Lifetime offspring production in relation to breeding lifespan, attractiveness, and mating status in male collared flycatchers

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Abstract

As a comprehensive fitness parameter, lifetime reproductive success (LRS) is influenced by many different environmental and genetic factors, among which longevity is one of the most important. These factors can be reflected in secondary sexual characters, which may contribute to the life-history of individuals via social relations with conspecifics. Facultative polygyny in birds is another conspicuous reproductive trait that potentially increase male reproductive success, but lifetime success data in relation to polygyny are scarce. Here we used 17 years of breeding data to quantify the LRS of male collared flycatchers (*Ficedula albicollis*) on the basis of lifetime recruitment of offspring. Breeding lifespan showed a positive relationship with LRS, and it was also significantly associated with mean recruitment of offspring per breeding year. Body size and sexually selected forehead patch size did not predict the number of recruits. Polygyny was positively associated with LRS, but probably only due to the correlation between lifespan and polygyny. Our results demonstrate that the relationship between longevity and LRS is not explained by the larger number of reproductive attempts when living longer, and question the adaptive value of polygyny in this population. The lack of association between forehead patch size and recruitment suggests that forehead patch is a poor indicator of phenotypic quality in our birds.

Key words: reproductive success, recruitment, longevity, polygyny, *Ficedula albicollis*

Introduction

In species with overlapping iteroparity, the most accurate method to estimate the contribution of their genes to the subsequent generations (i.e. fitness; Clutton-Brock 1988) is the calculation of lifetime reproductive success (LRS), which is given by the number of lifetime recruits, i.e. sexually mature offspring contributing to the breeding population (Brommer et al. 2004). There are two main determinants of the number of lifetime recruits: lifespan and the number of recruits per breeding attempt. Several studies have identified longevity or the number of breeding attempts as an important determinant of LRS (birds: Gustafsson 1986; Merilä and Sheldon 2000; Blums and Clark 2004; mammals: Clutton-Brock 1988; Bérubé et al. 1999). However, a prolonged lifespan in itself is not sufficient to be successful, as a considerable proportion of individuals do not produce any recruits despite their long reproductive life (Gustafsson 1989; Blums and Clark 2004), and the successful individuals also vary greatly in productivity (Newton 1989). In fast-living species, which live for a short time but may produce numerous offspring per breeding attempt, the reproductive output in a single year is more important for LRS than in slow-living species (Saether and Bakke 2000).

Annual reproductive success can be affected by individual characteristics such as body size (Grant and Grant 2000) as well as sexually selected traits (Gustafsson et al. 1995; Hasselquist et al. 1996). Individuals with more elaborate sexual traits are often of better quality (Møller 1994; Hasselquist et al. 1996). Hence, a positive relationship is also expected between the elaboration of these characters and the number of recruits (Møller 1994; Petrie 1994, but see Brooks 2000). Similarly, the number of mates also has an important role. Polygyny is usually considered beneficial to immediate male reproductive success, but its effect on LRS is poorly understood (Gustafsson 1989; Hasselquist 1998). In addition, care is needed when interpreting the relationship between polygyny and fitness, as polygynous males may have a high LRS because of their high quality and viability, irrespective of their mating status (Hannon and Dobush 1997, also see Lambrechts and Dhondt 1986).

It is generally quite difficult to measure LRS in natural population, as long-term studies are required to follow a sufficient number of individuals throughout their lives. In this study, using a 17-year dataset, we investigated potential determinants of male LRS in a small passerine bird, the collared flycatcher (*Ficedula albicollis*). We measured LRS as the number of lifetime recruits, and examined how individual variation in LRS was explained by differences in breeding lifespan. We were also interested in the lifetime success consequences of body size, forehead patch size (a sexually selected character; Hegyi et al. 2002), and polygyny, which is a regularly encountered reproductive status of males (Garamszegi et al. 2004).

