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Female survival, lifetime reproductive success and mating status in a passerine bird

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Abstract In facultatively polygynous birds, secondary females of polygynously mated males typically have reduced annual reproductive success, because polygynous males provide less paternal care than monogamous males. Life history theory predicts that, as a result of increased reproductive investment, secondary females should suffer from reduced survival and lifetime reproductive success, but previous studies provided only weak support for this hypothesis. We used 7 years of data to study the fitness of female collared flycatchers *Ficedula albicollis* in relation to mating status by estimating survival and lifetime reproductive success. Taking differences in recapture probability into account, a mark-recapture analysis revealed that females observed at least once to breed as secondary female had higher survival than other females. This relationship was not confounded by laying date, because when we assessed the impact of laying date on survival, we found similar survival patterns. Females of polygynous males had reduced breeding success in terms of number of young fledged during the current reproductive event. However, during their lifetime females found at least once in primary or secondary mating status produced significantly more eggs, and at least the same number of fledglings and recruits as monogamous females. Thus, in the collared flycatcher, females of polygynously mated males seem to suffer from mating status during the most

recent reproductive event, but considering survival and lifetime reproductive success, the apparently disadvantageous mating event is not necessarily associated with reduced residual reproductive value.

Keywords Collared flycatcher · Fitness · Mark-recapture analysis · Polygyny · Secondary female

Introduction

Scientists interested in avian polygyny attempt to answer a basic question: why do females in some species choose to mate with already mated males (Verner 1964; Weatherhead and Robertson 1979; Alatalo et al. 1981; Searcy and Yasukawa 1989; Slagsvold and Lifjeld 1994)? This question arises because secondary females of polygynously mated males typically have reduced reproductive success during a single reproductive event, probably due to the decreased paternal care that polygamous males provide. Hypotheses from theoretical and empirical studies explain the maintenance of polygyny from the female's perspective (Searcy and Yasukawa 1989; Bensch 1997). In many cases there is a clear difference in fitness between females mated monogamously and females mated bigamously leading to a cost of polygyny for females. According to Searcy and Yasukawa (1989, 1995), it is crucial to first assess this cost before testing predictions.

However, the effect of polygyny on female fitness is usually underestimated, since it is difficult to predict which fitness component of females is determined by mating status (Searcy and Yasukawa 1989). In most studies, reproductive success related to pairing status is measured by using current reproductive parameters such as clutch size, nestling size, and fledging success (e.g. Johnson et al. 1993; Searcy and Yasukawa 1996; Smith and Sandell 1998; Lubjuhn et al. 2000). However, estimates of reproductive success should also include future consequences of current reproductive investment (Gustafsson 1989; Gustafsson and Pärt 1990). If polygyny is predicted to affect offspring or female fitness, the effect

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of mating status on fledgling recruitment or survival, mating success of sons, female survival, or lifetime reproductive success must be assessed. However, there are only a few examples available where future consequences of polygyny are investigated from the female's point of view.

For example, in great reed warblers *Acrocephalus arundinaceus*, Bensch (1996) examined female fitness to the level of offspring recruitment, and female survival rate was also included as a variable in the study. Wheelwright et al. (1992) used recapture data to estimate the effect of polygyny on nestling survival and female survival and future fecundity in the savannah sparrow *Passerculus sandwichensis*. Kempenaers (1995) measured apparent survival of primary and secondary female blue tits *Parus caeruleus* until the next breeding season. Recently, Both (2002) reported fitness estimations, including survival and the number of recruiting offspring, for female pied flycatchers *Ficedula hypoleuca* of different mating status. All of these studies, based on return rate data, found only weak support for the notion that secondary females suffer from reduced fitness as a result of polygyny. Furthermore, no study has taken into account differences in recapture probability related to female mating status. This omission may be particularly important, because females differing in mating status may also differ with respect to recapture probability, thereby causing bias in female fitness estimates.

Here we explore the potential relationship between current female mating status and future survival possibilities in a Hungarian collared flycatcher *Ficedula albicollis* population. To examine the trade-off between reproduction and survival, we used 7 years of breeding data in a mark-recapture analysis that takes recapture probability into account. In this paper, we also focus on lifetime fitness consequences of polygyny and investigate the effect of mating status on lifetime reproductive success. We estimated lifetime reproductive success and investment by recording the total number of eggs, fledglings and recruits produced by females during their lifetime. We included laying date in our analyses, since the relative date of breeding in a given year is known to affect both mating status and current reproductive output in flycatchers (Lundberg and Alatalo 1992; Garamszegi et al. 2003; Both 2002).

