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Article

Descriptive and experimental evidence for timing-mediated polygyny risk in a pied flycatcher *Ficedula hypoleuca* population

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In polygynous species with biparental care, mates are often acquired in succession. Most research has focussed on the cost of polygyny in secondary females, but primary females may also suffer from reduced paternal care. The likelihood of sharing a male may be higher for early laying females, which could counteract the fitness benefits of breeding early. In this study, we use 12 years of data on pied flycatchers *Ficedula hypoleuca*, to show that the likelihood of becoming a primary female of a polygynous male declines over the season. Moreover, we provide experimental evidence that early breeding elevates polygyny risk, through an experimental manipulation that introduced early breeding females to a population with later breeding phenology. We found that, independently of breeding date, primary females slightly more often experienced complete brood failures than monogamous females, but did not differ in number of fledged offspring among successful broods or number of locally returning recruits. However, apparent survival in subsequent years was substantially lower in primary females, indicating that they may compensate for reduced male care at the expense of future reproduction. Our study reveals that polygyny risk indeed increases with early breeding and entails a local survival cost for primary females. However, this cost is likely largely outweighed by fitness benefits of early breeding in most years. Hence it is unlikely that the increased polygyny risk of early breeding counteracts the fitness benefits, but it may reduce selection for breeding extremely early.

Keywords: *Ficedula hypoleuca*, life history, mating system, pied flycatcher, polygyny, reproductive success, timing

Introduction

Individual optimal behaviour can strongly depend on the behaviour of conspecifics. For example, in species with biparental care, both male and female benefit from a greater investment from their partner, leading to sexual conflict over parental investment (Trivers 1972). Conflict can arise due to a female's interest to monopolize paternal care for her offspring, whilst males benefit from mating polygynously.

Polygyny is relatively common in birds with 39% of 122 well-documented European passerine species sometimes mating polygynously, of which 20% do so regularly (Møller 1986). In such species, polygynous males aid in nestling feeding less frequently than their monogamous counterparts (Møller 1986). Generally, the mates are acquired in succession, and the brood of the first-acquired mate receives the majority of male investment (Alatalo et al. 1982, Lifjeld and Slagsvold 1989, 1990, Bruun et al. 1997). Male food provisioning behaviour can significantly affect reproductive success and secondary females typically suffer reduced reproductive output under reduced paternal care (Lundberg and Alatalo 1992, Johnson et al. 1993, Lubjuhn et al. 2000, Both 2002, Moreno et al. 2002, Huk and Winkel 2006) (Table 1). This raises the question of why females mate with already-mated males.

Polygyny in pied flycatchers *Ficedula hypoleuca* results in secondary females often suffering fitness costs (von Haartman 1951). It is typically reported that the first-mated ('primary') females receive the majority of paternal care, whereas male care at secondary broods can even be non-existent (Lundberg and Alatalo 1992). Explanations for females ending up as secondary have focussed on deceptive behaviour of males hiding their mating status (Alatalo et al. 1981, 1982, Searcy et al. 1991) through polyterritoriality (Alatalo and Lundberg 1984, 1990). Because extensive searching for an unmated male could be costly (Slagsvold et al. 1988), mate sampling is restricted (Slagsvold and Dale 1994) and females may choose an already mated male as the best of a bad job.

While primary females are often reported to receive the majority of male care, they receive fewer feeds than monogamous females during incubation (Lifjeld et al. 1987). Furthermore, males feed primary broods at rates comparable to monogamous broods in the early and mid-nestling phase, but reduce feeding rates in the late nestling stage as they then may divert care to secondary nests (Alatalo et al. 1982). The costs to primary females may be particularly difficult to assess, because cost measures that are incurred at the end of the nestling phase and over a longer time scale (such as recruitment and survival) may be the most relevant. This may

Table 1. Summary table of studies investigating fitness costs of pairing status through comparisons to monogamous females (or monogamous+primary females) in females of the pied flycatcher *Ficedula hypoleuca* (PF), collared flycatcher *Ficedula albicollis* (CF), Savannah sparrow *Passerculus sandwichensis* (SaS), house wren *Troglodytes aedon* (HW), great reed warbler *Acrocephalus arundinaceus* (RW), tree swallow *Tachycineta bicolor* (TS) and spotless starling *Sturnus unicolor* (SS). Whether the laying date of the female's brood is taken into account in comparisons between females of different mating status is noted. In many studies, primary females are not assessed, or monogamous and primary females are pooled as a combined category against which secondary female reproduction is compared. Signs +, − and 0 indicate respectively statistically significant positive, negative or null effects on the listed fitness components in comparison to monogamous females. Trends are also noted.

	Study	Species	Accounted for timing	Clutch size	Fledgling number	Recruit number	Return rate/survival
Secondary females	Askenmo 1977	PF	no		−		−
	Alatalo et al. 1981	PF	yes	−	−		
	Alatalo et al. 1982	PF	yes		−		
	Alatalo and Lundberg 1984	PF	yes	−	−		
	Alatalo and Lundberg 1990	PF	yes	?	−		
	Potti and Montalvo 1993	PF	yes	0	−	−	0 (trend −)
	Lubjuhn et al. 2000	PF	no	0	−	−	
	Both 2002	PF	yes			0/−	0
	Huk and Winkel 2006	PF	yes	0	−	−	0
	Garamszegi et al. 2004	CF	yes	0	−	0	trend +
	Wheelwright et al. 1992	SaS	no	0		0/− (in one year)	0/− (in one year)
	Johnson et al. 1993	HW	yes	− (late broods)	− (brood failure and fledgling number)		
	Bensch 2006	RW	yes	0 (trend +)	fledgling success: −	0	0.
	Ferretti and Winkler 2009	TS	no	0	−		
	Moreno et al. 2002	SS	yes	0	− (early broods)/0 (late broods)		
Primary females	Askenmo 1977	PF	no		0		
	Alatalo et al. 1981	PF	yes	0	0		
	Alatalo and Lundberg 1984	PF	yes	−	0 (trend −)		
	Potti and Montalvo 1993	PF	yes	0	0	0	0 (trend +)
	Lubjuhn et al. 2000	PF	no	0	0		
	Huk and Winkel 2006	PF	yes	0	−	0 (trend −)	0
	Garamszegi et al. 2004	CF	yes	0	−	0	+
	Bensch 2006	RW	yes	0	0	0	0
	Ferretti and Winkler 2009	TS	no	0	−		
	Moreno et al. 2002	SS	yes	0	− (early broods)/0 (late broods)		

