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SURVIVAL COSTS AND FUTURE REPRODUCTIVE OUTPUT IN THE FACULTATIVELY POLYGYNOUS PIED FLYCATCHER

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**SURVIVAL COSTS AND FUTURE REPRODUCTIVE OUTPUT IN THE
FACULTATIVELY POLYGYNOUS PIED FLYCATCHER**

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Abstract

One of the most debated questions in evolutionary biology is the evolution of polygyny. In facultatively polygynous birds, polygynously-mated females typically incur higher reproductive costs due to reduced male assistance. By contrast, polygynous males should increase their reproductive success by mating with multiple females. However, little is known on whether and how the female and male mating status affects their survival and future reproduction. We performed a multi-state study using 26 years of mark-recapture data of a Spanish pied-flycatcher population in order to test whether the mating status of females and males affected their probabilities of surviving and breeding in the next season. We found that polygynously-mated females (primary, i.e. 1st mate, and secondary, i.e. 2nd mate, females) had lower probability to survive and breed in the next season than monogamous ones. In contrast, polygynous males did not suffer survival costs, but they had a lower probability of breeding in the next year. Also, we found that the probability of breeding two consecutive years in a polygynous state was very low (polygynous male: 0.15; primary female: 0.19, secondary female: 0.24) confirming our modelling approach based on the idea that the mating status is not an inherent, fixed, characteristic of an individual. Furthermore, males >one-year old had a higher probability of being polygynous than younger ones, while females >one-year old were more likely to be monogamous. Overall, our findings confirm that polygyny impose survival costs for females and suggest the possibility of a trade-off between survival and reproduction for males, providing new information within the study of the evolutionary processes related to the polygyny.

INTRODUCTION

Sexual selection is the process by which individuals of the same sex and species compete for access to mates and reproduction opportunities (Darwin 1871). This process determines the evolution of animal mating systems, a main issue in Evolutionary Biology (Emlen and Oring 1977, Simmons and Andersson 2006). Sexual selection can operate through two different mechanisms: competition within a sex for access to mates (intrasexual selection) and mate choice (intersexual selection) (Jones and Ratterman 2009, Sirkiä and Laaksonen 2009).

Classical sexual selection theory predicts that the intensity of sexual selection and the evolution of different mating systems depends on the operational sex ratio, i.e. the ratio of males to females ready to mate in a population (Emlen and Oring 1977). However, modern theory of sexual selection has shown that more complex relationships may exist between sex roles (as choosy sex and competitive sex) and different components of the mating systems (as parental investment and mating costs) (see e.g. Kokko and Johnstone 2002, Shuster and Wade 2003). Moreover, the different reproductive strategies of females and males often generates a conflict between both sexes because, while females tend to allocate more in the offspring, males tend to maximize the number of mates (Bateman 1948, Trivers 1972).

Polygyny, namely when a male pairs with more than a female and the females only mates with a male, is the most common form of polygamy. According to Emlen and Oring (1977), males often invest less in parental care than females, which allows them to spend more time and energy searching for other females to mate, what may lead to the development of polygyny. This mating strategy can be found in a wide variety of taxa (Shuster and Wade 2003). Although social monogamy is the most common mating strategy among birds (Orians 1969, Shuster and Wade 2003), social polygamy is found in a number species (Møller 1986, Huk and Winkel 2006). This mating strategy seems to be beneficial for males, as by mating with several females they may increase their number of offspring (Kempnaers et al. 1995,

Ferretti and Winkler 2009, Walker and Marzluff 2017). In contrast, for females the benefits of mating with polygynous males are unclear because they have to share key resources as the territory or the male parental care with other females, which may entail fitness costs (Emlen and Oring 1977, Searcy and Yasukawa 1989, Saetre et al. 1997). During the last decades, a plethora of studies have focused on the adaptiveness of this strategy for females, and several hypotheses postulated to explain the evolution of polygyny. The Polygyny Threshold Model (PTM), based on female choice and direct benefits, predict that a female will prefer to mate with an already mated male rather than a single mate when the territory of the former can compensate the potential costs of the reduced male assistance (Orians 1969). As an expansion of the PTM, Weatherhead and Robertson (1979) proposed The Sexy Son Hypothesis (SSH), also based on female choice, but referring to indirect fitness. As for the PTM, also according to the SSH, females paired with already-mated males are assumed to experience a cost in their direct fitness. However, this cost would be compensated by their sexy sons, which are supposed to inherit their father's attractiveness and social mating status, having a higher reproductive success.

A number of works have investigated the costs and benefits of polygyny for both males and females, but only a few examples have evaluated their costs on individual survival (Both 2002, Marzolin 2002, Garamszegi et al. 2004a, Huk and Winkel 2006), one of the most important parameters determining individual fitness. The parental investment of birds during the breeding period is strictly related to the mating status (Both 2002). It has been suggested that polygynously-mated females increase their allocation in parental care to compensate the lower assistance from their mate, which distributes its investment among multiple partners (Lundberg and Alatalo 1992, Garamszegi et al. 2004a). Then, the increase in reproductive effort paid by the polygynously-mated female could affect negatively her future survival or reproduction. On the other hand, it is most often assumed that polygynous males do not pay

any cost by mating with multiple females, but this hypothesis has been barely tested (Gustafsson et al. 1995, Saetre et al. 1997). Therefore, survival may be an important parameter to measure the reproductive costs of polygamous species (Both 2002). As an example, Marzolin (2002) studied the survival rate in the Eurasian dipper (*Cinclus cinclus*), a territorial bird who lives along the stream and rivers and whose females choose breeding sites based on their quality. He found that polygynous males had higher survival probability than monogamous ones, probably because they had better territories where they were protected from drought and floods.