The collared flycatcher is a socially monogamous bird, but polygyny occurs regularly. Therefore, the collared flycatcher and its sibling species, the pied flycatcher, have been extensively studied in terms of polygyny (Stenmark et al. 1988; Gustafsson 1989; Alatalo et al. 1990; Lundberg and Alatalo 1992; Král et al. 1996). These studies found that males having two mates divide their parental investment between primary and secondary females, with most effort devoted to the brood of the primary female. By using automatic feeding visit recorders and radio-telemetric techniques in our collared flycatcher population we also found asymmetrical male contribution to provisioning of chicks (Török et al. 1998). This phenomenon is known to be the main factor negatively

affecting the reproductive success of females paired with already-mated males (Lifjeld and Slagsvold 1989; Lundberg and Alatalo 1992).

The cost of polygyny for female flycatchers has been reported in many studies, and triggered the development of hypotheses suggesting mechanisms to explain why some females choose already mated males (Lundberg and Alatalo 1992). The deception hypothesis (Alatalo et al. 1981) and the female-female aggression hypothesis (Stenmark et al. 1988) are the best-known explanations for polygyny in flycatchers, and have provided a long lasting disagreement between research groups (e.g. Rätti et al. 1995; Slagsvold and Dale 1995). Nevertheless, a more thorough estimation of fitness of all participants (male, primary female, secondary female) is required to understand the mechanisms playing a role in the evolution of polygyny in these species. Our paper is an attempt in this direction.

Life history theory predicts that the cost of reproduction has profound effects on subsequent performance reducing parental fitness via reduced future reproduction and survival (Williams 1966a, 1966b; Gustafsson 1989). Secondary female pied flycatchers receiving reduced or no male assistance during chick feeding experience reduced reproductive output in terms of fledging and breeding success (Lundberg and Alatalo 1992). They are also assumed to pay additional costs of polygyny if the detrimental effect of caring for young alone on female condition is taken into account, since increased reproductive investment can have negative future consequences (Nur 1988). Alternatively, if females mated to polygynous males are of poor phenotypic quality, mating status should appear to be associated, without causal linkage, with measures of female fitness such as survival and lifetime reproductive success. As a consequence, we hypothesise that polygynous mating is negatively related to survival and future reproduction of secondary females.

However, secondary females can be compensated in the future for the cost of polygyny, thereby eliminating its harmful fitness consequences leading to no detectable effect of mating status on female survival and lifetime reproductive success (Searcy and Yasukawa 1989, 1995). Alternatively, females may decrease their current reproductive investment when they share or lack male assistance, thereby increasing the probability of survival and future reproductive success due to a reproductive strategy dependent on their mating status. This tactic may cause diminished reproductive output in the given year, but can be adaptive if the decision of secondary females is to achieve increased survival and hence future reproductive success.

Materials and methods

Data collection

We analysed the breeding data of a collared flycatcher population, collected between 1995 and 2001 at Pilis Field Station (47°43'N,

19°01'E), Pilis Mountains, Budapest, Hungary. To establish a breeding population of hole-nesting passerines more than 600 artificial nest-boxes were set up in 1981 in a 32-ha area in eight plots of an oak-dominated woodland. During the breeding season, we checked all nest-boxes a minimum of 3 times a week. We recorded standard breeding variables such as the calendar laying date of the first egg, clutch size and the number of nestlings at age 13 days. We also measured tarsus length and body mass of nestlings at age 13 days. The condition of nestlings was assessed in an ANCOVA with body mass as the dependent variable and tarsus length as a covariate. Standardised relative laying date for each breeding attempt was calculated as the difference between calendar laying date of the given brood and calendar laying date of the first brood appearing in a given year. Nesting females were trapped and measured during the incubation or the nestling periods between 0800 and 1200 hours. Each year we applied the same capture protocol and, according to estimates based on mark-recapture analysis, about 86% of females nesting in our study sites were captured and measured.

In our population the annual frequency of polygyny averaged 6.040% (SE=0.950, $n=935$). The mating status of females was estimated by applying a unique combination of colour rings on males. Polygynous males were identified during pair formation by binocular observations and verified during the nestling period if we caught a male a second time in his secondary nest. Females were classified as (1) secondary females, if they were observed at least once to breed as a secondary female of a polygynous male; (2) primary females, if they were found at least once to be primary females; and (3) monogamous females if they were always mated with monogamous males. If a bird was observed once as primary and once as secondary female it was treated as secondary female. This classification of mating status allowed us to investigate the relationship between survival and mating status, but the consequences of potential changes in mating status among years were thus neglected. Initially, we intended to handle mating status transitions among years by using status categories for each year in multi-strata analysis of survival (Brownie et al. 1993). Our intention was to test whether immediate mating status is a function of mating status during the preceding year. However, since we also included laying date as a covariate into the survival analyses (see below), to avoid very complex models, we decided to disregard the potential variation caused by mating status changes. Our preliminary calculations indicated, however, that the probability of secondary females being observed as secondary females in the subsequent year is not significantly different from random mating status transitions (Yates corrected $\chi^2=0.220$, $P=0.641$). In our data there were only two females observed to breed twice as secondary females. The exclusion of these birds from the analysis gives similar results. We only used data for females with known laying dates and mating status. This selection gave us a sample of 464 females (387 monogamous, 34 primary and 43 secondary females).

