.2), male identity: 0.61 (0.00 to 2.2), female identity: 3.6 (0.00 to 9.3).

[11]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown).

[12]Posterior mean (95% CI) for random effects variances: year: 2.6 (0.73 to 5.4), male identity: 4.1 (3.0 to 5.4), female identity: 8.7 (6.8 to 10.9).

[13]Posterior mean (95% CI) for random effects variances: year: 1.1 (0.09 to 2.8), male identity: 1.1 (0.19 to 2.1), female identity: 2.6 (1.3 to 3.9).

[14]Posterior mean (95% CI) for random effects variances: year:1.1 0.09 to 2.8), male identity: 1.1 (0.19 to 2.1), female identity: 2.6 (1.3 to 3.9).

Table S14. Patterns of extra-pair paternity in relation to mating status. Shown are results from generalized linear mixed-effect models with categorical error structure for probabilities (estimates on logit-scale) and Poisson error structure for number of extra-pair young (EPY, estimates on log-scale) and with year and male and female identity as random intercepts, as appropriate (model 15a–h).

	Estimate	95% CI	P (MCMC)
MALE-BASED ANALYSIS			
Probability that young is extra-pair (all males)[1,2]			
Intercept	–5.56		
Polygynous vs. monogamous	1.98	1.02 to 3.00	<0.001
Male age (older vs. yearling)	–0.43	–0.85 to 0.002	0.04
Hatch date[3]	0.03	–0.03 to 0.09	0.35
Probability that young is extra-pair (males with paternity loss)[4]			
Intercept	–2.34		
Polygynous vs. monogamous	–0.41	–1.09 to 0.19	0.20
Male age (older vs. yearling)	–0.50	–0.86 to –0.17	0.005
Hatch date[3]	0.05	0.002 to 0.09	0.04
Probability that male sires EPY[5,6]			
Intercept	–7.89		
Polygynous vs. monogamous	0.44	–1.20 to 2.55	0.66
Male age (older vs. yearling)	3.41	2.51 to 4.12	<0.001
Hatch date[3]	–0.06	–0.15 to 0.03	0.18
Number of EPY sired (all males)[5,7]			
Intercept	–6.87		
Polygynous vs. monogamous	0.17	–1.23 to 1.50	0.80
Male age (older vs. yearling)	2.41	1.77 to 2.96	<0.001
Hatch date[3]	–0.04	–0.12 to 0.03	0.23
Number of EPY sired (males with paternity gain)[8]			
Intercept	–0.13		
Polygynous vs. monogamous	–0.09	–1.85 to 1.73	0.90
Male age (older vs. yearling)	0.32	–0.47 to 1.24	0.48
Hatch date[3]	–0.001	–0.10 to 0.10	0.96
FEMALE (NEST–WISE) ANALYSIS			
Probability that nest contains ≥ 1 extra-pair young[9]			
Intercept	–1.09		
Primary vs. monogamous	1.73	–0.49 to 3.74	0.13
Secondary vs. monogamous	2.99	0.96 to 5.18	0.004
Secondary vs. primary[10]	*1.36*	*–1.54 to 4.19*	*0.38*
Male age (older vs. yearling)	0.09	–0.57 to 0.85	0.80
Hatch date[3]	–0.02	–0.10 to 0.08	0.74
Probability that young is extra-pair (all nests)[1,11]			
Intercept	–5.59		
Primary vs. monogamous	1.15	–0.21 to 2.48	0.11
Secondary vs. monogamous	2.80	1.45 to 4.06	<0.001
Secondary vs. primary[10]	*1.69*	*0.05 to 3.43*	*0.05*
Male age (older vs. yearling)	–0.44	–0.89 to 0.0005	0.05
Hatch date[3]	0.02	–0.05 to 0.08	0.63

Table S14. Continued.