The pied flycatcher *Ficedula hypoleuca* is a small insectivorous, migratory, hole-nesting passerine with biparental care. This species is typically monogamous, but some males (3-25%) (Lundberg and Alatalo 1992) after mating with a female (which will be the primary female), occupy another cavity and attract a second female (namely, the secondary female), becoming socially polygynous. Polygamous males often provide less parental care to their secondary brood, which may reduce the reproductive success of such brood (Alatalo et al. 1981). Several works have studied different fitness components in order to explain the evolution and maintenance of polygyny in the pied flycatcher and its sister species. Haartman (1969) reported in a pied flycatcher population that males mated with two females had higher annual reproductive output than monogamous males. By contrast, Herényi et al. (2014) showed in collared flycatchers that polygyny was advantageous for males in years with high food supplies but not in years with low food supplies, when the reproductive success of polygynous and monogamous males was similar. Gustafsson et al. (1995) found in a collared flycatcher population that polygynous males did not pay a survival cost when they increase their effort in order to care the two broods. However, they experimented a reduction of the forehead patch in the following year. While only few studies focused on the consequences of polygyny on males, the consequences on females have been widely studied. In the same pied

flycatcher population object of this study, Canal et al. (2012) found that secondary females did not occupy worse territories than the primary female of their male. Thus, contrary to the PTM rationale, females mated with polygynous males would hardly compensate the cost of mate sharing by obtaining a better territory. Also conflicting with the PTM, Alatalo et al. (1981) found that the number of fledglings of secondary females was lower than that of primary or monogamous females laying in the same date, even when the nest of the secondary female was located in a high quality territory. Huk and Winkel (2006) reported that secondary females of pied flycatchers had fewer young than monogamous and primary ones. However, they did not find a relationship between female survival probability and her mating status. The previous studies showed that pairing with an already mated male have a cost for females, but Garamszegi et al. (2004a) found that the opposite may also occur. Performing a mark-recapture analysis they found that primary and secondary collared flycatcher females had higher survival probability than monogamous ones, despite receiving less parental help from their male.

The aim of this paper was to investigate whether the mating status of females and males affects their probabilities of surviving and breeding in the next season. We used 26 years of breeding data from a Spanish pied flycatcher (*Ficedula hypoleuca*) population and a mark-recapture approach to perform a multi-event study, in which we evaluated the effect of the social mating status, considered as a dynamic characteristic (i.e. potentially changing between years) of individuals, on survival and breeding of males and females. This statistical approach allowed us also to estimate and test hypotheses on the probabilities of changing of mating status. Many empirical studies support the life-history theory (Stearns 1992) evidencing that reproduction is costly for the individuals' future reproductive value (see e.g. Gustafsson et al. 1995, Saetre et al. 1997). Therefore, we expect that secondary, primary and monogamous females would have, in this order, from the lowest to the highest survival and breeding

probabilities. By contrast, we do not expect differences in survival and breeding probability between monogamous and polygynous males as they typically reduce parental care in the secondary brood (Lundberg and Alatalo 1992, Garamszegi et al. 2004a).

METHODS

Study area and study population

We analysed the breeding data from a Spanish pied flycatcher population, collected between 1990-2016 (with no data for 2003), except for the year 2003, as a part of a long-term study of this species in central Spain (ca. 41°N, 3°W, 1200-1300m asl). The study area consists of two plots in two different montane habitats separated by 1.3 km, including 236 nest boxes. One habitat consists of an old deciduous oak (*Quercus pyrenaica*) forest and the other one of a managed mixed coniferous (mainly *Pinus sylvestris*) forest. The nest boxes have remained stable in the same trees since 1988 (pine wood) and 1995 (oak wood) (for details see Camacho et al. 2013 and Potti and Montalvo 1991a).

Fieldwork and data collection

Nest boxes were regularly checked to ascertain exact laying date, clutch size, hatching date and number of fledglings. Bird parents were captured with a nestbox trap while incubating (females) or feeding 8-day-old nestlings (both sexes; for details see Camacho et al. 2017) and marked with a numbered metal ring and a unique combination of colour ring for individual identification. They were measured for tarsus (± 0.01 mm), weighed (± 0.1 g), wing length (± 0.5 mm) and height and width of the forehead patch (± 0.01 mm). A high number of breeding birds (53%) were born in the nest boxes and, therefore, their age was known with precision (Potti and Montalvo 1991b). Unringed birds were aged as first-year or older on the basis of plumage traits following aging criteria described in Karlsson et al. (1986) and Potti and Montalvo (1991a). All nestlings were ringed, measured and weighed at the age of 13 days. Blood samples were taken from all individuals by puncturing the brachial vein and stored in ethanol.

Polygynously-mated males were detected when they were captured and/or individually identified while feeding young in two nest boxes (Canal et al. 2011; Potti and Montalvo 1993). A polygynous male was defined as a male which, after mating, acquire a second female, becoming socially polygamous. Polygynously-mated males were detected when they were captured and/or individually identified while feeding young in two nest boxes (Canal et al. 2011; Potti and Montalvo 1993). We distinguished three different status for females according to their male mating status: (i) monogamous females, i.e. mated with monogamous males; (ii) primary females, i.e. the first female mating with a polygamous male; and (iii) secondary females of a polygynous male, defined as those with later laying dates in relation to the primary female. In a few cases, primary and secondary females had the same laying date, so the brood status was assigned according to the male assistance in each brood, which is typically lower in secondary broods (Alatalo and Lundberg 1984, Lifjeld and Slagsvold 1988, Potti and Montalvo 1993). In some others, it was not possible to assign a female mating status since the identity of male remained unknown.

Multi-Event Capture-Recapture models

We used multi-event Capture-Recapture models (Pradel 2005) to test how the mating status of males and females affects their probabilities of: (i) apparent survival (i.e. of surviving and do not leave the area permanently), (ii) breeding tenacity (i.e. of breeding in $t+1$ if alive during the interval $t \rightarrow t+1$), and (iii) state-transition (i.e. of changing of mating status). These models make a distinction between events, i.e. characteristics of captured individuals that are directly assessed by the observer, and states, i.e. hidden features of the individuals that cannot be directly observed. By using these models, we have been therefore able to investigate the

effects of mating status on demographic parameters although the mating status of some captured individuals was unknown.

Multi-event models are defined by three types of parameters: Initial State probabilities, Transition probabilities and Event probabilities. The Initial state parameter refers to the probability of being in a certain state at the first capture and is calculated from a vector of all the possible states except the dead state (the model assumes that an individual is alive at the moment of being captured). Transition and Event parameters refer, respectively, to the probability of transition between states and of an event given the underlying state. All these probabilities are described by matrices, with departure states in rows and, in columns, arrival states for Transition and events for Event (Appendices S1 and S2 in Supplementary material). In our study, we defined the Transition matrix as the product of two matrices: Survival and State Transition. Similarly, we defined Event as formed by two steps: Capture (or “Breeding Tenacity”, see below) and State Assignment. More in detail, we considered the following parameters:

- Initial State: the probability of being in a specific mating status at the first encounter. In the case of males, it is the probability of being monogamous or polygynous; for females, it is the probability of being monogamous, primary or secondary females.
- Transition:
 - Survival: the probability of surviving and not emigrating permanently from the population of nest boxes between year t and year $t + 1$.
 - State transition: the probability of an alive bird of changing state between year t and $t+1$.
- Event:
 - Capture/Breeding Tenacity: the probability of an alive bird in a certain state of being recaptured at time $t+1$. Note that this parameter depends on two

processes (see Kendall and Nichols 1995): (i) the true probability of recapture, i.e. of an individual alive and present in the area, and (ii) the probability of presence, that in our case is the probability of breeding in a nest box. In populations with individuals exhibiting high fidelity to their breeding sites and close-to-one (true) probability of being recaptured, this parameter can be considered a proxy of the probability of breeding tenacity (Jenouvrier et al. 2003, Lee et al. 2007). Because of the high natal philopatry of individuals in our population (Potti and Montalvo 1991b) and the close-to-one probability of capturing an individual nesting in one of our nest boxes, we interpret this parameter as the probability of breeding tenacity.