Materials and methods

Study species and field methods

The collared flycatcher is a small, long-distance migratory, hole-nesting, insectivorous passerine that breeds in deciduous woodlands of Central Europe. Our data were collected between 1987 and 2003 in the Pilis Mountains, Hungary, in an oak-dominated forest, where more than 750 nestboxes were placed. The nuptial plumage of collared flycatcher males is black and white with a prominent white collar, forehead patch and wing patches. This species is ideal for long-term studies of reproductive success. It shows a preference for nestboxes, can easily be captured, and has high breeding site fidelity (Pärt and Gustafsson 1989; Könczey et al. 1992; Hegyi et al. 2002) and considerable local recruitment rates (Pärt 1990; Török et al. 2004). Nestboxes were checked multiple times a week throughout the nesting period, so breeding attempts were followed from nest building to fledging. Most parents were captured and ringed when feeding young, but some females were caught during incubation.

The forehead patch of males is an important sexually selected trait which, however, shows complicated links to individual life history. Studies in a population on Gotland, Sweden, showed among others that the size of this trait was related to age and body condition during the previous breeding season (Gustafsson et al. 1995; Qvarnström 1999). In addition, a positive relationship was found between a male's mean lifetime patch size and his mean recruitment of offspring per breeding attempt (Gustafsson et al. 1995; for more information about forehead patch see Gustafsson and Qvarnström 2006 for a review). In our population, in contrast, forehead patch size did not reflect the body condition of males, its dependence on age and yearly environmental conditions was weak and there was no relationship between forehead patch size and breeding lifespan either (Hegyi et al. 2002, 2006a). However, the trait is still a sexually selected character as an important determinant of social mating success: males with a larger forehead patch find a mate more rapidly relative to their arrival date (Hegyi et al. 2010). The yearly means of forehead patch sizes strongly varied among years in our population showing a linear temporal decline (Hegyi et al. 2006a), so patches of the same size could be relatively small in earlier years and relatively large in later years. The forehead patch size of males was estimated as a product of maximum height and maximum width. Forehead patch dimensions and tarsus length (to estimate body size) were measured with a calliper to the nearest 0.1 mm. The within-season repeatability of measurements between the major measurers was $r = 0.76$ for tarsus and $r = 0.60$ for forehead patch. (We calculated r – the intra-class correlation coefficient – from variance components as described in Lessells and Boag (1987), $n = 32$.) We did not mention here the other main secondary sexual character of male flycatchers, the white wing patch, because of the more limited dataset available for that trait.

The collared flycatcher is predominantly monogamous, but a fraction of males successfully attract two females and become polygynous. During the study period 83 out of 1558 breeding males were polygynous in our population. Several studies have found that males that had two mates divided their parental investment between the two nests with most effort devoted to the primary brood (Král et al. 1996), which may increase LRS compared to monogamy. In contrast, both primary and secondary nests experience similarly reduced reproductive success in our population (Garamszegi et al. 2004), so the positive effect of polygyny on LRS should be weaker.

Statistical analyses

We used a 17-year dataset, which contained data from 683 male flycatchers after excluding individuals that were the subject of experiments that could have influenced their breeding success. However, missing data for different variables resulted in different sample sizes among tests. In our population, returning male collared flycatchers occupy a nestbox within a mean of 129 metres from the box that they used in the preceding year (Könczey et al. 1992) and movement between plots is very rare, so it is possible to follow individuals throughout their entire breeding lifespan. Only males with complete recapture records (that is, those that were recaptured in each year between their first and last captures) were included in the analyses (95.9% of non-manipulated males).

The LRS of males was characterized by the number of lifetime recruits. As a significant proportion of recruits return only at the age of two or three years, males that bred after the year 2000 were excluded from the analyses, as their recruits may have returned after 2003, the end of the study period. Birds that were first captured in 1987 or 1988 as an adult (i.e. at least 2 years old, as indicated by the absence of subadult plumage) were also omitted, because very few males had been trapped before 1987, so it was not known if these birds had bred prior to the study period. In the morphological database, each individual had at most one measurement. Males with records from multiple years were represented by the measurement from their earliest year in the dataset. If there were more than one measurement from an individual in a given year, we randomly selected one of them. As the yearly means of forehead patch size in the population varied strongly among years, showing a linear temporal decline, and because body size also declined during the study period (Hegyi et al. 2006a), we used year-standardized forehead patch size and tarsus length in the analyses (mean of 0, standard deviation of 1). A male was considered polygynous if it was caught in two nestboxes while feeding nestlings. It was possible that we did not detect polygyny in some cases, so the observed rate of polygyny (4.9 %) is an underestimate (but it is similar to that found in the Swedish population with a similar approach (4.3 %); Qvarnström et al. 2003). Given the high capture effort, polygynous males caught at only one nest probably allocated nearly all of their care to this nest (included here as a monogamous nest) while neglecting the other nest (not used here due to the lack of the male). A secondary brood without the male caring for the offspring presumably produces little reproductive output, so the misclassification of these birds as monogamous is likely to bias polygynous LRS upwards. In this study, males were included in the analyses as polygynous if they were polygynous during at least one year of their entire lifespan. We adopted this binary categorization because only three males were polygynous in more than one year. Breeding date was not considered in our analyses because it was not repeatable within males (results not shown), so the timing of individual breeding attempts would not directionally bias the estimates of LRS. Indeed, models controlling for mean breeding date yielded the same conclusions as those reported here.