	Estimate	95% CI	P (MCMC)
FEMALE (NEST–WISE) ANALYSIS			
Probability that young is extra-pair (nests that contain EPY)[12]			
Intercept	–2.35		
Primary vs. monogamous	–0.03	–1.04 to 0.93	0.95
Secondary vs. monogamous	1.00	0.15 to 1.82	0.02
Secondary vs. primary[10]	*1.02*	*–0.21 to 2.36*	*0.11*
Male age (older vs. yearling)	–0.47	–0.78 to –0.12	0.006
Hatch date[3]	0.04	–0.004 to 0.09	0.08

[1]n = 9799 young (from 1085 breeding attempts of 699 individual females, 24 of which are primary and 30 of which are secondary females, and 650 individual males, 34 of which are polygynous), of which 1026 are extra-pair, 210 are from primary, and 206 from secondary nests.
[2]Posterior mean (95% CI) for random effects variances: year: 0.06 (0.00 to 0.17), male identity: 0.97 (0.53 to 1.4), female identity: 1.8 (1.3 to 2.3).
[3]Relative to annual mean.
[4]n = 4392 young (from 483 breeding attempts of 369 individual females, of which 22 are primary and 27 are secondary females, and 363 individual males, of which 31 are polygynous), of which 1026 are extra-pair and 375 are from nests of polygynous males. Posterior mean (95% CI) for random effects variances: year: 0.02 (0.00 to 0.06), male identity: 0.04 (0.00 to 0.14), female identity: 0.16 (0.02 to 0.29).
[5]n = 1095 annual male breeders (661 individuals), of which 316 sired extra-pair young and 35 are polygynous.
[6]Posterior mean (95% CI) for random effects variances: year: 0.02 (0.00 to 0.08), male identity: 0.05 (0.00 to 0.15), female identity: 0.11 (0.00 to 0.22).
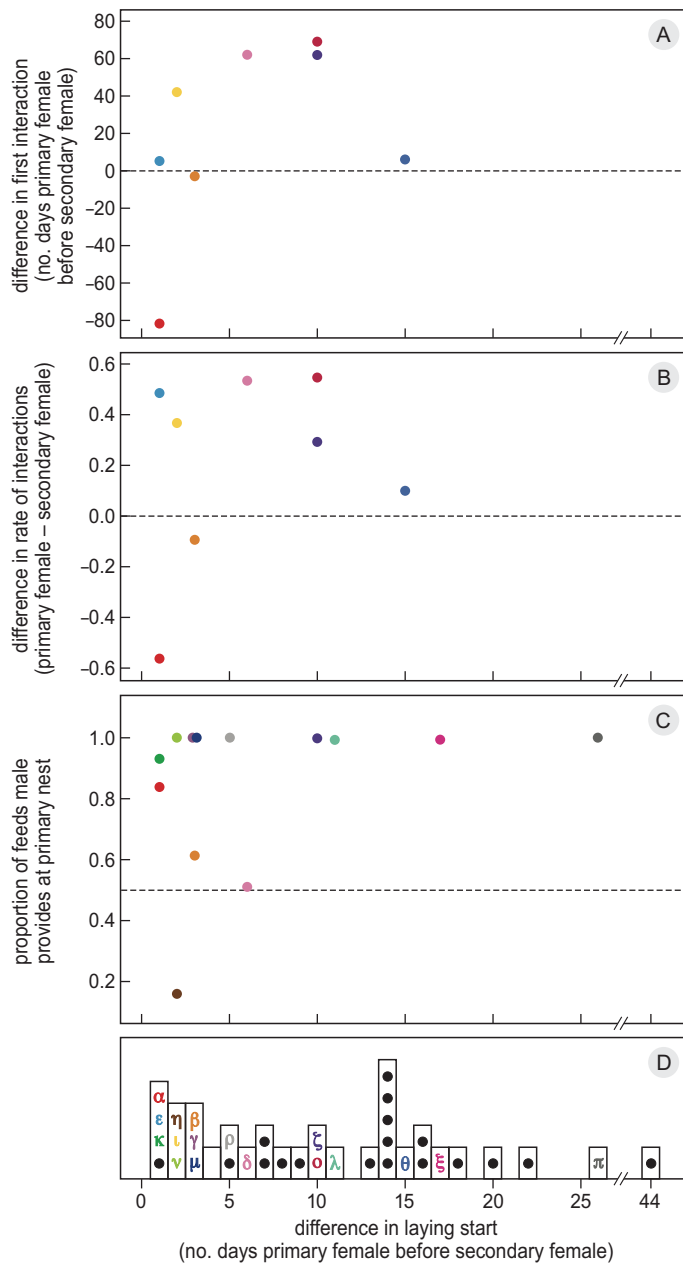[7]Posterior mean (95% CI) for random effects and residual variances: year: 0.09 (0.00 to 0.26), male identity: 0.47 (0.00 to 0.86), residual: 1.9 (1.3 to 2.5).
[8]n = 316 annual male breeders (232 individuals), of which 14 are polygynous. Posterior mean (95% CI) for random effects and residual variances: year: 0.01 (0.00 to 0.05), male identity: 0.05 (0.00 to 0.11), residual: 0.05 (0.00 to 0.13).
[9]n = 1117 nests (from 660 individual males and 716 individual females), of which 469 contain extra-pair young, 26 are primary and 32 are secondary. Posterior mean (95% CI) for random effects variances: year:0.09 (0.00 to 0.28), male identity: 0.43 (0.00 to 1.2), female identity: 1.6 (0.46 to 2.8).
[10]This estimate was obtained by reordering the levels of the explanatory variable, i.e. the corresponding intercept is different (not shown).
[11]Posterior mean (95% CI) for random effects variances: year:0.06 (0.00 to 0.17), male identity: 0.98 (0.63 to 1.4), female identity: 1.8 (1.3 to 2.3).
[12]n = 4286 young (from 469 breeding attempts of 360 individual females, 14 of which are primary and 21 of which are secondary females, and 362 individual males, 29 of which are polygynous), of which 1026 are extra-pair, 123 are from primary nests, and 146 are from secondary nests. Posterior mean (95% CI) for random effects variances: year: 0.02 (0.00 to 0.08), male identity: 0.05 (0.00 to 0.15), female identity: 0.11 (0.00 to 0.22).