- State Assignment: the probability that the mating status of a captured individual is ascertained. We assumed no state misclassification.

We used the encounter histories of all the marked birds ($N_{\text{females}}=1641$; $N_{\text{males}}=1436$) that were detected at least once breeding in the study area between 1990 and 2016. These data were obtained by captures and recaptures of marked individuals and by establishing the biological events according to their mating status (see below). We ran separate analyses for each sex, considering four biological states for females: alive monogamous breeder (MBF), alive primary breeder (PBF), alive secondary breeder (SBF) and dead or permanently emigrated (†); and five events, numbered as they appear in the encounter histories: (0) non-captured, (1) captured as monogamous breeder, (2) captured as primary breeder, (3) captured as secondary breeder and (4) captured of unknown mating status. Females of unknown status (14,3%) were those for which we did not know the identity of the mate after repeated visits at the nest box. These females could be of any mating status and the mate being absent or very sporadically visiting the nest. For males, instead, we considered three biological states: alive monogamous

breeder (MBM), alive polygynous breeder (PBM) and dead or permanently emigrated (†), mediated by four events: (0) non-captured, (1) captured as monogamous, (2) captured as polygynous, (3) captured of unknown mating status. Males of unknown mating status (3,8%) were those for which we could not determine with certainty their mating status. For both sexes, we established two age classes, one consisting of individuals of one-year-old (41.74% females; 26.46% males), and the other one of individuals of more than a year (58.26% females; 73.54% males). This classification allowed us to include in our analyses the breeders that were not born in the population (immigrants), i.e. we did not know their exact age, but we could determine if they were young or adults.

Models were built and fitted to the data using E-SURGE 2.1.2 (Choquet et al. 2009b). As our data were annually collected and we had no data for 2003, in E-SURGE we marked the “Unequal Time Intervals” option to consider a two-year period between time sessions corresponding to that interval (2002-2004).

Goodness of fit

There are no tests to assess the goodness of fit for multi-event models. Therefore, we transformed our data to single state and used the software U-CARE 2.3.2 (Choquet et al. 2009a) to test the goodness of fit of the Cormack-Jolly-Seber model, i.e. a model that accounts uniquely for time variation in survival and capture probabilities. We consider this approach conservative as the CJS model is more restrictive than our models that do allow for different survival and recapture probabilities according to the individuals' mating status. We ran a global test, which evaluates the overall fit of data to the CJS as proceeding by all the components of the test. Of these components, the test 3.SR evaluates if there is a transient effect (i.e. heterogeneity in survival between first and subsequent intervals after marking) and

the test 2.CT assess the presence of trap dependence (i.e. individuals whose recapture probability is affected by being captured or not in the previous session). All the tests were run for males and females separately.

The global tests were non-significant for both males [$\chi^2=72.57$, $df=103$, $p=0.99$; $N(0,1)$ statistic for transient (>0) = -0.49, $p=0.69$; $N(0,1)$ signed statistic for trap-dependence = -0.84, $p=0.99$] and females [$\chi^2=76.13$, $df=122$, $p=0.99$; $N(0,1)$ statistic for transient (>0) = -2.51, $p=0.69$; $N(0,1)$ signed statistic for trap-dependence = -1.22, $p=0.22$]. Transient effect and trap dependence were not found in any of the groups (i.e. one-year old and $>$ one-year old) analysed separately for both males and females. For the complete results of 3.SR and 2CT tests see Appendix S3 in Supplementary material.

Model selection

Model selection was based on Quasi-Akaike Information Criterion corrected for small sample sizes (QAIC_c) (Burnham and Anderson 2002). We retained the structure of models with the lowest QAIC_c. For each sex, in a preliminary and exploratory analysis of data, we built a global model whose complexity (number of parameters) was chosen in such a way that it allowed us to test our pre-defined hypotheses without serious consequences on parameters' identifiability. For females, the global model (is3 in Table 1) included the non additive effect of time and mating status for Initial State, Capture and State Assignment parameters; the non-additive effect of age and mating status for Transition parameter; and age plus the non-additive effect of time and mating status for Survival parameter. The global model of males (is3 in Table 2) only differed of that of females in that it included only the time effect on Initial State parameter. From these models, we tested different effects on Initial State probability, maintaining fixed the effect established in the global model for the other

parameters. We then fixed the structure of Initial State parameter of the model with the lowest QAIC_c value, and continued modeling, in this order, State Assignment, Capture, Transition and Survival parameters following the same criteria.

RESULTS

Model selection and estimations

The steps of the model selection procedure for survival, breeding tenacity and transition probabilities of females and males are provided in tables 1 and 2 respectively. The model selection for the remaining parameters for both sexes are shown in Table S1 and Table S2 in Supplementary material.

Females

For females, the best model (s1 in Table 1) estimated the survival probability depending on their mating status and age in an additive way, considering that females paired with polygynous males (i.e. primary and secondary females) had the same survival probability. This model was more supported than a model that considered the same survival for monogamous and primary females ($\Delta\text{QAIC}_c = 1.87$) and another that considered a different survival for each mating status ($\Delta\text{QAIC}_c = 2.03$). According to the best model, polygynously mated females had a lower survival probability than monogamous females, and this probability was lower for older than for one-year females (1-yr old pol.: 0.55, 95%CI: 0.49-0.60; 1-yr old mon.: 0.63, 95%CI: 0.58-0.68; >1-yr old pol.: 0.47, 95%CI: 0.42-0.51; >1yr old mon.: 0.55, 95%CI: 0.52-0.58).

The breeding tenacity probability (i.e. the time-specific p of an alive individual to breed) was time-varying and different for each mating status. The probability of breeding tenacity of monogamous females was estimated on the upper boundary ($p=1$) for most of the sessions being considerably higher than that of polygynously-mated females (Fig. 1). The higher breeding tenacity of monogamous females with respect to the primary and secondary females was confirmed by an extra model, with the structure of the lowest QAIC_c model except the constant probability of breeding tenacity for monogamous females (0.95, 95%CI: 0.86-0.98).