explain why relatively little research has assessed the potential costs from the primary female's perspective (Table 1). Costs for primary females may include reduced reproductive output (Huk and Winkel 2006) or provisioning compensation, which may trade-off against future reproduction (Trivers 1972). Observed female aggression towards other females close to their nest box, and at their mate's secondary territory during the nest-building and egg-laying phases, may also indicate that monopolizing paternal care is a valuable asset (Breiehagen and Slagsvold 1987, Slagsvold et al. 1992). Thus, primary females may suffer reduced male assistance, but as noted by Alatalo and Lundberg (1984), they cannot forecast additional pairings of their mate to other females, and thus do so without choice.

While it has been suggested that late-nesting flycatcher females are more likely to become secondary mates of polygynous males (Alatalo et al. 1982), the selective pressures acting on early-nesting females in light of their risk of becoming a primary female of a polygynous male have rarely been explored. Moreover, early arrival in males has often been proposed to lead to increased fitness; through among other factors more opportunities to find a mate (Alatalo et al. 1984, Møller 1994, Canal et al. 2012, Samplonius and Both 2017), and also specifically due to increased chances of attracting multiple mates (Alatalo et al. 1984, Canal et al. 2012). This carries the implication that early breeding females may be more likely to be subjected to polygyny as primary females (have increased 'polygyny risk'). If a female settles with a mate early in the season, many more females are still to arrive and find a partner, giving the male many opportunities of finding another mate. On the other hand, constraints on a male's time and energy in attracting mates or the behaviour of his first female may limit the males' opportunity to acquire another mate shortly after pairing (Leonard and Picman 1987). This would also limit the polygyny risk of females that arrive more synchronously. If polygyny risk shows a temporal pattern and primary females experience reduced male investment, this could exert selection pressures on females to modulate polygyny risk through later and synchronous breeding.

This study aims to investigate whether selection on early breeding in female pied flycatchers is affected by an increased risk of becoming a primary female of a polygynous male. We investigate the relationship between polygyny and timing of breeding within a wild population of pied flycatchers in the Netherlands and present findings of an experiment that introduced early-timed females to a population with later breeding phenology, and report on their polygyny risk. Finally, we analyse the costs that polygyny carries for primary females through investigating fledgling and recruit production. Since life-history theory predicts that greater reproductive investment should result in reduced survival (Reznick 1985), we also analyse the relationship between pairing status and apparent survival rate of females within the Dutch population.

Material and methods

Study population

Data were collected in a nest box breeding population of pied flycatchers *Ficedula hypoleuca* in Drenthe, The Netherlands (52°49′N, 6°22′E). The population of ca 300 breeding pairs each year, nests in around 1100 nest boxes that have been established in the forested area since 2007 (Both et al. 2017) and includes data up to 2018. Male pied flycatchers usually arrive at the breeding grounds first, preceding females by a week (Lundberg and Alatalo 1992, Both et al. 2016), and occupy one or multiple territories which they start defending.

Fieldwork methods

Nest boxes were checked at least once every five days to record reproductive parameters (as described in Both et al. 2017). Laying dates are the date on which the first egg was laid. Most females were taken out of the nest to be ringed or identified during the incubation period. Females that were missed and males were caught in the nest box with a spring trap at a chick age of at least seven days to read their rings or to be ringed. Of all nests started, over 90% of breeding females and 82% of males were identified in this manner (Both et al. 2017). All chicks were ringed seven days after the first chick hatched, and again measured at an age of 12 d. Fledgling numbers could be determined by re-visiting the nest box after fledging and subtracting the number of dead chicks from the number of ringed chicks when the brood was 12 d old. We determined brood success as whether or not a female fledged any offspring, and this may include predation events, since we did not exclude predated broods. Number of recruits is defined as the total number of offspring in a brood that bred as adult in our study area in any year after hatching. The recruitment rate in this population is on average 0.07 (2007–2018 data). Broods of 2017 and 2018 were excluded from recruitment data, because local pied flycatcher recruits often do not breed in their first year (Both et al. 2017). Return rate of adult females were calculated by determining whether females returned to the population any subsequent year after the breeding attempt. This is a composite measure that includes the propensity to breed again, dispersal tendency and actual survival. Although we do capture at least 90% of the females of all nests that get started, female annual capture rates estimated previously with mark–recapture methods were lower (67%, Both et al. 2017), which either is caused by temporary breeding dispersal away from our study area, or individuals skipping a breeding season.