Figure S1. Classification of primary and secondary females. (A) Relationship between difference in laying date (days apart) and mating order (days between first interaction of male with primary and with secondary female). (B) Relationship between difference in laying date and rate of pre-breeding interactions. From the days where data were available, we calculated the proportion of days the male interacted with a given female. Shown is the difference of this proportion between the primary and the secondary female. (C) Relationship between difference in laying date and male provisioning (proportion of male feeds provided at primary nest). (D) Distribution of difference in laying date. Black points indicate cases where no behavioural information is available. Symbols refer to cases listed in Table S3. Colours in panels A–C refer to the symbol of the same colour in panel D.

Figure S2. Case of replacement polygyny (case ν in Table S3). The x-axis shows time (month of the year). Grey horizontal lines separate sites (boxes or feeders, labels on the left). The two boxes on the top are the nestboxes of the primary (first row, blue) and the secondary (second row, green) nest. Shading in light and dark grey indicate the periods when nests contained eggs and nestlings, respectively. Symbols at the bottom indicate when an individual received a transponder (the start of transponder data). Symbols left of the vertical grey line indicate individuals that were already equipped with a transponder at the beginning of the period shown. Days of visits to sites by the polygynous male and the two females are indicated with orange squares (polygynous male), blue circles (primary female) and green circles (secondary female). The secondary female initially interacted with a male indicated by red squares. This male disappeared from the study site after 28 March (indicated by vertical dotted line) and was replaced by an already paired male.
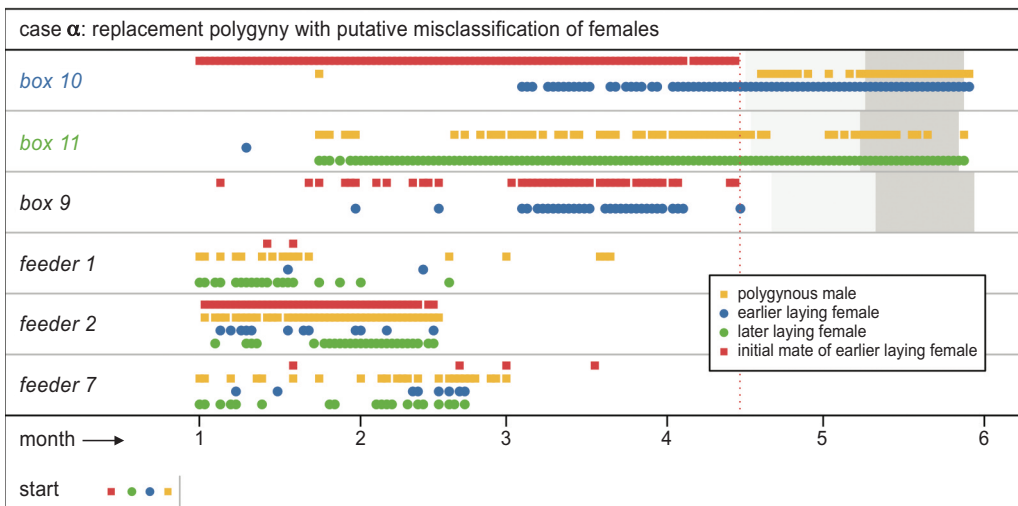