Mark-recapture analysis

Females differing in mating status were recaptured a different number of times. Monogamous females were recaptured in our study sites on average 1,375 times (271 individuals once, 94 twice, 15 three times and 7 four times), while primary and secondary females were captured 1,529 times (20 individuals once, 10 twice and 4 three times) and 1,837 times (21 individuals once, 12 twice, 6 three times and 4 four times), respectively (Kruskal-Wallis ANOVA: $H=12.295$, $P=0.002$, $n=464$). These results suggest that apparent survival of females estimated from recaptures might be related to their mating status, and therefore the need to model these phenomena using a mark-recapture approach. Although a priori we hypothesised a correlation between mating status and survival due to the consequences of polygyny on survival (see Introduction), an opposite causal relationship may also be at work, for example, due to differences in female quality (see Discussion for further details). However, note that a correlative approach does not have the

potential to reveal causal relationships. Thus, any correlative evidence of such relationship should be treated with caution.

We investigated the relationship between mating status, survival and recapture probabilities relying on individually marked animals, following a model selection strategy proposed by Lebreton et al. (1992). For this mark-recapture survival rate estimation we used the MARK 1.9 computer program (White and Burnham 1999, <http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>). We applied live recapture data only, as exact time of death is often unknown.

Live recaptures are the basis of the standard Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965; Pollock et al. 1990). Under the CJS scheme, marked animals are released into the population, and later these marked animals are encountered by catching them alive and then re-releasing them. Survival (Φ) for each interval between successive recapture sessions and recapture probability (p) for each recapture session can be estimated. The CJS approach offers hypothesis testing through a model selection algorithm based on Maximum Likelihood (ML) estimation, which allows investigation of the potential effect of capture year (t) and/or a priori defined grouping variables (g). Additionally, it is possible to assess the importance of continuous variables on survival and recapture probability by using covariates.

First, we generated CJS survival models to detect time (t ; 7 recapture events providing 6 measures of survival, $k=7$) and group (g ; mating status: monogamous, primary and secondary) effects on female recapture (p) and survival (Φ). Altogether 25 models were created representing all possible permutations of group, time and interaction effects on recapture and survival. Because we expected possible differences in mating status-specific survival rates, we started with the $[\Phi(g \times t)p(g \times t)]$ global model involving the maximum number of estimable parameters and a flexible structure. For all models, the number of estimable parameters and the deviance were computed and the models were compared and ordered based on Akaike's Information Criterion (AIC) in order to find the best model that fitted the distribution of our observed data (Akaike 1985; Lebreton et al. 1992). This was done because we had to consider numerous models, and the Akaike's approach allows comparison of models that are not necessarily nested. If the difference in AIC between two models is larger than two, there is a considerable support for a significant difference. If $\Delta AIC < 2$, then both models have approximately equal weight in the data (Burnham and Anderson 1998).

Second, to address the importance of the relative date of breeding as a confounding factor on mating status, we constrained the previously selected best model with laying date as an individual covariate. Using AIC, we compared the model including laying date effects with the previously selected best model that was not constrained. Since it is impossible to handle covariates separately year by year for each observed individual in MARK, for each female we used the average laying date if they bred more than once during the study years. Using the average values, we indirectly applied the assumption that laying date is an individual attribute that can be repeatedly measured across years. We tested this assumption and found that although highly significant, the repeatability of laying date was low ($R=0.183$, $P=0.005$). Hence, we also controlled for potential laying date effects by using a different approach. Laying date effects are in part due to the fact that by definition primary females necessarily breed earlier than later arriving secondary females [monogamous females: mean standardised laying date (+SE) = 8.524(+1.032); primary females: mean (+SE) = 5.905(+1.078); secondary females: mean (+SE) = 11.235(+1.081); Kruskal-Wallis ANOVA: $\chi^2=27.011$, $df=2$, $P<0.001$]. Therefore, we repeated the survival analysis with a data set that only contained secondary and monogamous females. In this second survival analysis, for each secondary female, we randomly chose a monogamous female from the same year that commenced its breeding on the same day. Then we performed the same model selection procedure as before without constraining the final model with laying date.

For a recapture analysis to be feasible, the basic assumptions of the CJS model should be met (Lebreton et al. 1992). We assumed that (1) rings are not lost or missed; and (2) all sampling sessions are

instantaneous, relative to the interval between occasion (i) and ($i+1$), and each release is made immediately after the sample. However, it is also required that all marked animals in the population (3) should have the same chances of being captured at any time; and (4) should have the same probability of surviving, regardless of when they were marked. For these prerequisites Burnham et al. (1987) recommended the use of TEST 2 and 3 to check how well a given model fits the observed data. These TESTs are computed for the relevant input capture histories by pooled chi-square statistics yielding the goodness-of-fit to the CJS model. In this flycatcher survey, there were insufficient data available to perform TEST 2.