Polygyny categories

We classified polygyny categories for individually marked and identified pairs. Second broods (Both et al. 2019) and replacement clutches of identified females in the same year were excluded, as were females whose mate was not

identified. Females were classified as monogamous females when their mate was not identified attending any other broods that year. If a female's mate was attending another female's brood, the female was either classified as a primary or secondary female, based on laying date (earliest laying date is of primary female). Our choice for laying date as opposed to hatching date, the main determinant for male care allocation (Lifjeld and Slagsvold 1990, Bruun et al. 1997), is due to this distinction being most relevant to our hypotheses on the 'polygyny risk' of the first-acquired female. In one case in which a male attended three females, the female with the earliest laying date was classified as primary female and both additional females as secondary females. For one male that had an interbrood interval of zero, the female with the earliest hatching date was assigned the primary female, and the female with chicks that hatched a day later was categorized as secondary female. We excluded the single case in which two females shared the same nest box and incubated together on their shared clutch. Centred laying dates were calculated for each brood through subtracting the year-specific median first egg date. We calculated interbrood timing interval as the difference between the egg laying dates of the primary and secondary female.

Experimental translocations and polygyny

In the spring of 2017 and 2018, we performed an experiment in which we experimentally introduced females from an early breeding population to a later population. We performed female translocations from our study population in the Netherlands (described above) to a nest box population in Vombs fure (55°40′N, 13°33′E), southern Sweden (as described in Burger et al. 2013). The breeding phenology of the Swedish (SE) study site is approximately two weeks later than the study population in Drenthe (NL). The average first egg laying date of unmanipulated females in the Netherlands and Sweden, respectively, was 5 and 21 May ($n_{NL} = 215$, $n_{SE} = 71$) in 2017 and 4 and 20 May ($n_{NL} = 270$, $n_{SE} = 73$) in 2018. Dutch females were translocated to Sweden in two different groups per year; one earlier and one later group (caught on 2 May and 12 May in 2017 and 26 April and 3 May in 2018). In addition, some Swedish females were also caught and translocated within the study site. All females were caught just after pair-formation when building nests and kept in small individual transport cages. They were covered with a light cloth and provided two perches, and ad libitum mealworms and water. Dutch females were transported to Sweden by car during the night, whereas Swedish control translocated females were captured throughout the nest-building period and kept overnight at the nearby field station. Females of both treatment groups were randomly assigned to and released into outdoor aviaries ($2 \times 2 \times 2$ m) at the field site in the next morning. These aviaries were built adjacent to a tree, which had a nest box inside the aviary. Females in the aviaries were provided with ad libitum water and food (waxmoths, crickets and ad libitum mealworms) on a feeding table, nesting material and large bushes and branches for

perching and shelter. Aviaries were covered in double netting to prevent predator attacks. An unpaired Swedish male displaying nearby the aviary was captured for each female and released into the aviary. After a period of three (2018) to five (2017) days, the aviaries were opened and removed to release the birds, after which food was still provided at the site for another day. Translocated Dutch females and Swedish control translocation females that settled to breed in either the provided nest box or elsewhere in the study site were used for analysis of polygyny rates. This resulted in a sample size of 15 settled translocated Dutch females (out of 50) and 16 settled Swedish local control females (out of 18). Moreover, 111 unmanipulated Swedish females were also monitored within the study site and were added as a third category in the analysis. Population and nest monitoring in Sweden, and data processing for polygyny classification, were performed separately for Sweden but were otherwise identical to the Dutch population.

Statistical analyses

As several studies have shown fitness consequences for secondary females, and our hypothesis focusses on consequences for primary females, we restrict our comparisons to two polygyny categories: monogamous females and females subjected to polygyny as primary females ('primary females'). Secondary females were not included in the analyses, but are displayed as ecologically relevant reference in the figures. The relationship between the likelihood of a female to be subjected to polygyny as a primary female and her centred timing of egg laying were analysed for the Dutch population using a generalized linear mixed model (GLMM) with a binomial error distribution and a logit-link function from the R package 'lme4' (Bates et al. 2015). Centred laying date was thus included as explanatory variable, whilst year (2007–2018) and female identity were included as random effects. The model fit was evaluated using a likelihood ratio test. Statistical models were analysed in R ver. 3.5.1 (R Core Team). To investigate whether interbrood intervals were larger than expected by chance, we generated 10 000 permutated datasets. This was done by shuffling the male identities for all the years separately, thereby keeping the existing laying date distribution intact. We then recalculated the interbrood intervals between the mates of polygynous males to construct a distribution of mean interbrood intervals that could be expected under a random mate choice and polygyny distribution.

Within the Swedish population, we analysed the effects of the experimental treatment (Dutch translocation, Swedish local translocation and Swedish unmanipulated) on the likelihood of a female to become mated to a polygynous mate as a primary female. We fitted generalized linear models with binomial error distribution. These models included treatment category, laying date and year as explanatory variables. Multiple comparisons of treatment means (Tukey contrasts; package 'multcomp') were performed post-hoc.

To quantify the fitness consequences of polygyny, variation in female annual reproductive output (brood success

as fledged at least one young, fledgling number and local recruit number) were analysed in GLMM with binomial (brood success) or Poisson (fledgling and recruit number) error distribution. All models analysing the costs of polygyny included laying date centred by year, as an approximation for the pairing date of the females. This allowed for comparisons between the pairing strategies that control for timing effects. Moreover, we tested whether adding the female's age as a fixed effect (distinguishing between first-year females and older individuals) affected the results on the female's reproductive output. Ages of adult birds were based on plumage characteristics observed when caught. If historic captures (as chicks or adults in prior years) were available, age was instead assigned using the database. However, since adding age in the models resulted in a lower sample size, we report on the models without age when this did not affect the model selection or model results. Female identity, male identity and year were added as random factors to account for non-independence of the data and variation between years. In the case of brood success, the random effects on female identity and male identity were not fitted due to singularity issues. For the models of experimental timing and costs of polygyny, model selection was performed based on Akaike information criterion (AIC) value (Burnham and Anderson 2002). Model parameter full averages were obtained through model averaging using the R package 'MuMIn' (Barton 2018).