The breeding lifespan of a bird was defined as the number of consecutive years (see above) in which it was caught as a potential breeder (irrespective of the actual breeding success). Because of the high site fidelity of breeding males (Könczey et al. 1992; Hegyi et al. 2002) and the high capture effort in our population, birds that bred in one of our study plots in a given year but were not recaptured in subsequent years were considered dead. We tested if including cohorts (year of birth) in the analyses changed the results. Year of birth was obvious in birds that ringed as a nestling or as one-year-old (which wear subadult plumage). In newly ringed adult males, the youngest possible age assignment (2-year-old) was used because males that had been ringed as a nestling and bred first as an adult were mostly 2 years old (our unpublished data).

We found a significant relationship between breeding lifespan and mating status (polygynous males had a longer lifespan; also see the Results section), so using both as independent variables in the same model would have led to questionable results (Graham 2003). We resolved the situation in two steps. First, we ran two models that contained only one of these two variables. This informed us about the relationship of one variable with LRS without correction for the other. Second, to see whether the effect of mating status is due to its correlation with lifespan, we assessed the effect of mating status on LRS among males of the same breeding lifespan. We used the most common lifespans of 1 and 2 only, as for the other values there were very few polygynous data.

Individuals with a long lifespan can produce more recruits than those with a short lifespan simply because they have more breeding attempts. In connection with this, they have time to gain experience, and have more chance to become polygynous etc. In this case, when comparing individuals with the same breeding lifespan, we would not expect a difference among them in terms of reproductive success. However, long-lived individuals can also produce more recruits independently of their lifespan, for example, due to their more viable offspring. In this case, they may realize higher reproductive success even on a yearly basis. To clarify this issue, we computed the mean recruitment of offspring per breeding year by dividing the number of lifetime recruits by the number of breeding years.

Data on LRS were analysed in two generalized linear models with Poisson error and log link, containing the number of lifetime recruits as the dependent variable, forehead patch size and tarsus length as continuous predictors, and either breeding lifespan as a continuous variable, or mating status as a factor. Polygynous and monogamous males with the same breeding lifespan (1 or 2, see above) were compared with respect to LRS by using the number of lifetime recruits as the dependent variable, mating status as a factor and forehead patch size and tarsus length as continuous predictors. We used binomial error and logit link when comparing individuals producing versus not producing a recruit during their breeding lifespan. In this analysis binary recruit production was the dependent variable and breeding lifespan was a continuous variable. The dispersion parameters of the models were less than 1.34 and we corrected for them in the analyses. In all models we employed a backward stepwise model selection procedure. Statistics presented for non-significant terms reflect their reintroduction to the final model one by one. Since the mean recruitment of offspring per breeding year could not be transformed to conform to any standard distribution, it was analysed using non-parametric statistics (Spearman’s rank correlation, Mann–Whitney U-test). All statistical tests were calculated in Statistica 5.5. Means are represented with their standard errors. We report effect sizes estimated as Pearson’s correlation coefficients and the associated 95% confidence intervals as suggested previously (Nakagawa and Cuthill 2007).