Figure S3. Case of replacement polygyny with putative misclassification of females (case α in Table S3). The x-axis shows time (month of the year). Grey horizontal lines separate sites (boxes or feeders, labels on the left). The two boxes on the top are of the two females mated to the polygynous male, one laying earlier (first row, blue) and one later (second row, green). Shading in light and dark grey indicate the periods when nests contained eggs and nestlings, respectively. Symbols at the bottom indicate when an individual received a transponder (the start of transponder data). Symbols left of the vertical grey line indicate that all individuals were already equipped with a transponder at the beginning of the period shown. Days of visits to sites by the polygynous male and the two females are indicated with orange squares (male), blue circles (earlier laying female) and green circles (later laying female). The earlier laying female initially interacted with a male indicated by red squares. This male disappeared from the study site after 15 April (indicated by vertical dotted line). The earlier laying female then started to interact with a male that was already associated with the later laying female and was the owner of the nestbox used by the later laying female. The polygynous male provided care at both nests (see also Figure 5B).
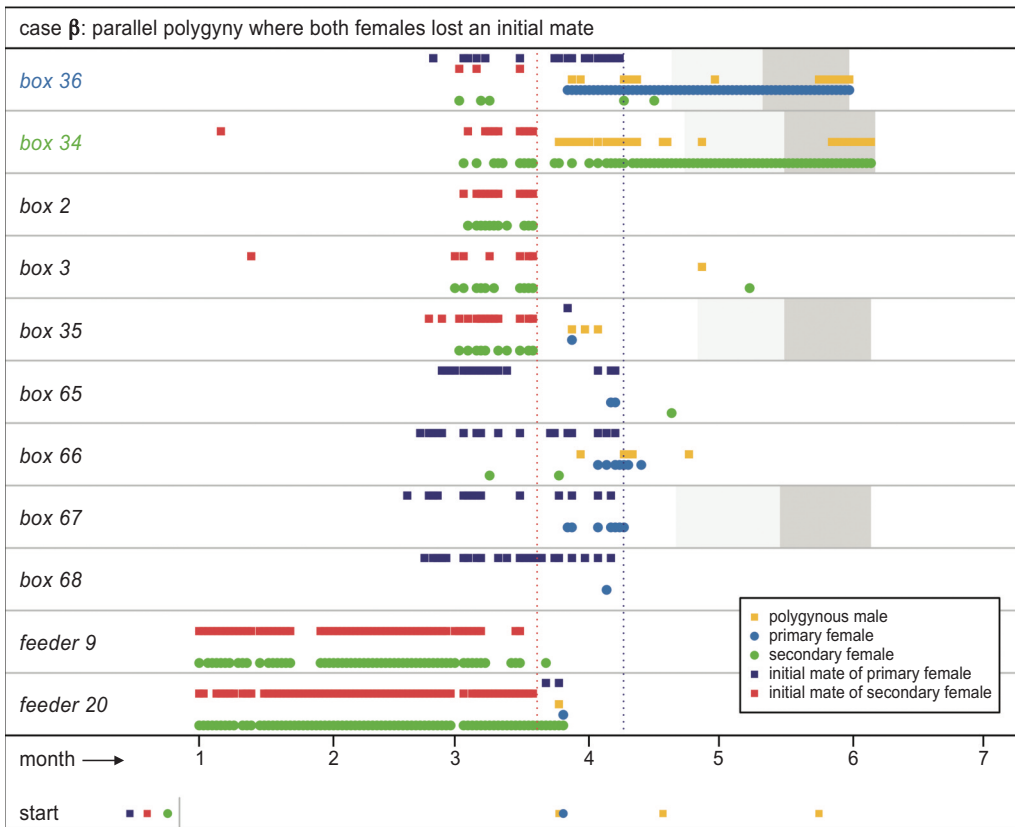
Figure S4. Case of parallel polygyny where both females lost an initial mate (case β in Table S3). The x-axis shows time (month of the year). Grey horizontal lines separate sites (boxes or feeders, labels on the left). The two boxes on the top are the nestboxes of the primary (first row, blue) and the secondary (second row, green) nest. Shading in light and dark grey indicate the periods when nests contained eggs and nestlings, respectively. Symbols at the bottom indicate when an individual received a transponder (the start of transponder data). Symbols left of the vertical grey line indicate individuals that were already equipped with a transponder at the beginning of the period shown. Multiple starts occur for the polygynous male, because he had lost his transponder. Days of visits to sites by the polygynous male and the two females are indicated with orange squares (polygynous male), blue circles (primary female) and green circles (secondary female). The primary female initially associated with the male indicated by purple squares, who disappeared from the study site after 8 April (indicated by purple vertical dotted line). The secondary female initially associated with the male indicated by red squares, who disappeared from the study site after 19 March (indicated by red vertical dotted line). The polygynous male associated with the two females around the same time. He also provided care at both nests (see also Figure 5C).