Since TEST 3 usually lacks statistical power to detect lack of fit, Buckland and Garthwaite (1991) have suggested using a parametric bootstrap procedure provided in MARK to evaluate the goodness-of-fit of the global model. With the bootstrap procedure, the estimates of the model being assessed for goodness-of-fit are used to generate data, i.e., a parametric bootstrap. The simulated data exactly meet the assumptions of the model, and data are simulated based on the number of animals released at each occasion.

Consequently, we first computed TEST 3 and also bootstrap-based goodness-of-fit tests for the $[\Phi(g \times t)p(g \times t)]$ basic model in order to assess its fit with the observed data. These tests revealed that the deviance of the basic model fitted the deviance coming from the original data (total database: TEST 3, $\chi^2=9.145$, $df=18$, $P=0.956$, bootstrap GOF: $P=0.508$; database for monogamous and secondary females: TEST 3, $\chi^2=12.836$, $df=12$, $P=0.381$, bootstrap GOF: $P=0.411$). Therefore, we concluded that these tests allowed inquiry of the basic assumptions to subsequent analyses, and we continued creating models and selecting them by using AIC differences (Lebreton et al. 1992).

Within-season reproduction and lifetime reproduction

First, we compared within-season reproductive success of females of different mating status. To control for laying date effects in a pairwise comparison, we randomly chose a monogamous female laying its first egg on the same day for each primary and secondary female. We then compared their clutch size and the number and condition of the fledglings. Offspring surviving until 13 days were used to estimate fledgling success, because there is hardly any mortality between age 13 days and age 14 days, when fledging usually occurs. Therefore, throughout the study we assumed that, if any, there was no mating-status-dependent mortality between age 13 days and age 14 days that may bias the estimation of fledging

success. This assumption was supported by the fact that nestling condition at age 13 days did not differ among mating status groups in any of the studied years (ANCOVAs: $P>0.452$).

Second, lifetime reproductive output and success were calculated. In these analyses, we only included females that were first time breeders during the monitored years, and were not seen during the study to have died. We used the total number of eggs laid and the total number of young fledged to estimate lifetime reproductive output for each female. In our lifetime analysis, we did not include average nestling condition, because this variable was not repeatable among years. We estimated lifetime reproductive success of females from the number of recruits found till 2002. Since the distribution of the number of eggs, fledglings and recruits was significantly different from a normal distribution (Lilliefors test: $P<0.01$ in all cases), we applied non-parametric tests to compare the effect of different mating status on within-season and lifetime reproductive variables.

Results

Mating status related survival and recapture probability

In our mark-recapture framework on survival and recapture probabilities in relation to mating status, the basic assumption of the Jolly-Seber model was met for the $[\Phi(g \times t)p(g \times t)]$ global model. We created 25 models, for which the variance and the number of parameters are given in Table 1. According to Akaike's Information Criterion, the best models selected to explain the distribution of our seven years of recapture data indicated that without applying laying date control, there was a strong effect of mating status [group effect, (g)] on female survival (Φ). The models $[\Phi(g+t)p(\cdot)]$, $[\Phi(g)p(\cdot)]$ and $[\Phi(g)p(g+t)]$ had the lowest AIC values (<2). These models showed that in addition to group effects, survival and recapture probability varied among years [time effects (t)]. However, since our aim in this study was to investigate female survival in relation to mating status,

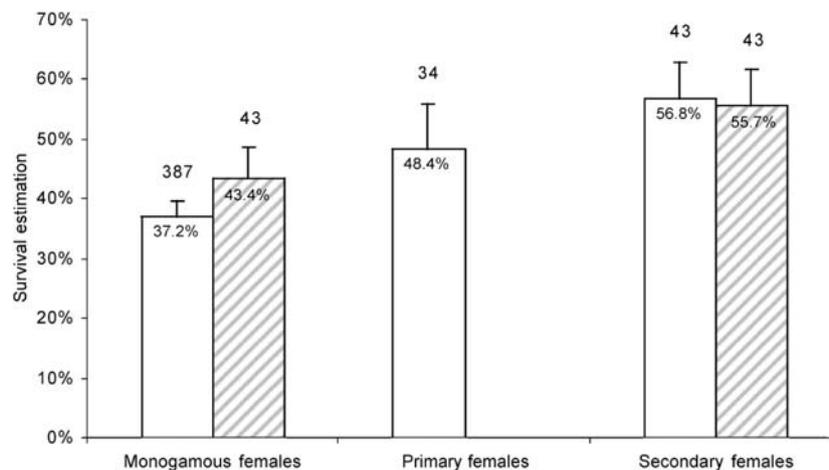


Fig. 1 Estimates of survival rate of monogamous, primary and secondary collared flycatcher *Ficedula albicollis* females breeding in Hungary 1995–2001 based on mark-recapture analysis. *White columns* represent the survival estimates of the model denoted $[\Phi(g)p(\cdot)]$, which according to Akaike's Information Criterion (AIC) has been selected as the second best model without laying date

control (Table 1). *Striped columns* indicate the survival estimates of the selected model $[\Phi(g)p(\cdot)]$ of an independent analysis, in which for each secondary female a monogamous female that commenced its breeding on the same day was selected randomly. Standard error bars and sample sizes are given