Our best model considered that the probability of state transition was different depending on the departure state. Females being monogamous at year t were more likely to remain as monogamous at year $t+1$ ($P_{\text{mon} \rightarrow \text{mon}}$: 0.70, 95%CI: 0.67-0.74) than changing of status ($P_{\text{mon} \rightarrow \text{prim}}$: 0.11, 95%CI: 0.06-0.20; $P_{\text{mon} \rightarrow \text{sec}}$: 0.19, 95%CI: 0.12-0.28). However, both primary and secondary females in year t had a higher probability of being monogamous at year $t+1$ than remaining in the same mating status ($P_{\text{prim} \rightarrow \text{prim}}$: 0.19, 95%CI: 0.08-0.39; $P_{\text{prim} \rightarrow \text{mon}}$: 0.71, 95%CI: 0.56-0.82; $P_{\text{prim} \rightarrow \text{sec}}$: 0.10, 95%CI: 0.03-0.31; $P_{\text{sec} \rightarrow \text{sec}}$: 0.24, 95%CI: 0.14-0.36; $P_{\text{sec} \rightarrow \text{mon}}$: 0.69, 95%CI: 0.59-0.77 ; $P_{\text{sec} \rightarrow \text{prim}}$: 0.08, 95%CI: 0.02-0.24). However, a model with age additive effect differed 1.01 units in QAIC_c (t2 in Table 2) from the best model in the selection step for the Transition parameter, suggesting that the probability of remaining in the monogamous state was slightly higher for females older than a year ($P_{\text{mon} \rightarrow \text{mon}}$: 0.70, 95%CI: 0.64-0.74) than for younger ones ($P_{\text{mon} \rightarrow \text{mon}}$: 0.66, 95%CI: 0.59-0.72).

The probability of each mating status at the first capture was affected by the age. In females, the probability of being monogamous at first encounter was higher than that of being primary or secondary. The probability of being monogamous was higher for females older (>1-yr old mon.: 0.82, 95%CI: 0.79-0.85) than for younger ones (1-yr old mon.: 0.75, 95%CI:0.72-0.79). Between polygynously-mated females, the probability of being secondary at the first capture was higher than that of being primary, and one-year females had a higher probability of being secondary than older ones (1-yr old sec.:0.18, 95%CI:0.13-0.23; 1-yr old prim.: 0.07, 95%CI:0.04-0.13; >1-yr old sec.: 0.11, 95%CI: 0.08-0.15; >1-yr old prim.: 0.07, 95%CI: 0.04-0.11).

Males

In the case of males, the best model (s1 in Table 2) considered that survival probability was constant ($p=0.539 \pm SE=0.01$ [95%CI 0.519-0.559]), with no effect of mating status.

However, we cannot discard a slight difference between ages (s_2 in Table 2; $\Delta\text{QAIC}_c=0.99$; 1-yr old: 0.57, 95%CI: 0.51-0.63; >1yr-old: 0.54, 95%CI: 0.51-0.56) and between monogamous and polygynous males (s_3 in Table 2; $\Delta\text{QAIC}_c= 1.98$; mon: 0.54, 95%CI: 0.51-0.56; pol: 0.55, 95%CI: 0.46-0.64).

Mating status and time affected additively the probability of breeding tenacity. Monogamous males were considerably more likely to breed in the next session than polygynous males (Fig. 2).

A male being polygynous at year t had a higher probability of becoming monogamous at year $t+1$ ($P_{\text{pol} \rightarrow \text{mon}}$: 0.85, 95%CI: 0.74-0.92) than remaining in the same mating status ($P_{\text{pol} \rightarrow \text{pol}}$: 0.15, 95%CI: 0.08-0.26). In contrast, a monogamous male at year t was more likely to persist in the same mating status at year $t+1$ ($P_{\text{mon} \rightarrow \text{mon}}$: 0.79, 95%CI: 0.75-0.83) than to change to the polygynous state ($P_{\text{mon} \rightarrow \text{pol}}$: 0.21, 95%CI: 0.17-0.25). The model including age plus mating status effect (t_2 in Table 2) had a similar QAIC_c ($\Delta\text{QAIC}_c=0.23$). Therefore, we cannot discard an age effect ($P_{\text{mon} \rightarrow \text{mon}}$ 1-yr old: 0.84, 95%CI: 0.75-0.90; $P_{\text{mon} \rightarrow \text{mon}}$ >1-yr old: 0.78, 95%CI: 0.73-0.83; $P_{\text{mon} \rightarrow \text{pol}}$ 1-yr old: 0.16, 95%CI: 0.10-0.26; $P_{\text{mon} \rightarrow \text{pol}}$ >1-yr old: 0.22, 95%CI: 0.17-0.27 ; $P_{\text{pol} \rightarrow \text{pol}}$ 1-yr old: 0.22, 95%CI: 0.11-0.39; $P_{\text{pol} \rightarrow \text{pol}}$ >1-yr old: 0.16, 95%CI: 0.09-0.27; $P_{\text{pol} \rightarrow \text{mon}}$ 1-yr old: 0.78, 95%CI: 0.61-0.89; $P_{\text{pol} \rightarrow \text{mon}}$ >1-yr old: 0.84, 95%CI: 0.73-0.91).

Initial state probabilities depended on age. One-year old males had a lower probability of being polygamous when first captured (1-yr old pol.: 0.01, 95%CI: 0.00-0.03) than older males (>1yr old pol.: 0.04, 95%CI: 0.03-0.05), being higher for both age classes the probability of being monogamous than polygamous (1-yr old mon.: 0.99, 95%CI: 0.97-1.00; >1-yr old mon.: 0.96, 95%CI: 0.95-0.97).

DISCUSSION

Consistent with our predictions, primary and secondary females had a lower probability of surviving and breed in the next season than monogamous ones, contrary to what (Garamszegi et al. 2004a) found in a similar mark-recapture analysis with the collared flycatcher. This lower survival may be consequence of the higher breeding investment of primary and secondary females, as male assistance is often reduced, in relation to monogamous broods (Haartman 1951, 1969, Alatalo et al. 1982, 1984). However, contrary to our expectations, we found also a cost for polygynous males which had consistently lower probabilities of breeding in the next season than had monogamous males. Furthermore, the female and male probability of remaining in the polygynous state was low compared to that of monogamous, which supports our idea that the mating status should be treated as a dynamic, and not a fixed, characteristic of the individuals.