To investigate differences in subsequent apparent survival between monogamous and primary females we used Cormack–Jolly–Seber capture–mark–recapture models (Lebreton et al. 1992). We modelled apparent survival (Φ) depending on category and centred laying date while recapture probability (p) model had only an intercept. Because monogamous females comprised the majority of the observations (see Results for sample sizes) and primary females were never observed again as primary or secondary, we assumed that in all cases in which a female was not observed it was monogamous. We also assigned the median laying date to all the cases for which laying date was not known. The interaction in slope of survival probability by laying date was not statistically significant (ΔDIC = 52.28) and therefore our final model contained only category specific intercept and a common slope by laying date. The models were formulated in Bayesian framework and fitted in JAGS ver. 3.0.0 (Plummer 2003) with five chains of 4000 iterations each, burn-in of 1000 and no thinning). All parameters in the models had Gelman–Rubins statistic lower than 1.01. These analysis were performed in R using the 'jagsUI' package (Kellner 2015).

Apparent survival and recruit number were further combined into a measure of overall fitness to evaluate the importance of polygyny risk for evolutionary processes. Model estimates (intercept and laying date slope) for survival rate and half the number of recruits from the breeding attempt (to reflect genetic contribution; Both 2002) were added to estimate fitness as a function of laying date for monogamous and primary females. Recruits are more dispersive than adults, which could lead to underestimation of the recruitment component. The mean detection probability of recruits in our population was previously estimated to be 0.42 (0.33 for females and 0.50 for males; Both et al. 2017). Therefore, we accounted for the underestimation of the recruitment component by multiplying recruit number by 2.4 (1/0.42). The difference between the fitness of monogamous and primary females was then calculated. Then, we calculated the cost of polygyny risk by multiplying the difference in fitness and the model estimates of the effect of laying date on polygyny risk. Finally, we subtracted this from the fitness of monogamous females to generate the fitness curve incorporating polygyny risk.

Results

Out of all broods in our Dutch population with known female identity, 90% of social fathers were identified in all broods that were started (2650 out of 2942 broods). This was 92% for all broods that had any hatchlings and 95% of fathers for all broods with fledged young. One reason why males could be missed is due to low male feeding frequencies at secondary broods. Apart from potentially misclassifying some primary females as monogamous females and thereby reducing potential effect sizes, this is otherwise not expected to bias our results. Another reason is nest predation (mostly by martens) after we identified the female during incubation. The proportion of broods attended by polygynous males was on average 6% from 2007 to 2018 (annual range 1–20%). All in all, our results on timing and apparent survival are based on a total of 2488 monogamous females and 81 primary females. Some females however had broods for which fledgling numbers were unknown. These were excluded from analyses on reproductive success, resulting in 2194 monogamous and 79 primary females.

Timing and polygyny

Females breeding earlier were significantly more likely to be subjected to polygyny as primary females (χ = 73.4, $p < 0.0001$, $\beta \pm$ SE: laying date: -0.22 ± 0.03, intercept: -4.07 ± 0.30, Fig. 1a–b). We also simulated the relationship between polygyny risk and laying date assuming that this relationship only depended on the proportion of females with later timing. For this, we calculated for each female what proportion of females had later timing of egg laying. We then defined polygyny risk as a linear function of the proportion of females with later timing, and calculated the slope of this relationship by scaling this to the overall proportion of polygyny in our observed population. The total rate of polygyny in this statistically simulated population was therefore equal to the observed occurrence. This gave us a function over time of the proportion of females that would be subjected to polygyny as primary females if a male had an equal chance of becoming mated to any female in the area with later timing than his original mate (Fig. 1b). Males, whose first-acquired mate is early, then have a greater likelihood to acquire another mate because many females in the area have yet to find a mate,

thus subjecting early timed females to higher rates of polygyny. Our observed data fits this expected pattern upon visual inspection (Fig. 1b).

The interbrood interval between primary and secondary females of the same male was on average 8.73 d ± 0.55 SE (n = 80, range = 0–21). Permutations of the dataset for polygyny risk unrelated to female timing, which were generated by shuffling male identities within the years, generated a mean interval of 6.40 d ± 0.65 SE (range = 0–34). This indicates that the interbrood interval was greater than expected by chance (Supplementary material Appendix 1 Fig. A1).

Experimental timing and polygyny

The proportion of broods in Sweden attended by polygynous males was 6% in 2017 and 14% in 2018 (mean 10%). Translocated Dutch females breeding in Sweden laid their first eggs on average four days earlier than control and unmanipulated females (Supplementary material Appendix 1 Fig. A2) and 31% of them paired as primary female, compared to only 2 or 7% in unmanipulated and control females respectively (Fig. 1c). The proportion of females subjected to polygyny as primary females was assessed for the treatment categories. Models including treatment category were a better fit with the data than those without, but we could not unambiguously confirm whether a negative effect of laying date should be included (Supplementary material Appendix 1 Table A1). Post-hoc testing revealed a significant difference between translocated females and natural brood females in their likelihood to become mated as primary females to a polygynous mate (Table 2). Due to low sample size, differences between the translocated control group and the other treatment groups were not significant.