Table 1 Cormack-Jolly-Seber survival and recapture models generated to fit female collared flycatcher *Ficedula albicollis* recapture data. For each model we present the number of estimable parameters (*NP*), the deviance (*DEV*) and the Akaike's Information Criterion (*AIC*). Models are ordered according to increasing *AIC* value, and the *AIC* differences compared to the first model are also given (ΔAIC). Models shown in bold were used for further survival estimations (see Figs. 1, 2). *Phi* survival, *p* recapture rate, *t* time, *g* mating status (monogamous, primary and secondary), *LD* laying date constrain, . constant. Monogamous females $n=387$, primary females $n=34$, secondary females $n=43$

Model	NP	DEV	AIC	ΔAIC
[Phi($g \times LD$) <i>p</i> (.)]	7	770.65	784.86	0.00
[Phi($g+LD$)<i>p</i>(.)]	5	775.63	785.74	0.88
[Phi($g+t$) <i>p</i> (.)]	9	771.78	790.12	5.26
[Phi(g)<i>p</i>(.)]	4	782.43	790.50	5.64
[Phi(g) <i>p</i> ($g+t$)]	9	772.37	790.70	5.84
[Phi($g+t$) <i>p</i> (t)]	13	766.62	793.30	8.44
[Phi(g) <i>p</i> (t)]	9	775.17	793.50	8.64
[Phi($g+t$) <i>p</i> (g)]	11	771.25	793.74	8.88
[Phi(g) <i>p</i> (g)]	6	781.79	793.95	9.09
[Phi($g \times t$) <i>p</i> (.)]	19	754.72	794.16	9.30
[Phi(t) <i>p</i> (.)]	7	780.91	795.11	10.25
[Phi(.) <i>p</i> (.)]	2	792.55	796.57	11.71
[Phi($g \times t$) <i>p</i> (g)]	21	753.33	797.09	12.23
[Phi($g+t$) <i>p</i> ($g+t$)]	15	766.22	797.12	12.26
[Phi($g \times t$) <i>p</i> (t)]	23	749.71	797.82	12.96
[Phi(t) <i>p</i> (g)]	9	779.73	798.06	13.20
[Phi(t) <i>p</i> (t)]	11	776.12	798.62	13.76
[Phi(.) <i>p</i> (t)]	7	784.64	798.85	13.98
[Phi(.) <i>p</i> (g)]	4	791.21	799.29	14.43
[Phi(.) <i>p</i> ($g+t$)]	9	781.08	799.41	14.55
[Phi($g \times t$) <i>p</i> ($g+t$)]	25	748.48	800.98	16.12
[Phi(t) <i>p</i> ($g+t$)]	13	774.38	801.06	16.20
[Phi(g) <i>p</i> ($g \times t$)]	21	759.93	803.69	18.83
[Phi($g+t$) <i>p</i> ($g \times t$)]	25	754.34	806.83	21.97
[Phi(.) <i>p</i> ($g \times t$)]	19	768.26	807.70	22.84
[Phi(t) <i>p</i> ($g \times t$)]	23	762.21	810.32	25.46
[Phi($g \times t$) <i>p</i> ($g \times t$)]	33	740.20	810.57	25.71

Table 2 Pairwise comparisons of current reproductive variables (clutch size, fledgling success and fledgling condition) of females starting to breed on the same day with different mating status. Results of Wilcoxon matched-pairs signed-ranks tests (clutch size