Results

Individual males produced up to five recruits during their breeding lifespan of 1 to 6 years, but 67.8% of males did not recruit any offspring. Mating status was significantly related to breeding lifespan (polygynous males had a longer lifespan; Wald $\chi^2_{(1)} = 13.44$, $P < 0.001$, $n = 467$, $n_{mono} = 444$, $n_{poly} = 23$; effect size $r = 0.170$ (0.080 / 0.256), Fig. 1), so we did not enter the two parameters into the same model (see Methods). Breeding lifespan had a positive effect on the number of lifetime recruits (Table 1, Fig. 2a). The probability of producing a recruit also increased with lifespan (binary data, Wald $\chi^2_{(1)} = 54.28$, $P < 0.001$, $n = 683$; effect size $r = 0.282$ (0.211 / 0.350), Fig. 2b), though there were several long-lived birds that did not produce any breeding offspring. Forehead patch size and tarsus length were not correlated with the number of recruits (Table 1). Polygynous males had two clutches in at least one season of their life, and so we could expect them to have more nestlings that fledged and more offspring that returned to the breeding population. Indeed, polygyny, when assessed in isolation from lifespan, had a positive effect on the LRS of male collared flycatchers (Table 1). However, when we compared polygynous and monogamous males with the same breeding lifespan, the success of polygynous males was no different from that of monogamous males (breeding lifespan of 1: Wald $\chi^2_{(1)} = 0.48$, $P = 0.49$, $n_{mono} = 291$, $n_{poly} = 9$; effect size $r = 0.040$ (-0.074 / 0.153); breeding lifespan of 2: Wald $\chi^2_{(1)} = 1.97$, $P = 0.16$, $n_{mono} = 119$, $n_{poly} = 8$; effect size $r = 0.125$ (-0.051 / 0.292)). The above results suggest that polygyny is positively related to LRS, but this relationship is explained by the correlation between lifespan and polygyny. Including cohorts (year of birth) in the model did not affect the outcome of the analysis.

The mean recruitment of offspring per breeding year did not differ between polygynous and strictly monogamous males (Mann–Whitney U-test: adjusted Z = -1.181, P = 0.24, n_{mono} = 444, n_{poly} = 23; effect size r = -0.055 (-0.145 / 0.036)), but it was positively related to breeding lifespan (Spearman's rank correlation: r = 0.142, P = 0.002, n = 467; effect size r = 0.142 (0.052 / 0.230)). This finding means that the lifespan effect on LRS is not simply due to the larger number of breeding attempts by longer-lived males. Forehead patch size and tarsus length did not have any effects in this model either.

Discussion

Here we found that the LRS of male collared flycatchers was mainly associated with their breeding lifespan and that this was in a positive direction. Moreover, longevity was also positively related to the mean number of recruits per breeding year. The morphological traits we considered (forehead patch size and tarsus length) were not related to the number of lifetime recruits. There was a positive relationship between mating status and LRS, but this association could not be detected when comparing polygynous and monogamous males with the same breeding lifespan. Polygyny did not increase the mean yearly reproductive success of males either. These findings show a more complex picture on the relation of breeding lifespan and LRS than generally expected, and also have interesting implications for the evolution of visual signals and alternative reproductive tactics in our population.

In many bird species extra-pair paternity plays an important role in influencing the reproductive success of males. Unfortunately, we could not assess this component, because we did not have blood samples from individuals for most years of the study period. Given that paternity in the own nest is apparently not related to male ornaments or body size in our population (Rosivall et al. 2009), a directional effect of extra-pair paternity on our results is unlikely in this respect. However, the relationship between paternity and polygyny could be negative (Pilastro et al. 2002), very weak (Pearson et al. 2006) or positive (Soukup and Thompson 1998), so, our data on polygyny must be treated with caution. Studies conducted in different populations of the sibling species pied flycatcher (*Ficedula hypoleuca*) consistently showed that polygynous males had extra-pair young in their broods more frequently than monogamous males (Brün et al. 1996; Lubjuhn et al. 2000; Drevon and Slagsvold 2005). These findings suggest that considering extra-pair paternity would further reduce the advantage of polygynous over monogamous males, thereby strengthening our conclusions.