In contrast to our results, in other bird populations, females did not experience survival costs in relation to their mating status. Both (2002) found that the survival probability of polygynously mated females did not differ significantly from the survival probability of monogamous females in a Dutch pied flycatcher population. Huk and Winkel (2006) also found no differences between secondary and monogamous females of a German pied flycatcher population. The survival estimates of the two previous studies were based on return rates, which consider that the probability of capturing an individual alive and present in the study is one. To our knowledge, there is only one study taking into account a lower detection probability (imperfection detectability) for testing the relationship between survival probability and mating status (Garamszegi et al. 2004a). In that study, conducted in the sister species, the collared flycatcher, Garamszegi et al. (2004a) found that primary and secondary females had higher survival probability than monogamous females. A possibility to explain the discrepancy between studies is that Garamszegi et al 2004 treated the mating status a fixed

trait and each female was attributed to a different group according to the number of breeding seasons they were observed in a given mating status. They defined as secondary females those observed at least once in that state through all their life, as primary females those observed at least once as primary and never as secondary, and as monogamous females the remaining ones. By doing so, we suspect that they inflated the estimation of the survival probability in the group of the secondary females because the higher the number of times they were captured, the higher was the probability of surviving and the probability of been assigned to the group of secondary females. In our study, given that mating status is not a fixed characteristic of the individual (for more details see below), we used a generalization of the multi-state capture-recapture approach (Lebreton et al. 1992) which allowed us to estimate the survival probabilities related to the mating status as a dynamic state varying at the individual level among different sessions.

We expected to find that secondary females had a lower survival probability than primary females, as secondary females often receive lower male assistance (Lifjeld and Slagsvold 1989) and, subsequently, are supposed to increase their investment to fledge their young (eg. Potti and Montalvo 1993; Saetre et al. 1997). Primary and secondary females had similar survival probabilities. A possible explanation is that, as a consequence of the reduced male assistance, they had to compensate it with a similar expenditure, as the energy females can invest is constrained (Moreno et al. 1999). The consequences of the lack of male assistance in nests of secondary females has been shown to affect fledgling survival as it has been shown, for example, in secondary broods by Huk and Winkel (2006). However, we cannot discard slight differences in survival of primary (1-yr old prim: 0.56, 95%CI 0.45-0.66; >1-yr old prim: 0.48, 95%CI 0.38-0.57) and secondary females (1-yr old sec: 0.54, 95% 0.47-0.61; >1 yr-old sec: 0.46, 95%CI 0.39-0.53), as suggested by a model accounting for different survival for each mating status and similar QAICC value (s_3 in Table 1; $\Delta QAICC=2.03$) than our best

females' model. This would be consistent with the hypothesis that the females pay a cost for the lack of male assistance, given that primary females typically are assisted more than secondary females (Haartman 1951, 1969, Alatalo et al. 1982, 1984).

Apparently, polygynous males did not experience survival costs, as they showed similar survival probability than monogamous males. Possibly, this is due to the frequently low feeding assistance provided by polygynous males in the secondary brood (Lundberg and Alatalo 1992). Although we did not find survival costs in males related to their mating status, we found that polygynous males had a lower probability of breeding locally in the following year. We suggest that the possibility of skipping breeding is related to the effort that adult birds invest while breeding. The effort invested by males involves searching for a place to nest, attracting a female and mating with her and providing care and food to the offspring and to the female. This investment is higher for polygynous than for monogamous males because the former have to occupy two (or more) territories, defend them from other males and to feed both primary and secondary females and their broods. In addition, polygynous males may also increase their costs when they are travelling between the primary and secondary nest, although in our study population distances among nest boxes of primary and secondary females of the same polygynous male are not large (Potti and Montalvo 1993). Another explanation could be that males being polygynous a year, arrive late in the season in the following year, decreasing their probability of breeding, as there are fewer females available to mate (Canal et al. 2012). Gustafsson et al. (1995) also showed some indirect cost of polygynous males of a Swedish population of collared flycatchers. They found that polygynous males experienced a reduction in their forehead patch in the next year of being polygynous, which makes them less attractive to females. We think that our results can be in line to what they found. If polygynous males become less attractive in the following year of

being polygynous, their probability to find a mate will be lower, and thus, they will have a lower probability of breeding.

Like the males, also the polygynously-mated females showed a lower probability of breeding tenacity than monogamous, a difference more remarkable for the secondary females. We think that this result can be explained by worsening physical conditions, consequence of the high investment in the breeding season when they were primary or secondary females.

Females need to invest a high amount of energy to produce gametes and eggs (Monaghan and Nager 1997), thus, when they are in poor quality, it may be hard for them to breed. Several experimental works have found that the future reproductive success can be altered by increasing effort in different reproductive stages. For example, Bowers et al. (2012) remove some eggs from nests of a house wren population, forcing females to produce more eggs. They found that females investing a higher effort producing extra eggs, were less likely to breed again in the same breeding season. Hanssen et al. (2005) manipulated the incubation demand of common eiders and found that females investing higher in incubation reduced their clutch size and started later to nest in the following year. Milonoff et al. (2004) studied the costs of brood rearing of the common goldeneye, a species with uniparental female care. They found that brood rearing females also reduced their future reproductive output, in the way that their clutch size decreased and they started egg laying later, compared to females that had not rear a brood in the previous year.

Our estimates of the transition probabilities between-mating status may seem an obvious consequence of the frequency of each mating status in the pied flycatchers populations (Lundberg and Alatalo 1992). However, according to the Sexy Son Hypothesis (Weatherhead and Robertson 1979), secondary females compensate the cost of mating to a polygynous male with their sexy and polygynous sons. This involves that there would be a genetic component underlying the individual mating status, namely that birds are genetically predisposed to be of

a certain mating status. If the mating status were genetically determined, we would expect to find that a polygynous male had 100% probability of being polygynous the following years, and the same for the other mating status. However, we found that the probability of remaining in the same mating status in successive years, was lower than 100% for every mating status, especially for the polygynous states. This result confirms our expectation that mating status is not a fixed trait of the individuals, but a characteristic that can change through their life. Our findings are coherent with other studies that have shown very weak heritability of the mating status in polygynous species. For example, Gustafsson and Qvarnström (2006) found that the sons of polygynously mated females of collared flycatchers did not inherit their father attractiveness or their mating status.

We found that males older than a year were more likely to be polygynous than younger ones. This may be due to the fact that older males are experienced, and arrive earlier in the season (Alatalo et al. 1984, Askenmo 1984, Potti and Montalvo 1991a, 1993). These males have a high probability of finding better places to nest, and of occupying two nest boxes in order to attract two females and become polygynous (Haartman 1951, Potti and Montalvo 1991a). In addition, one-year-old males are less likely to reproduce than older individuals (manuscript in preparation). However, females older than a year were more likely to be monogamous than younger ones. The explanation is similar to that of males. Inexperienced and younger females arrive later in the season, when the best quality males are already paired. Although there are unmated males, some females prefer to pair with an already mated male (Alatalo et al. 1981), becoming secondary females. Our analyses have been performed using two age classes in order to not exclude immigrant adults and to maximize the sample size. We cannot discard that the age may affect in a more intricate way the probability of being polygynous, as well as the interplay between mating status and survival and breeding tenacity (see for e.g. Péron et al. 2010). Future studies are needed to clarify this specific aspect.