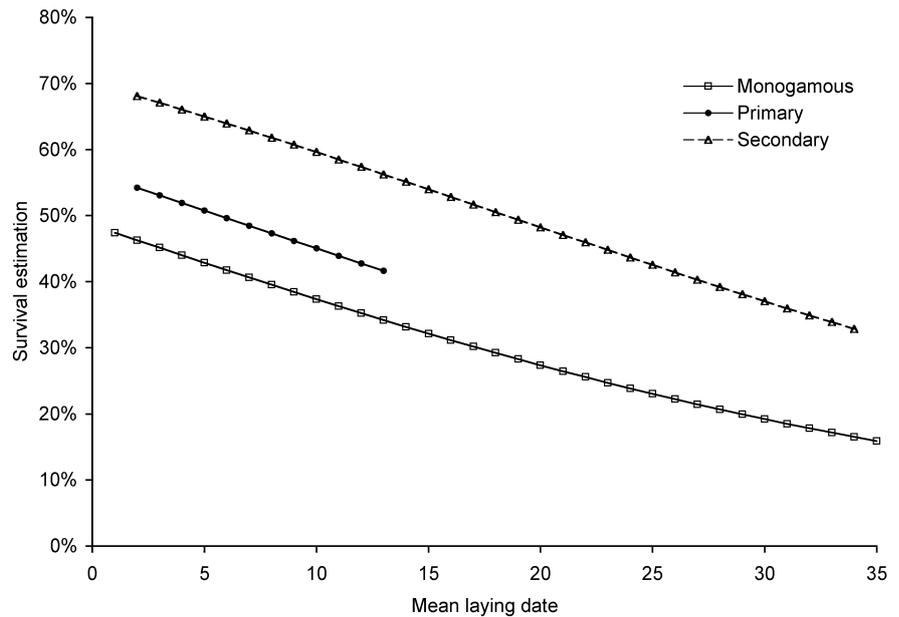
	Mean (SE)		Statistical tests
	Monogamous	Polygamous	
Monogamous—primary			
Clutch size	6.552 (0.117)	6.421 (0.104)	$Z=-1.034$; $P=0.301$
Number of fledglings	5.182 (0.341)	4.269 (0.428)	$Z=-2.193$; $P=0.028$
Condition of fledglings	138.273 (1.906)	135.407 (2.948)	$F=0.051$; $P=0.822$
Monogamous—secondary			
Clutch size	5.913 (0.128)	6.087 (0.128)	$Z=-1.437$; $P=0.151$
Number of fledglings	4.571 (0.326)	3.382 (0.375)	$Z=-2.357$; $P=0.018$
Condition of fledglings	137.207 (1.993)	131.158 (2.771)	$F=1.615$; $P=0.228$

we did not address hypotheses concerning survival differences among years. For simplicity, we used model [Phi(g)*p*(.)] for further analysis $\{\Delta AIC$ between models [Phi($g+t$)*p*(.)] and [Phi(g)*p*(.)] were 0.39}. The bootstrap-based goodness-of-fit results showed that the deviance of the selected [Phi(g)*p*(.)] model was likely to be observed with a probability of 0.568. Based on this model, the estimates for survival for secondary females were larger than those of monogamous and primary females, and the survival of primary females also exceeded the survival of birds always breeding in monogamous pair-bonds (Fig. 1). When we constrained survival in model [Phi(g)*p*(.)] with laying date averages as a covariate, we found that models denoted [Phi($g \times LD$)*p*(.)] and [Phi($g+LD$)*p*(.)], taking laying date effects into account were the best selected with the lowest AIC value (Table 1). The difference in AIC between these two models were 0.88, suggesting that both models fit equally well with the data. Because the model [Phi($g \times LD$)*p*(.)] that assumes an interaction between mating status and laying date had more parameters to estimate (7), we have chosen the model [Phi($g+LD$)*p*(.)] that assumes the additive effects of mating status and laying date (number of parameters =5) for further estimation. This model predicted that later arriving birds have lower survival, and polygynous females realised higher survival than monogamous females, with secondary females achieving the maximum values (Fig. 2). A separate mark-recapture survival analysis with secondary and randomly chosen monogamous females of the same laying date revealed a relationship between mating status and survival {model [Phi(g)*p*(.)] had the lowest AIC value: 261.80, number of parameters: 3, deviance: 68.053}. This model estimated higher survival for secondary females (Fig. 1).

It is plausible that apparent differences in survival (number of recaptures) could be due to differences in dispersal rather than survivorship. We investigated dispersal of females in relation to mating status. About 4 km from the study site from which we used data for the analyses presented in this paper, there is another nest box plot where we applied the same ringing protocol. We counted the number of breeding plot shifts of females

and number of fledglings) and of ANCOVAs (fledgling condition: repeated measure analysis of body mass with tarsus length as a covariate), 34 monogamous-primary pairs and 43 monogamous-secondary pairs

Fig. 2 Laying date, mating status and survival estimated by the model $[\Phi(g+LD)p(\cdot)]$, which is the laying date constrained model of the model $[\Phi(g)p(\cdot)]$, and predicts additive effects between mating status and laying date. Using seven years of data, the sample sizes are $n=387$ for monogamous females, $n=34$ for primary females and $n=43$ for secondary females. Laying date is the mean standardised relative laying date, which is the difference between calendar laying date of a brood and calendar laying date of the first brood



between years, and checked if these shifts were dependent on mating status. We found that one secondary and ten monogamous females shifted breeding plot, and this pattern was not significantly different from random ($\chi^2=0.080$, $df=2$, $P=0.961$). These results imply that dispersal has not seriously biased the detected survival patterns.