In species that breed more than once, breeding lifespan is often one of the most important correlates of LRS (Newton 1989) and this holds true in our case as well: breeding lifespan has a strong positive effect on the number of lifetime recruits. Such a relationship is expected because the presence or absence of a reproductive attempt often makes a numerically greater difference to LRS than lower or higher reproductive success in a given season. However, we also found that breeding lifespan positively predicted not only the number of lifetime recruits but also the mean recruitment of offspring per breeding year, which means that individuals with a long lifespan attained a higher LRS than expected from the number of their breeding bouts. The higher yearly reproductive performance of long-lived individuals may be explained by accumulating experience, that is, improving ability to raise offspring with ageing, which experience could not be reached by short-lived individuals. This may either be due to a better knowledge of the resource distribution and quality (i.e. foraging ability) or a better ability to occupy a cavity in a favourable area (whereby e.g. reducing the risk of predation). Alternatively, only birds with given genetic or phenotypic properties can survive to a certain age (Forslund and Pärt 1995). These individuals may also better cope with the costs of reproduction and may attain higher success independently of their lifespan. This explanation may be more consistent with our results than improving experience as a large number of individuals produce no returning young despite breeding several times during their life (also see Gustafsson 1989; Blums and Clark 2004). Females of many species apparently prefer older males (Enstrom 1993; Richardson and Burke 1999), or traits that indicate the expected lifespan of males (Jennions et al. 2001), thereby often enhancing the quality of young they produce (Saetre et al. 1995; Hegyi et al. 2006b). In addition, females may also invest preferentially in such offspring (Burley 1986; de Lope and Møller 1993), which may further increase their mate's reproductive success. This implies that, in some cases, individual attributes may influence both breeding lifespan and, indirectly, other aspects of fitness.

The forehead patch is a well-studied secondary sexual character of male collared flycatchers. It is sexually selected, but it seems that its information content differs between populations. Our results show that male forehead patch size did not predict lifetime offspring recruitment and this result is consistent with those of earlier studies performed in this population, suggesting that the forehead patch is a poor indicator of phenotypic quality in our birds (Hegyi et al. 2002, 2006a, but see Hegyi et al. 2010), in contrast to the Swedish population (Gustafsson et al. 1995; also see Gustafsson and Qvarnström 2006). It is possible that the advantage of large forehead patch can be detected only in extra-pair paternity, but within-brood paternity at least was not robustly related to forehead patch size in this population (Rosivall et al. 2009, but see Michl et al. 2002). Alternatively, large-patched males may be successful in some years, but variation in year quality may swamp the overall effect (Török et al. 2004). Long-term data on within- and extra-brood paternity would be helpful to further clarify the selection pressures on forehead patch size.

Many studies have shown that polygyny increases seasonal reproductive success of male birds due to the increased number of offspring from multiple broods (Davies and Houston 1986; Soukup and Thomson 1998). However, the increase may not be very large in cases when the reduced male help impairs the success of secondary or both females (Slagsvold and Lifjeld 1994; Garamszegi et al. 2004). Our results imply that polygynous males realized a higher LRS only because of their longer lifespan. This points out that, if polygyny is connected with lifespan, a positive relationship between the occurrence of polygyny and LRS may have nothing to do with the causal effect of polygyny on reproductive success. To our knowledge, the only study to date that has examined the effects of mating status on LRS while correcting for lifespan was conducted in a Swedish population of collared flycatchers. That study found that polygyny increased lifetime success irrespective of lifespan (Gustafsson 1989). In our collared flycatcher population, which lives in more variable environmental conditions (Török et al. 2004), the situation is different (also see Garamszegi et al. 2004).

Our findings raise the fundamental question of whether it is adaptive for males to build polygynous partnerships. It is possible that polygyny is not adaptive at present and the net selection pressure operating on polygyny is very low. Indeed, as in collared flycatcher polygynous males spend most of their life monogamously (also see Gustafsson 1989) the potential benefits to polygynous males in terms of yearly reproductive success are expected to become smaller when viewed across the whole breeding lifespan. Alternatively, polygyny may be advantageous only in years of good food supply, but males may still try to become polygynous every year because they cannot predict the food supply at the beginning of the season (Lubjuhn et al. 2000). This explanation may easily apply in our population, where the unpredictable among-year fluctuations of food availability even prevent the individual optimization of clutch size (Török et al. 2004). Finally, fitness benefits to polygynous males may also appear in the attractiveness of their offspring (Gwinner and Schwabl 2005; Huk and Winkel 2006), which will increase the number of grandoffspring, a variable we did not assess here. Even data from the Swedish population did not suggest a reproductive advantage for the offspring of polygynous males (Gustafsson and Qvarnström 2006), which makes such an advantage unlikely in our population. Further investigations are currently underway to clarify the determinants of polygyny in our population and its consequences for LRS in more detail. Note that the potential detection failure of polygyny may lead to overestimated polygynous LRS (see Methods). However, this supports rather than weakens our results, i.e. this likely overestimated LRS is not higher than that of monogamous males.