Arrival time and, consequently, laying date are related to breeding success in flycatchers (Lundberg and Alatalo 1992, Garamszegi et al. 2004b) and to female social mating status (see Fig. S1 in Supplementary material). Thus, laying date may exert a confounding effect on survival probability of individuals of different mating status. In order to take this effect into account, we should have considered laying date as a time-varying individual covariate. However, this kind of effects are not handled by frequentist capture-recapture models because of missing data for each non-detection events of the marked individuals (Gimenez et al. 2006). An alternative could have been to calculate the average of laying date values for each individual and testing its effect on survival. However, we discarded this option because both arrival time and mating status are dynamic, not fixed, characteristics of the individuals (Potti 1998, Moreno et al. 2002). Nevertheless, we feel confident that our findings do suggest a survival cost of female depending on their mating status, regardless of any associated effect of laying date on this parameter. A strong support in this direction comes from the observation that primary and secondary females share a similar cost in survival (see model s1 [f(1,2,3)] vs. model s2 [(f(1,2,3))] in Table 1) even though primary females typically breed early in the season whereas secondary females do it late (Fig. S1).

To conclude, our results show that polygyny has strong effects on the future survival and reproduction of females. This result is important because it confirms theoretical expectations that received little support by empirical studies. Moreover, and surprisingly, we found evidences for costs of polygyny also for the males, that suffered lower breeding tenacity after a polygynous event. This result strives with the classical assumption that polygyny is beneficial for males (Alatalo et al. 1981); however, it is consistent with life-history theory predicting a trade-off between survival and reproduction (Stearns 1989) and with previous findings suggesting that male attractiveness decreases after a polygynous event (Gustafsson et

al. 1995). With this work we provide new information and open new questions within the study of the evolutionary processes related to the polygyny.

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LITERATURE CITED

- Alatalo, B. Y. R. V., A. Lundberg, and K. Stahlbrandt. 1982. Why do pied flycatcher females mate with already-mated males? *Animal Behaviour* 30:585–593.
- Alatalo, R. V., A. Carlson, A. Lundberg, and S. Ulfstrand. 1981. The conflict between male polygamy and female monogamy: the case of the pied flycatcher *Ficedula hypoleuca*. *The American Naturalist* 117:738–753.
- Alatalo, R. V., and A. Lundberg. 1984. Polyterritorial polygyny in the pied flycatcher *Ficedula hypoleuca*: evidence for the deception hypothesis. *Annales Zoologici Fennici* 21:217–228.

- Alatalo, R. V., A. Lundberg, and K. Ståshlbrandt. 1984. Female mate choice in the pied flycatcher *Ficedula hypoleuca*. *Behavioral Ecology and Sociobiology* 14:253–261.
- Askenmo, C. E. H. 1984. Polygyny and nest site selection in the pied flycatcher. *Animal Behaviour* 32:972–980.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- Both, C. 2002. Fitness costs of polygyny in female pied flycatchers *Ficedula hypoleuca*. *Ardea* 90:129–138.
- Bowers, E. K., S. K. Sakaluk, and C. F. Thompson. 2012. Experimentally increased egg production constrains future reproduction of female house wrens. *Animal Behaviour* 83:495–500.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Page (Springer, Ed.) *Ecological Modelling*. Second. New York.
- Camacho, C., D. Canal, and J. Potti. 2013. Nonrandom dispersal drives phenotypic divergence within a bird population. *Ecology and Evolution* 3:4841–4848.
- Camacho, C., D. Canal, and J. Potti. 2017. Lifelong effects of trapping experience lead to age-biased sampling : lessons from a wild bird population. *Animal Behaviour* 130:133–139.
- Canal, D., R. Jovani, and J. Potti. 2012. Multiple mating opportunities boost protandry in a pied flycatcher population. *Behavioral Ecology and Sociobiology* 66:67–76.
- Canal, D., J. Potti, and J. A. Dávila. 2011. Male phenotype predicts extra-pair paternity in pied flycatchers. *Behaviour* 148:691–712.
- Choquet, R., J. D. Lebreton, O. Gimenez, A. M. Reboulet, and R. Pradel. 2009a. U-CARE:

- Utilities for performing goodness of fit tests and manipulating CAPture-REcapture data. *Ecography* 32:1071–1074.
- Choquet, R., L. Rouan, and R. Pradel. 2009b. Program E-SURGE: A Software Application for Fitting Multievent Models. Pages 845–865 in D. Thomson, E. G. Cooch, and M. J. Conroy, editors. *Modeling Demographic Processes in Marked Populations*. Springer Science+Business Media.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science* 197:215–223.
- Ferretti, V., and D. W. Winkler. 2009. Polygyny in the tree swallow *Tachycineta bicolor*: a result of the cost of searching for an unmated male. *Journal of Avian Biology* 40:289–295.
- Garamszegi, L. Z., J. Török, G. Michl, and A. P. Møller. 2004a. Female survival, lifetime reproductive success and mating status in a passerine bird. *Oecologia* 138:48–56.
- Garamszegi, L. Z., J. Török, L. Tóth, and G. Michl. 2004b. Effect of timing and female quality on clutch size in the Collared Flycatcher *Ficedula albicollis*. *Bird Study* 51:270–277.
- Gimenez, O., R. Covas, C. R. Brown, M. D. Anderson, M. B. Brown, and T. Lenormand. 2006. Nonparametric estimation of natural selection on a quantitative trait using mark recapture data. *Evolution* 60:460–466.
- Gustafsson, L., and A. Qvarnström. 2006. A test of the “sexy son” hypothesis: sons of

- polygynous collared flycatchers do not inherit their fathers' mating status. *American Naturalist* 167:297–302.
- Gustafsson, L., A. Qvarnström, and B. C. Sheldon. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature* 375:311–313.
- Haartman, L. von. 1951. Successive Polygamy. *Behaviour* 3:256–273.
- Haartman, L. von. 1969. Nest-site and Evolution of Polygamy in European Passerine Birds. *Ornis Fennica* 46:1–7.
- Hanssen, S. A., D. Hasselquist, I. Folstad, and K. E. Erikstad. 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society B: Biological Sciences* 272:1039–1046.
- Herényi, M., L. Z. Garamszegi, R. Hargitai, G. Hegyi, B. Rosivall, E. Szölloosi, and J. Török. 2014. Laying date and polygyny as determinants of annual reproductive success in male collared flycatchers (*Ficedula albicollis*): A long-term study. *Naturwissenschaften* 101:305–312.
- Huk, T., and W. Winkel. 2006. Polygyny and its fitness consequences for primary and secondary female pied flycatchers. *Proceedings of the Royal Society B: Biological Sciences* 273:1681–1688.
- Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2003. Effects of climate variability on the temporal population dynamics of southern fulmars. *Journal of Animal Ecology* 72:576–587.
- Jones, A. G., and N. L. Ratterman. 2009. Mate choice and sexual selection: What have we learned since Darwin? *Proceedings of the National Academy of Sciences* 106:100001–

10008.