Mating status related to within-season and lifetime reproduction

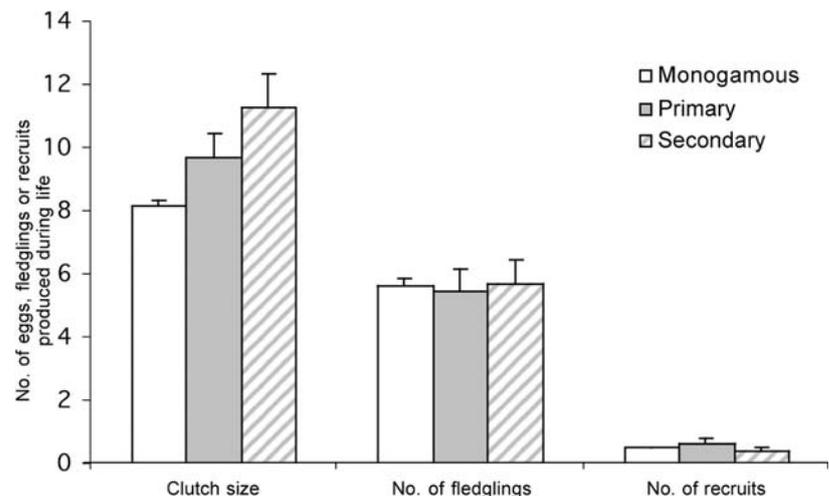
In pairwise comparisons of females of different mating status that started to breed on the same day, monogamous females produced more fledglings than primary and secondary females. However, clutch size and the condition of fledglings did not differ significantly among females of different mating status (Table 2). Although current reproductive success of secondary and primary females was

low, they laid significantly more eggs and fledged at least as many nestlings as monogamous females during their life (Kruskal-Wallis ANOVAs: clutch size, $\chi^2=11.060$, $df=2$, $P=0.004$; number of fledglings, $\chi^2=2.378$, $df=2$, $P=0.305$; Fig. 3). Lifetime reproductive success, estimated as the number of recruits produced, did not differ significantly among mating status groups ($\chi^2=1.876$, $df=2$, $P=0.392$; Fig. 3).

Discussion

The general viewpoint is that secondary female flycatchers caring for their young alone or with less male assistance work harder and are therefore less likely to survive and have reduced lifetime reproductive success compared to other females (Alatalo et al. 1982; Alatalo and Lundberg 1984; Gustafsson 1989). From this perspective, our results are surprising. We found that polygamously mated females

Fig. 3 Lifetime reproductive output and success of collared flycatcher females of different mating status expressed by cumulative clutch size (*white columns*), number of fledglings (*grey columns*) and the number of recruits produced till 2002 (*striped columns*). Monogamous females $n=291$, primary females $n=25$, secondary females $n=31$



had lower breeding success, which is probably the consequence of reduced male assistance during chick provisioning. However, primary and secondary females enjoyed higher survival and similar future reproductive success compared to monogamous females. Consequently, we conclude that the apparent reduction in current reproductive success of polygynously mated collared flycatcher females is not associated with reduced success in subsequent breeding attempts. This conclusion suggests that previous studies investigating the effects of mating status on current individual reproductive success may have underestimated the fitness consequences of mating status, because they neglected effects of future survival and reproductive performance.

There are at least four potential explanations for the observed patterns. First, our findings may be consistent with the cost-compensation models in Searcy and Yasukawa's (1989, 1995) classification of polygyny. These models predict that compensatory mechanisms should account for increased survival of females facing current reproductive costs in the season when they breed with polygynous males. For example, the polygyny threshold model assumes that female fitness is a function of breeding-situation quality (Verner 1964; Verner and Willson 1966; Orians 1969). Primary and secondary females may pay reproductive costs, but such costs could be compensated for by the opportunity to breed in a territory of superior quality belonging to a high quality male. If polygamous males have prime quality territories, their females may not suffer from lack of food or an abundance of parasites when they raise young on their own. Alternatively, it is also possible that compensation acts via the absence or the partial presence of a polygynous male during chick feeding. This may involve the benefits of a reduction in social contacts that enhance horizontal transmission of parasites (see Frank 1996). The absence of a conspicuous male may also decrease the probability of attracting predators (see Dale and Slagsvold 1996b). These effects in turn could positively affect the survival of females mated with polygamous males compared to monogamous females with mates present.

Second, search-cost models (Stenmark et al. 1988) may apply if searching for unmated males is costly for females. In this case, monogamous or primary females may pay this cost when ensuring the independence of their chosen mate. By contrast, if search costs negatively influence survival, we would expect secondary females, who do not ascertain the mating status of their male, to have higher survival. However, this mechanism would predict that primary and monogamous females have equal survival and lifetime reproductive success. This was not the case in our study. The low rate of polygyny in our population also suggests that the costs associated with searching for unmated males may be low. In addition, in the pied flycatcher, secondary females have also been demonstrated to spend time searching for unmated males (Slagsvold and Dale 1994; Dale and Slagsvold 1996a).