Breeding success of primary females

A total of 84% of females in our Dutch study population fledged at least one offspring during their breeding attempt (84.0 ± 0.77% SE of monogamous females and 86.1 ± 3.92% SE of primary females). The best fitting models explaining variation in brood success included both laying date and polygyny category (Supplementary material Appendix 1 Table A2). Including female age in the models did not change the model selection nor estimates, and we thus report on models excluding this. Brood success was negatively related to laying date. Whether the interaction between mating status and timing should be included was inconclusive, but there was a trend towards the likelihood of successfully fledgling at least one chick decreasing faster in primary females for later laying dates than in monogamous females (Table 3, Fig. 2a). When controlling for laying date, primary females appeared slightly more likely to experience complete brood failure. Primary females thus paid a slight reproductive cost in terms of brood failure, but this may not be independent of timing. Among monogamous and primary females that did not experience complete brood failures (respectively n = 1905 and n = 68), fledgling numbers were on average 5.53 ± 0.03 SE for monogamous females and 5.88 ± 0.14 SE for primary females. Including age did not improve the model fit nor change the outcome. Variation in fledgling numbers in successful broods was best explained by a negative relationship with laying date, while we found no support for an effect of polygyny category (Table 3, Fig. 2b, Supplementary
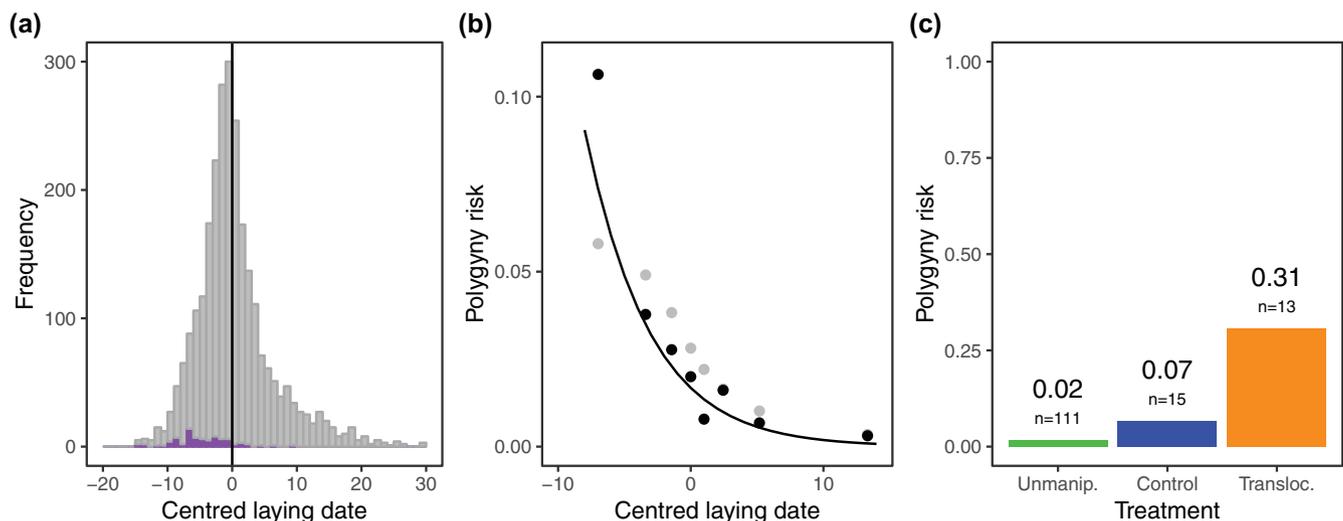

Figure 1. (a) The observed laying date frequency distribution of female pied flycatchers in Drenthe (NL, 2007–2018) experiencing polygyny as a primary female (purple) illustrated within population timing (grey histogram). (b) Polygyny risk (proportion of primary females) decreases with date. The observed data are represented by the black filled circles. The plotted line depicts the model estimates. Grey filled circles represent the expected 'polygyny risk' under a hypothesis of random mate choice for (either mated or unmated) males by females with later timing than the first-acquired female. For graphical purpose only, date is presented for eight different timing quantiles (each dot represents ca 12.5% of the data). (c) Polygyny risk (proportion of primary females) in the different treatments (unmanipulated females, Swedish control translocation females and Dutch females translocated to Sweden) in a Swedish pied flycatcher population (2017–2018).

Table 2. Effects of experimental treatment on the likelihood of becoming a primary female in Swedish pied flycatcher females (2017 and 2018). Model outputs are full averages of all the candidate models acquired by model averaging based on AIC value. Significance (p < 0.05) between groups, as calculated with a post-hoc test (Tukey contrasts), is indicated by the combination of the superscripts.

Fixed effect	Estimate	SE	Z value	p-value
Brood status (unmanipulated)[a]	−5.04	1.53	1.09	ac
Brood status (control)[b]	−3.34	1.49	2.24	
Brood status (translocation)[c]	−2.14	1.66	0.67	ca
Laying date	−0.13	0.15	0.83	
Year: 2018	1.24	1.25	0.91	

material Appendix 1 Table A3). Similar to fledgling numbers, recruit numbers decreased with laying date (Table 3, Fig. 2c, Supplementary material Appendix 1 Table A4). However, the second best supported model included polygyny category, indicating that there was a trend for primary females to have fewer recruits than monogamous females of the same timing. Female age again did not change the model estimates nor did inclusion change the model selection.

Apparent survival probability of primary females

The capture–mark–recapture analysis confirmed that the apparent survival rate of females was negatively correlated with their laying date (Table 3, Supplementary material Appendix 1 Fig. A3). The polygyny category state of a female predicted her survival rate to the following year. Females subjected to polygyny as primary females were less likely to return in subsequent years than monogamous females with the same timing. Our survival analysis shows that for females with the median laying date, the apparent survival was on average 0.38 (95% CI: 0.36, 0.40) for monogamous females but only 0.25 (95% CI: 0.15, 0.36) for primary females. This closely mimics the pattern in the raw return rates (Fig. 2d).