Karlsson, L., K. Persson, and G. Walinder. 1986. Ageing and sexing in pied flycatcher *Ficedula hypoleuca*. *Var Fagelvärld* 45:131–146.

Kempnaers, B., G. R. Verheyen, and A. A. Dhondt. 1995. Mate guarding and copulation behaviour in monogamous and polygynous blue tits: do males follow a best-of-a-bad-job strategy? *Behavioral Ecology and Sociobiology* 36:33–42.

Kendall, W. L., and J. D. Nichols. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22:751–762.

Kokko, H., and R. A. Johnstone. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical Transactions of the Royal Society B: Biological Sciences* 357:319–330.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modelling Survival and Testing Biological Hypotheses Using Marked Animals: a Unified Approach with Case Studies. *Ecological Monographs* 62:67–118.

Lee, D. E., N. Nur, and W. J. Sydeman. 2007. Climate and demography of the planktivorous Cassin's auklet *Ptychoramphus aleuticus* off northern California: Implications for population change. *Journal of Animal Ecology* 76:337–347.

Lifjeld, J. T., and T. Slagsvold. 1988. Female pied flycatchers *Ficedula hypoleuca* habitats in homogeneous choose male characteristics. *Behavioral Ecology* 22:27–36.

Lifjeld, J. T., and T. Slagsvold. 1989. Allocation of parental investment by polygynous Pied

- Flycatcher males. *Ornis Fennica* 66:3–14.
- Lundberg, A., and R. V. Alatalo. 1992. The pied flycatcher. Poyser.
- Marzolin, G. 2002. Influence of the Mating System of the Eurasian Dipper on Sex-Specific Local Survival Rates. *Journal of Wildlife Management* 66:1023–1030.
- Milonoff, M., H. Pöysä, P. Runko, and V. Ruusila. 2004. Brood Rearing Costs Affect Future Reproduction in the Precocial Common Goldeneye *Bucephala clangula*. *Journal of Avian Biology* 35:344–351.
- Møller, A. P. 1986. Mating systems among European passerines : A review. *Ibis* 128:234–250.
- Monaghan, P., and R. G. Nager. 1997. Why don't birds lay more eggs? *Trends in Ecology and Evolution* 12:270–274.
- Moreno, J., S. Merino, J. Potti, A. de León, and R. Rodríguez. 1999. Maternal energy expenditure does not change with flight costs or food availability in the pied flycatcher (*Ficedula hypoleuca*): costs and benefits for nestlings. *Behavioral Ecology and Sociobiology* 46:244–251.
- Moreno, J., J. P. Veiga, M. Romasanta, and S. Sanchez. 2002. Effects of maternal quality and mating status on female reproductive success in the polygynous spotless starling. *Animal Behaviour* 64:197–206.
- Orians, G. H. 1969. On the Evolution of Mating Systems in Birds and Mammals. *The American Naturalist* 103:589–603.
- Péron, G., O. Gimenez, a. Charmantier, J.-M. Gaillard, and P.-A. Crochet. 2010. Age at the onset of senescence in birds and mammals is predicted by early-life performance.

- Proceedings. Biological sciences / The Royal Society 277:2849–2856.
- Potti, J. 1998. Arrival time from spring migration in male pied flycatchers: individual consistency and familial resemblance. *The Condor* 100:702–708.
- Potti, J., and S. Montalvo. 1991a. Male arrival and female mate choice in pied flycatchers (*Ficedula hypoleuca*) in central Spain. *Ornis Scandinavica* 22:45–54.
- Potti, J., and S. Montalvo. 1991b. Return rate age at first breeding and natal dispersal of pied flycatchers *Ficedula hypoleuca* in central Spain. *ARDEA* 79:419–428.
- Potti, J., and S. Montalvo. 1993. Polygyny in Spanish pied flycatchers *Ficedula hypoleuca*. *Bird Study* 40:31–37.
- Pradel, R. 2005. Multievent : An Extension of Multistate Capture- Recapture Models to Uncertain States. *Biometrics* 61:442–447.
- Saetre, G.-P., T. Slagsvold, A. Kruszewicz, and H. Viljugrein. 1997. Paternal care in pied flycatchers *Ficedula hypoleuca*: energy expenditure in relation to plumage colour and mating status. *Ardea* 85:233–242.
- Searcy, W. A., and K. Yasukawa. 1989. Alternative Models of Territorial Polygyny in Birds. *The American Naturalist* 134:323–343.
- Shuster, S. M., and M. J. Wade. 2003. *Mating Systems and Strategies*. Princeton University Press.
- Simmons, L. W., and M. Andersson. 2006. Sexual selection and mate choice. *TRENDS in Ecology and Evolution* 21:296–302.
- Sirkiä, P. M., and T. Laaksonen. 2009. Distinguishing between male and territory quality: females choose multiple traits in the pied flycatcher. *Animal Behaviour* 78:1051–1060.

- Stearns, S. 1992. The evolution of life histories. Oxford University Press, Oxford.
- Stearns, S. C. 1989. Trade-Offs in Life-History Evolution. *Functional Ecology* 3:259–268.
- Trivers, R. 1972. Parental investment and sexual selection. Pages 52–97 *in* B. Campbell, editor. *Sexual Selection and the Descent of Man*. Aldine, Chicago.
- Walker, L. E., and J. M. Marzluff. 2017. Simultaneous polygyny by a male Black-capped Vireo (*Vireo atricapilla*) in central Texas. *The Wilson Journal of Ornithology* 129:212–215.
- Weatherhead, P. J., and R. J. Robertson. 1979. Offspring quality and the polygyny threshold: “the sexy son hypothesis.” *The American Naturalist* 113:201–208.