Third, females may adjust their reproductive strategy based on their mating status (see also Eens and Pinxten,

1995). For example, secondary females may reduce their parental investment relative to their mating status in order not to jeopardise survival and future reproductive success. Thus, females of polygynous males may have reduced success during current reproduction compared to monogamous females, and apparent reproductive success should result from decisions based on costs and benefits associated with the realised mating system. Under this scheme, our results would imply that applying the tactic of reduced investment, secondary and primary females may end up with similar lifetime reproductive success in terms of number of recruits as monogamous females, because polygynously mated females have more opportunities to breed due to their higher survival. This perfect compensation would result in that mechanisms of female defence against polygyny (e.g. female-female aggression), and mechanisms of male attempts to hide their mating status (e.g. deception) will not necessarily be maintained.

However, we suggest that a female adjustment strategy cannot explain the observed patterns entirely. A system allowing perfect fitness compensation for polygamously mated females that reduce their current reproductive investment for future benefits cannot be evolutionary stable. If a reduced investment strategy were so beneficial, polygynous mating status should be more common in the population, and we would expect monogamous females to decrease their current reproductive investment. In addition, a key assumption of the mating-status-dependent reproductive strategy is that polygynously mated females have reduced reproductive investment. However, this assumption is not supported by measurements of parental effort in the pied flycatcher. In fact, secondary or primary females that receive less parental help from their mates than monogamous females tend to compensate by increasing their own parental effort (Lundberg and Alatalo 1992). In an earlier study, we found that widowed females caring alone for nestlings increased their feeding rates and lost more body mass compared to females at biparental nests (Török et al. 1998). Therefore, if a reproductive strategy of females dependent on mating status applied to our collared flycatcher population, it should work as the "best of a bad job" in secondary and primary females when breeding in a disadvantageous situation.

Fourth, since it is possible that females of different mating status are not random samples in terms of individual quality, the observed differences in female survival and overall reproductive success may not be due to mating status, but to systematic differences in quality. If females of polygynous males are of superior phenotypic quality, an apparently disadvantageous mating status may actually be associated with increased female fitness without a causal link between the two. For example, the threshold for settling with an already mated male may be lower for a high quality female than for a low quality female. It is also possible that, if the mating system of females is randomly determined, long-lived females will have higher probability to become primary or secondary females, which also results in a covariation between survival and mating status. It is noteworthy that in the

spotless starlings *Sturnus unicolor*, female breeding success in relation to mating status seemed to be weakly affected by male assistance, but strongly dependent on inherent quality differences between females (Moreno et al. 2002).

Since our conclusions are based on correlations, it is necessary to address the importance of potentially confounding factors. To understand the exact mechanisms that generate a relationship between mating status and survival, control for potential age effects would be necessary. We initially made efforts to examine this issue, but we failed to handle age effects, because available sample sizes were too small (note that during seven years, we recorded less than 50 polygyny events). Flycatcher females could not be aged reliably in the field. Thus, it was only possible to obtain age information for birds that were born in our study site. Nevertheless, even if age effects were important, we would expect that secondary females mate with polygynous males during their first breeding season, as inexperienced, young females were more likely to end up as secondary females. This result would indicate no causal effect of mating status on survival. However, this conclusion was not supported with our data, because polygyny events appeared randomly within the recapture histories of individuals (Yates corrected $\chi^2 < 0.001$, $P = 0.977$). It is also noteworthy that Gustafsson and Pärt (1990) did not find that age affected apparent survival probability of the collared flycatcher.

We previously mentioned a possible role for female quality in driving associations between mating status, survival and lifetime reproduction, but female condition, which we left uncontrolled, may also be a potential determinant of this context. Condition may influence mate-searching behaviour, thus affecting mating status, but the costs of reproduction may also be dependent on condition, thus interacting with the future fitness consequences of female mating status.

Dispersal differences might also affect recapture probability and survival in relation to mating status. However, we did not find any indication of dispersal differing among groups. Pärt and Gustafsson (1989) also found no difference in breeding dispersal patterns in the subsequent year between monogamous and secondary collared flycatcher females. Therefore, we assume that the recapture patterns used in our survival study were unaffected by differences in dispersal.

There are obvious differences among studies of flycatcher populations in terms of fitness costs associated with mating status. For example, Gustafsson (1989) showed lower fitness of secondary females in terms of number of recruits in a Swedish population of the collared flycatcher. Composite fitness measures including number of recruits and apparent female survival (without controlling for differences in recapture probabilities) did not differ statistically between monogamous and secondary females in a Dutch population of pied flycatchers (Both 2002). In a Spanish population of the same species, secondary females had slightly lower apparent survival, as estimated by return rate, and produced fewer recruits than

monogamous females. (Potti and Montalvo 1993). These diverse patterns together with our findings suggest that selection pressures arising from polygyny might act differently in different populations.

We regard our results as an indication of the importance of correct fitness estimations in studies addressing questions concerning the cost of polygyny. We present observational evidence for current reproductive success being reduced in polygynously mated females, while future fitness components showed opposite patterns among females of different mating status. These findings call for alternative explanations for the variance in mating system including the mating-status-dependent reproductive adjustment strategy or the higher quality of secondary females. Future experiments that control for potentially confounding effects should be designed to decide which mechanism is applicable in the collared flycatcher.

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