Furthermore, excluding females that did not fledge any offspring in a given year did not change the overall pattern of lowered return rates of primary females (Supplementary material Appendix 1 Fig. A4).

Fitness and polygyny risk

We modelled an approximation of fitness, as a function of the sum of half times the recruit number and the apparent survival rate from the model outputs (Table 3). Monogamous broods had higher fitness relative to primary females (Fig. 3). As a result, when incorporating the relative laying date dependent likelihood for monogamous females to become primary females (Fig. 1b), the fitness benefits of breeding early are reduced. This is most pronounced in females breeding the earliest relative to the rest of the population. It is however not severe enough to counteract benefits of breeding relatively early.

Discussion

This study aimed at quantifying timing-dependent polygyny risk and its associated fitness consequences. Results show that polygynous primary broods in Dutch pied flycatchers disproportionally occurred amongst the earliest laying females. The breeding performance of primary females was overall comparable to monogamous females, but we did detect a cost to future reproduction through reduced apparent survival rates. We discuss below the ecological and evolutionary implications of our findings.

Determinants of timing-mediated polygyny risk

Early females may be more susceptible to becoming primary females if the probability of her male mating with an additional female is linked to the proportion of females with later

Table 3. Model parameters for the breeding success (brood success, number of fledged offspring, number of recruited offspring) and apparent survival of pied flycatcher females breeding in Drenthe, the Netherlands. Full averages of model coefficients are acquired by model averaging over all the candidate models based on AIC values. For fledgling number, the broods of females that did not fledge any young were excluded. Significance (p < 0.05) between groups, as calculated with a post-hoc test (Tukey contrasts), is indicated by the combination of the superscripts. Data are from GLMM, with year (brood success) and year, male identity and female identity (for fledgling number and recruit number) as random effects. For apparent survival, estimates of CMR MCMC simulation are given. The lower (2.5%) and upper (97.5%) bounds of the confidence interval are given, and significance between the groups is indicated by the superscript for non-overlapping confidence intervals.

	Brood success			Fledgling number			Recruit number			Apparent survival		
	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	95% CI	p
Polygyny category (monogamous)[a]	2.699	0.455	ab	1.713	0.010		−0.859	0.044		−0.487	−0.585, −0.389	ab
Polygyny category (primary female)[b]	1.871	0.514	ba	1.72	0.037		−0.876	0.138		−1.148	−1.768, −0.556	ba
Laying date	−0.086	0.012	***	−0.01	0.002	***	−0.038	0.006	***	−0.026	−0.043, −0.010	*
Polygyny category (primary female): laying date	−0.034	0.075		0.00	0.004		0.005	0.021				

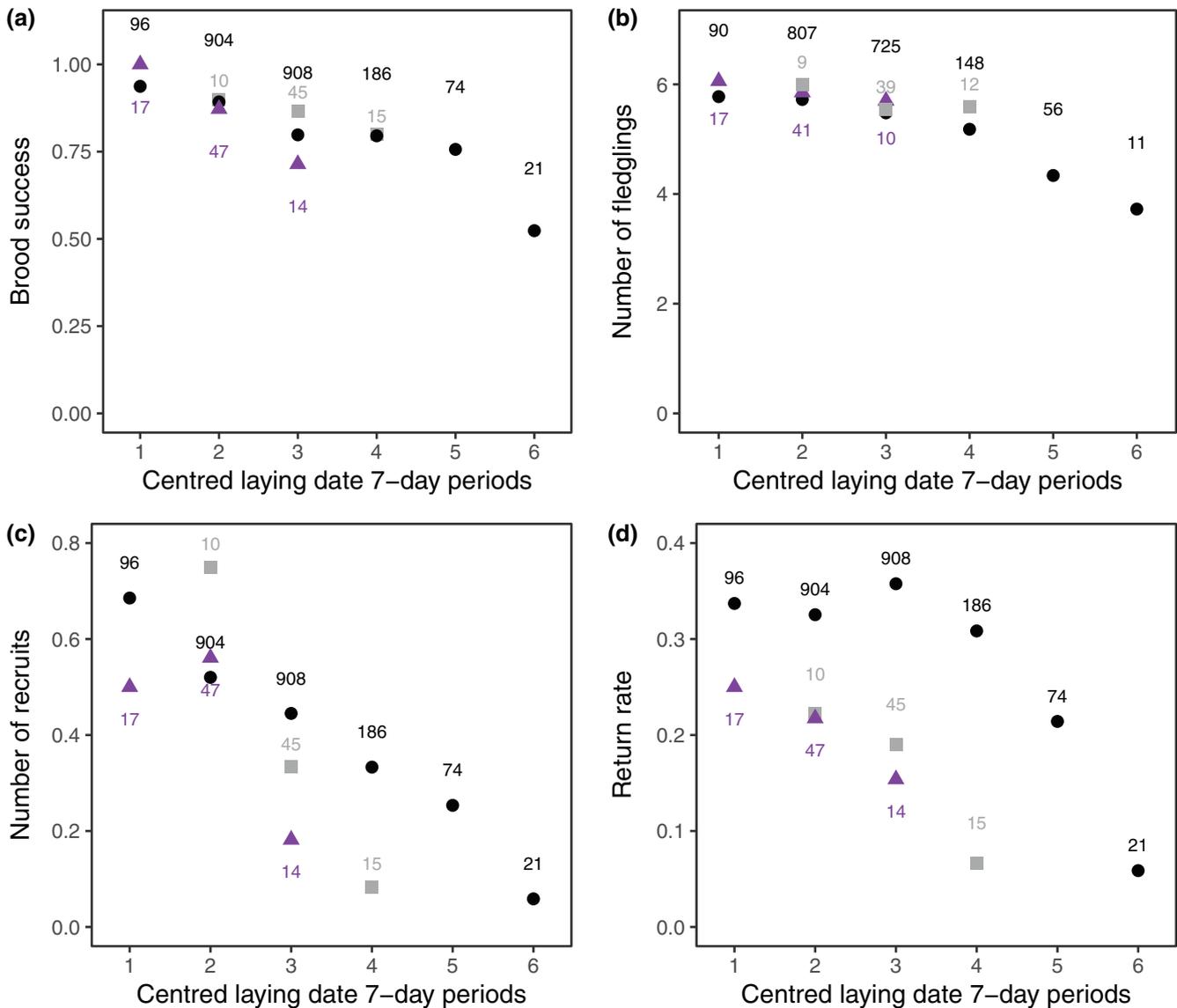Significance codes p: <0.001 '***', <0.01 '**', <0.05 '*'.