Figure S5. Case of parallel polygyny where the original female disappeared and the vacancy was filled by two females (case γ in Table S3). The x-axis shows time (month of the year). Grey horizontal lines separate sites (boxes or feeders, labels on the left). The two boxes on the top are the nestboxes of the primary (first row, blue) and the secondary (second row, green) nest. Shading in light and dark grey indicate the time when nests contained eggs and nestlings, respectively. Symbols at the bottom indicate when an individual received a transponder (the start of transponder data). The symbol left of the vertical grey line indicates that the polygynous male was already equipped with a transponder at the beginning of the period shown. Days of visits to sites by the polygynous male and the two females are indicated with orange squares (polygynous male), blue circles (primary female) and green circles (secondary female). The polygynous male was initially associated with the female indicated by the purple circles, but this female disappeared after 14 March (indicated by vertical dotted line). The male then associated with two new females. One of them received a transponder only late in the season, but the male visits to her nestbox suggest that he associated with both females at a similar time.
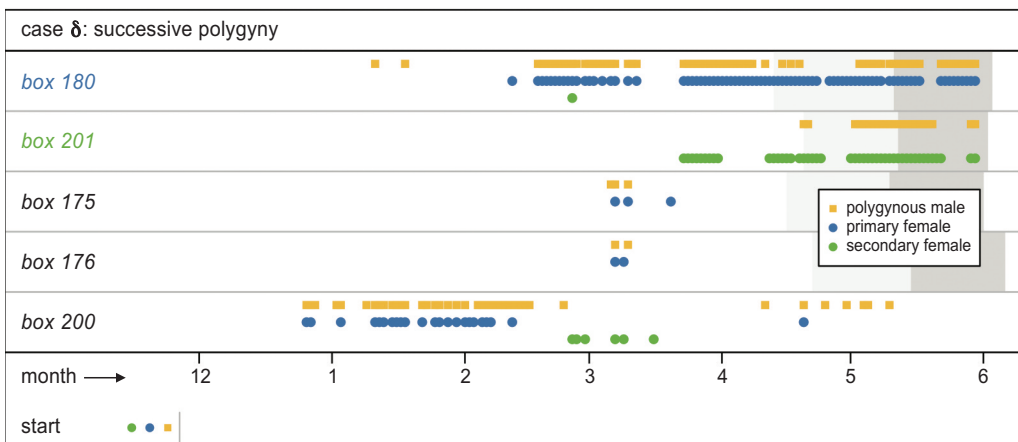