To summarize, our results show that the reproductive advantage of longer-living individuals does not always simply originate from their more breeding opportunities, and suggest that these individuals may also have other superior characteristics. The lack of effect of forehead patch size and polygyny on LRS indicates that the reproductive consequences of traits and strategies used in male mate acquisition are far from straightforward. Finally, our findings with polygyny and LRS highlight the need to consider the interrelations of various factors when assessing their importance in influencing LRS.

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Fig. 1 The probability of becoming polygynous in relation to breeding lifespan in male collared flycatchers. Sample sizes are shown

Fig. 2 a) The number of lifetime recruits (mean ± SE) and b) the probability of producing a recruit in relation to breeding lifespan. In Fig. 2a the values of breeding lifespan are shown only up to 4 years for better visibility as only three males lived longer than this. Sample sizes are shown

Fig. 1

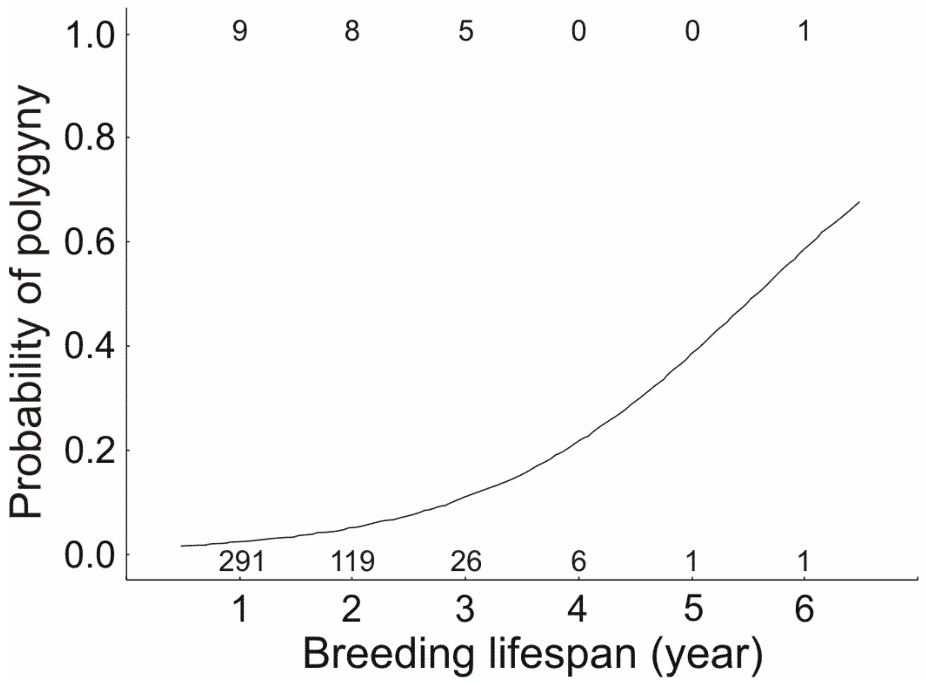
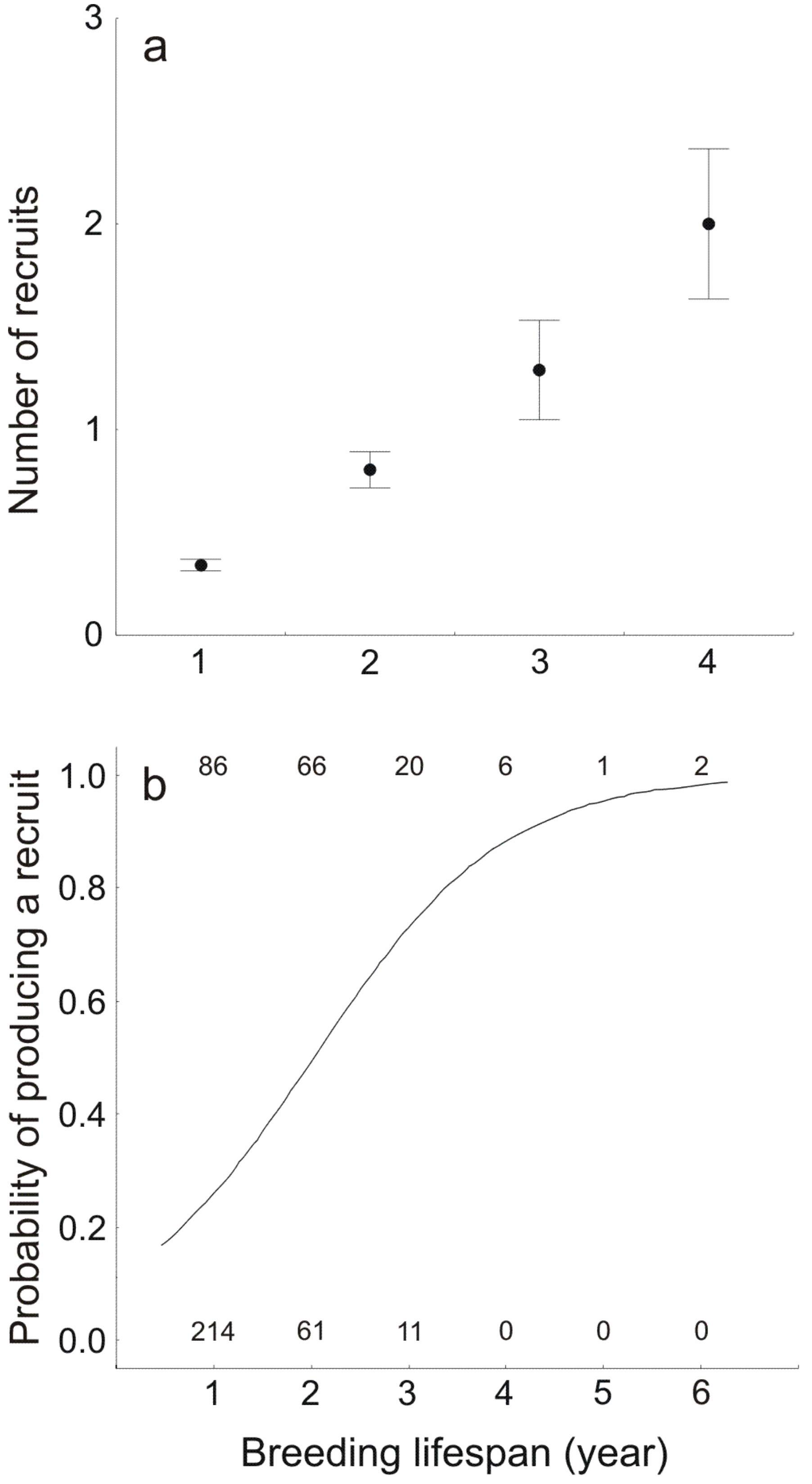