Figure 2. Proportion of brood success (a), fledgling numbers (b), recruit numbers (c) and return rates (d) of pied flycatcher females in Drenthe (NL, 2007–2018) as a function of laying date. Centred laying dates were grouped into seven-day units. Data points with sample sizes smaller than five were not depicted and sample size is indicated per point in text. Mating status of females is indicated by different symbols (black filled circles: monogamous females, purple triangles: primary females and grey squares: secondary females).

timing. Moreover, early females may have increased risk of having to share their mate if males' ability to acquire additional mates is limited by time and energy or the behaviour of their first mate (Alatalo et al. 1981). There are a number of additional ecological reasons why early-arriving males may more often become polygamous (Alatalo et al. 1981), predisposing early breeding females towards becoming primary females. Male competition over territories is lower early in the season. Early arriving males acquire the most attractive nest sites and territories (Askenmo 1984, Potti and Montalvo 1991) and even defend more cavities than later conspecifics (Potti and Montalvo 1991). Moreover, males chosen by early females may be males of better quality and therefore more able to acquire additional mates. We can thus present

multiple simple theoretical, as well as ecological reasons for our observation that early breeding females are more likely to be subjected to polygyny.

In line with this observed pattern of polygyny risk and timing, we moreover found that females from an early population that were introduced to a later breeding population showed a much greater risk than unmanipulated local females to become primary females of polygynous males. Alternatively, female quality may influence her ability to monopolize her mate (Slagsvold et al. 1992), or selection may have favoured males that intensively pursue polygyny when their first female is of inferior quality. Translocation and control translocation females were indeed subjected to an intensive experimental treatment, potentially lowering female
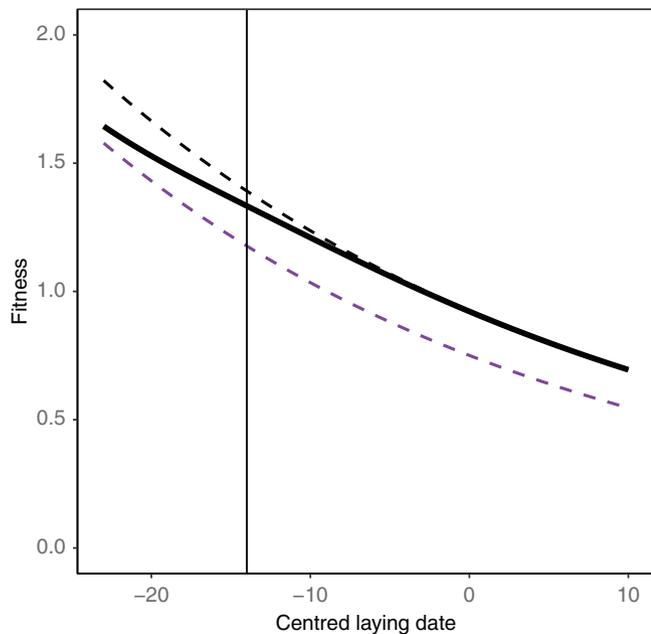
Figure 3. Fitness as a function of centred laying date in Dutch female pied flycatchers. Fitness of monogamous (black dashed) and primary females (purple dashed) is approximated by return rate $+ \frac{1}{2} \times 2.4 \times$ recruit number, and is based on model estimates with category-specific intercepts but identical slopes. Fitness incorporating polygyny risk (likelihood to become a primary female as a function of laying date) is represented by the solid line. The vertical line represents the earliest observed centred laying date in our population.

condition. Both control and Dutch translocated females had increased stress levels (Burger et al. 2013) and translocated Dutch females displayed a trend towards reduced reproductive output and differed in provisioned diet choice from control females and the natural population (Burger et al. 2013, unpubl.). Moreover, local selective pressures may potentially have shaped individuals of the two populations to differ in a variety of traits, resulting in translocated Dutch females being somewhat behaviourally or morphologically different from Swedish control females. The striking differences in polygyny rates therefore either provides experimental evidence that polygyny risk is increased for early females or alternatively illustrates the importance of female quality or other female characteristics as drivers in polygynous behaviour.