Figure S6. Case of successive polygyny (case δ in Table S3). The x-axis shows time (month of the year). Grey horizontal lines separate sites (boxes or feeders, labels on the left). The two boxes on the top are the nestboxes of the primary (first row, blue) and the secondary (second row, green) nest. Shading in light and dark grey indicate the periods when nests contained eggs and nestlings, respectively. Symbols at the bottom indicate when an individual received a transponder (the start of transponder data). Symbols left of the vertical grey line indicate that all individuals were already equipped with a transponder at the beginning of the period shown. Days of visits to sites by the polygynous male and the two females are indicated with orange squares (polygynous male), blue circles (primary female) and green circles (secondary female). The polygynous male associated earlier and more intensively with the primary female, but provided care at both nests (see also Figure 5D).
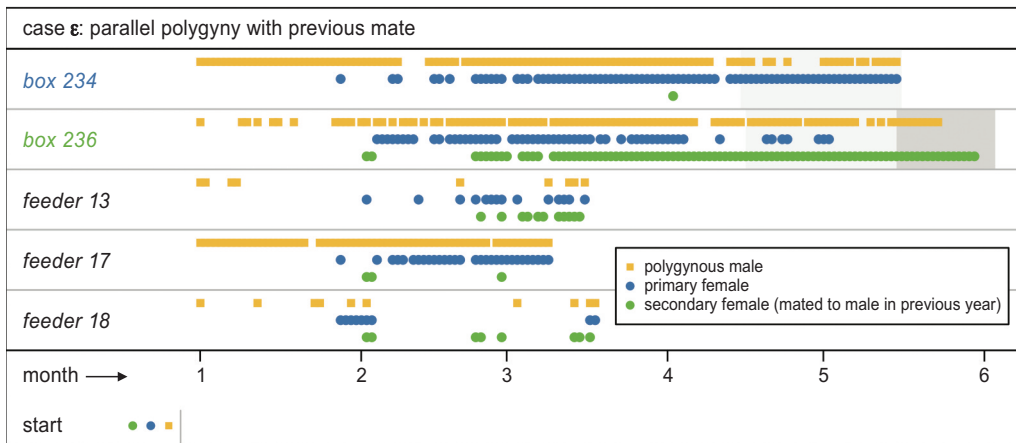
Figure S7. Case of parallel polygyny with a previous mate (case ε in Table S3). The x-axis shows time (month of the year). Grey horizontal lines separate sites (boxes or feeders, labels on the left). The two boxes on the top are the nestboxes of the primary (first row, blue) and the secondary (second row, green) nest. Shading in light and dark grey indicate the periods when nests contained eggs and nestlings, respectively. Symbols at the bottom indicate when an individual received a transponder (the start of transponder data). Symbols left of the vertical grey line indicate that all individuals were already equipped with a transponder at the beginning of the period shown. Days of visits to sites by the polygynous male and the two females are indicated with orange squares (polygynous male), blue circles (primary