Probability of polygyny
1.0
0.8
0.6
0.4
0.2
0.0
9
8
5
0
0
1
291
119
26
6
1
1
1
2
3
4
5
6
Breeding lifespan (year)

Fig. 2



a
3
2
1
0
Number of recruits
1
2
3
4
b
1.0
0.8
0.6
0.4
0.2
0.0
Probability of producing a recruit
86
66
20
6
1
2
214
61
11
0
0
0
1
2
3
4
5
6
Breeding lifespan (year)

Table 1 Correlates of lifetime reproductive success of male collared flycatchers. Generalized linear models with backward stepwise model selection. The number of degrees of freedom was 1 in all cases. n = 467 (monogamous 444, polygynous 23); CI, 95% confidence interval

	Breeding lifespan model					Mating status model				
	Wald χ^2	P	Effect size (r)	CI lower	CI upper	Wald χ^2	P	Effect size (r)	CI lower	CI upper
Breeding lifespan	94.24	<0.001	0.449	0.374	0.519					
Mating status						6.70	0.01	0.120	0.029	0.208
Forehead patch size	0.97	0.32	0.046	-0.045	0.136	1.24	0.27	0.052	-0.039	0.142
Tarsus length	0.007	0.93	0.004	-0.087	0.095	0.07	0.79	0.012	-0.078	0.103