Fitness consequences of polygeny for primary females

Whilst reduced reproductive success in secondary females has received much attention and has been well described, comparisons between primary females and monogamous females have been scarce. Huk and Winkel (2006) found reduced fledgling numbers in primary females compared to monogamous females and a negative trend in recruit numbers. Reduced fledgling numbers in primary females were also shown in a population of the closely related collared flycatcher *Ficedula albicollis* (Garamszegi et al. 2004). Long-term data on our study population showed a minor difference in one of the components of fledgling number: likelihood of complete brood failure was higher in primary females. It was unclear whether this was only the case for primary females with late timing. A disproportional effect on primary females with later timing could indicate the importance of interbrood interval in determining fitness costs for females of bigynous males (Lifjeld and Slagsvold 1989). Fledgling numbers in successful broods were similar, but we observed a trend towards primary females recruiting fewer offspring. However, differential dispersal tendency cannot be excluded as a factor determining recruit numbers of primary and monogamous females (Huk and Winkel 2006).

Discerning which aspects of the breeding situation are affected by mating status, and which fitness components should therefore be compared between females, is crucial for determining the effects of polygyny (Searcy and Yasukawa 1989). Males may shift care away from the primary to the secondary nest over time (Potti and Montalvo 1993), leading to reduced care for the primary female at the end of the nestling period (Alatalo et al. 1982) and most likely also after fledgling. Due to the great reproductive value of the offspring at that stage, primary females with older nestlings or fledglings may be more inclined to compensate for lost paternal care, potentially at their own expense (Wright and Cuthill 1990). Females in our population may compensate successfully for lost male care through increasing their own investment, resulting in negligible direct reproductive costs. However, such increased investment in current reproduction might well affect future survival (Reznick 1985) and for these reasons, survival rates of primary females may be of vital importance when studying the effects of polygyny on primary females.

In line with this, we found considerably lower survival rates of primary females compared to monogamous females. Reduced apparent survival could be caused by mortality, dispersal or a reduced propensity to breed in the following years, but are all indicative of costs. Our results contrast with mark–recapture survival analyses in collared flycatchers that showed a tendency for slightly higher return rates for primary females and even higher for secondary females compared to monogamous ones (Garamszegi et al. 2004). However, comparability between these studies may be low. Garamszegi et al. (2004) used Capture–Mark Recapture models with mating status as a fixed factor instead of allowing multiple states, thereby classifying a female as a primary or secondary female throughout her lifetime if she was mated as such on one occasion. Moreover, Huk and Winkel (2006) found no evidence in pied flycatchers for lower return rates of primary females to the next breeding season compared to monogamous females with an average return rate of 0.3. Their study population benefits from longer-term monitoring, but it has a smaller population size of pied flycatchers with higher polygyny rates. Both study populations have higher rates of polygyny, and future work could address whether there is a link between population

polygyny propensity and costs for females. Interestingly, Hemborg (1999) studied the effects of nest desertion by male pied flycatchers on the reproductive output and return probability of females, which can be argued to mimic lost paternal care due to polygyny in all relevant ways. Such deserted females had similar fledgling numbers indicative of successful compensation. They started moulting later than aided females with the same timing of breeding and had lower local return rates (Hemborg 1999). Additionally, Askenmo (1979) showed that pied flycatchers in south Sweden with experimentally enlarged brood sizes had reduced return rates. Similar experiments in collared flycatchers resulted in lowered breeding success in the subsequent year for adults whose broods had been enlarged (Gustafsson and Sutherland 1988). These results support that reduced primary female survival rates are a cost of lost male care.

Evolutionary implications of timing-mediated polygyny risk

Our results indicate that relatively early laying females experience an increased polygyny risk associated with a potential survival cost. Selection for early breeding might be reduced due to the combined effect of enhanced polygyny risk and other selection pressures, such as increased mortality of early arriving individuals (Brown and Brown 2000, Newton 2007). Polygyny risk and the associated fitness penalty for early-laying females, combined with increased pairing and polygyny likelihood in early arriving and breeding males, signifies a role for polygyny-mediated sexual conflict in determining the timing of breeding. Females could modulate the risk of their male acquiring another mate through their timing of reproduction relative to the rest of the population. Interestingly, later arrival of females than males to the breeding site (Lundberg and Alatalo 1992, Ouwehand et al. 2016) is in line with this. Early arrival of males can be explained by increased opportunities to acquire multiple mates (Canal et al. 2012), but the difference in arrival timing can also be attributed to reduced benefits for females of breeding early relative to conspecifics. Moreover, early arriving pied flycatcher females have greater arrival-laying intervals than later-arriving conspecifics (Potti 1999). Foregoing breeding early relative to the rest of the population may however go at the expense of first choice of mates and territories. Overall, polygyny risk is unlikely to counteract the strong observed benefits of early breeding (Perrins 1970, Both et al. 2006, Visser et al. 2015). However, polygyny risk can mitigate the selection pressures in females for early breeding, and may predominantly act upon and work against extremely early breeding.

Conclusions

This study shows a clear seasonal pattern in polygyny risk in Dutch pied flycatchers, which is supported by our experimental manipulation. Our study further indicates that pied flycatcher males acquire a second mate to the detriment of their first acquired female. We demonstrate a so far unappreciated selection pressure component against early breeding for females due to polygyny risk. This process can help prevent the establishment of extremely early laying dates, and reduces the amount of variation in timing on which evolution could act. The potential for timing-mediated polygyny risk and selection pressures stresses the importance of incorporating sexual conflict into predictions on the evolution of life history traits.

Data availability statement

Data available from DataverseNL (https://hdl.handle.net/10411/SARBDB) (Lamers et al. 2019).

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Supplementary material (available online as Appendix jav-02190 at <www.avianbiology.org/appendix/jav-02190>). Appendix 1.