female) and green circles (secondary female). The male associated with both females around the same time, but interacted more often with the primary female. The male had bred with the secondary female in the previous year (social monogamy). After the breeding attempt with the primary female failed, he continued to care for the brood of the secondary female.
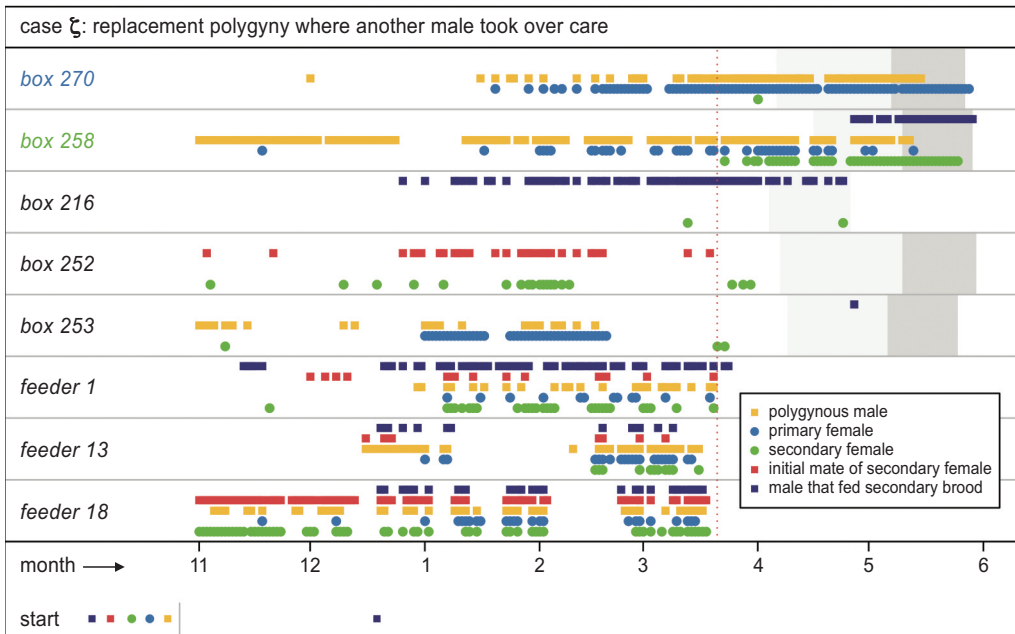
Figure S8. Case of replacement polygyny where another male took over parental care at one nest (case ζ in Table S3). The x-axis shows time (month of the year). Grey horizontal lines separate sites (boxes or feeders, labels on the left). The two boxes on the top are the nestboxes of the primary (first row, blue) and the secondary (second row, green) nest. Shading in light and dark grey indicate the periods when nests contained eggs and nestlings, respectively. Symbols at the bottom indicate when an individual received a transponder (the start of transponder data). Symbols left of the vertical grey line indicate individuals that were already equipped with a transponder at the beginning of the period shown. Two starts occur for the male indicated by purple squares, because he had lost his transponder. Days of visits to sites by the polygynous male and the two females are indicated with orange squares (polygynous male), blue circles (primary female) and green circles (secondary female). The secondary female initially associated with the male indicated by red squares, who disappeared from the study site after March 20 (indicated by vertical dotted line). The widowed female then associated with an already mated male, who sired most of her young. Later, the breeding attempt of the male indicated by purple squares failed (at box 216) and he started visiting the nest of the later laying female, although he did not sire any young there.