TABLE 1. Model selection for Breeding Tenacity/Capture, Transition and Survival probabilities of pied flycatcher females. For each model, we give deviance, number of estimable parameters (np), Quasi-Akaike Information Criterion corrected for small sample sizes ($QAIC_c$) and the difference in $QAIC_c$ between the current model and best model with the lowest $QAIC_c$ of the current parameter (ΔAIC_c).

Model notation: IS, Initial State; S, Survival, T, Transition, BT(C), Breeding tenacity/capture; SA, State Assignment; ms , mating status; t , time; i , constant. In s1 and s5 models, $ms(1, 2, 3)$ refers to a same survival probability for primary (2) and secondary (3) females, different from monogamous (1) females. In models s2 and s7, $ms(1, 2, 3)$ refers to a same survival probability for monogamous (1) and primary females (2), different from secondary (3) females.

No.	IS	S	Model			np	Deviance	QAIC _c	ΔAIC _c
			T	BT (C)	SA				
Model selection for Breeding Tenacity (Capture)									
c1	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms + t</i>	<i>ms + t</i>	147	8742.8698	9051.6547	0.0000
c2	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms</i>	<i>ms + t</i>	123	8818.9327	9075.2138	23.5591
c3	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>i</i>	<i>ms + t</i>	121	8841.7693	9093.7134	42.0587
c4	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>t</i>	<i>ms + t</i>	145	8801.1024	9105.4793	53.8246
Model selection for Transition									
t1	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	141	8749.7212	9045.3001	0.0000
t2	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age + ms</i>	<i>ms + t</i>	<i>ms + t</i>	142	8748.5367	9046.3128	1.0127
t3	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>i</i>	<i>ms + t</i>	<i>ms + t</i>	136	8954.7828	9239.3975	194.0974
t4	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age</i>	<i>ms + t</i>	<i>ms + t</i>	137	8953.4311	9240.2357	194.9356
Model selection for Survival									
s1	<i>age x ms</i>	<i>age + ms (1,2,3)</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	68	8860.3015	8999.4068	0.0000
s2	<i>age x ms</i>	<i>age + ms (1,2,3)</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	68	8862.1730	9001.2783	1.8715
s3	<i>age x ms</i>	<i>age + ms</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	69	8860.2413	9001.4389	2.0321
s4	<i>age x ms</i>	<i>age</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	67	8869.0880	9006.1022	6.6954
s5	<i>age x ms</i>	<i>ms (1, 2,3)</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	67	8870.9768	9007.9911	8.5843
s6	<i>age x ms</i>	<i>ms</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	68	8870.9751	9010.0803	10.6735
s7	<i>age x ms</i>	<i>ms (1,2,3)</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	67	8873.1271	9010.1413	10.7345
s8	<i>age x ms</i>	<i>i</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	66	8878.2240	9013.1486	13.7418
s9	<i>age x ms</i>	<i>age + ms + t</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	93	8833.5139	9025.3477	25.9409
s10	<i>age x ms</i>	<i>age + t</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	91	8839.6121	9027.1953	27.7885
s11	<i>age x ms</i>	<i>ms x t</i>	<i>ms</i>	<i>ms + t</i>	<i>ms + t</i>	140	8760.7823	9054.1654	54.7586

TABLE 2. Model selection for Breeding tenacity/capture, Transition and Survival probabilities of pied flycatcher males. For each model, we give deviance, number of estimable parameters (np), Quasi-Akaike Information Criterion corrected for small sample sizes (QAIC_c) and the difference in QAIC_c between the current model and best model with the lowest QAIC_c of the current parameter (Δ AIC_c).

No.	Model					np	Deviance	QAIC _c	Δ AIC _c
	IS	S	T	BT (C)	SA				
Model selection for Breeding Tenacity (Capture)									
c1	<i>age</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms + t</i>	<i>t</i>	109	5580.6774	5808.3234	0.0000
c2	<i>age</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>t</i>	<i>t</i>	108	5605.7456	5831.2125	22.8891
c3	<i>age</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms</i>	<i>t</i>	85	5657.6429	5833.4676	25.1442
c4	<i>age</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>i</i>	<i>t</i>	84	5700.6800	5874.3669	66.0435
Model selection for Transition									
t1	<i>age</i>	<i>age + [ms x t]</i>	<i>ms</i>	<i>ms + t</i>	<i>t</i>	107	5582.8144	5806.1038	0.0000
t2	<i>age</i>	<i>age + [ms x t]</i>	<i>age + ms</i>	<i>ms + t</i>	<i>t</i>	108	5580.8695	5806.3364	0.2326
t3	<i>age</i>	<i>age + [ms x t]</i>	<i>age</i>	<i>ms + t</i>	<i>t</i>	107	5649.6348	5872.9242	66.8204
t4	<i>age</i>	<i>age + [ms x t]</i>	<i>i</i>	<i>ms + t</i>	<i>t</i>	106	5652.3045	5873.4182	67.3144
Model selection for Survival									
s1	<i>age</i>	<i>i</i>	<i>ms</i>	<i>ms + t</i>	<i>t</i>	57	5641.3286	5757.9338	0.0000
s2	<i>age</i>	<i>age</i>	<i>ms</i>	<i>ms + t</i>	<i>t</i>	58	5640.2254	5758.9231	0.9893
s3	<i>age</i>	<i>ms</i>	<i>ms</i>	<i>ms + t</i>	<i>t</i>	58	5641.2203	5759.9180	1.9842
s4	<i>age</i>	<i>t</i>	<i>ms</i>	<i>ms + t</i>	<i>t</i>	81	5600.5897	5767.8737	9.9399
s5	<i>age</i>	<i>ms + t</i>	<i>ms</i>	<i>ms + t</i>	<i>t</i>	82	5600.5828	5769.9995	12.0657
s6	<i>age</i>	<i>ms x t</i>	<i>ms</i>	<i>ms + t</i>	<i>t</i>	105	5583.7606	5802.7004	44.7666

Model notation: IS, Initial State; S, Survival, T, Transition, BT(C), Breeding tenacity/capture; SA, State Assignment; *ms*, mating status; *t*, time; *i*, constant.

LEGENDS TO THE FIGURES

FIGURE 1. Ninety-five confidence interval estimates of annual breeding tenacity, i.e. the probability of breeding in the following year, of pied flycatchers females according to their mating status during the previous breeding season (monogamous, primary and secondary). Estimates for monogamous are at the boundary ($p=1$, except in 2002), which motivates why confidence intervals are not estimated. MON= monogamous, PRIM= primary, SEC= secondary.

FIGURE 2. Ninety-five confidence interval estimates of annual breeding tenacity, i.e. the probability of breeding in the following year, of pied flycatcher males according to their mating status during the previous breeding season (monogamous and polygynous). MON= monogamous, POL= polygynous.

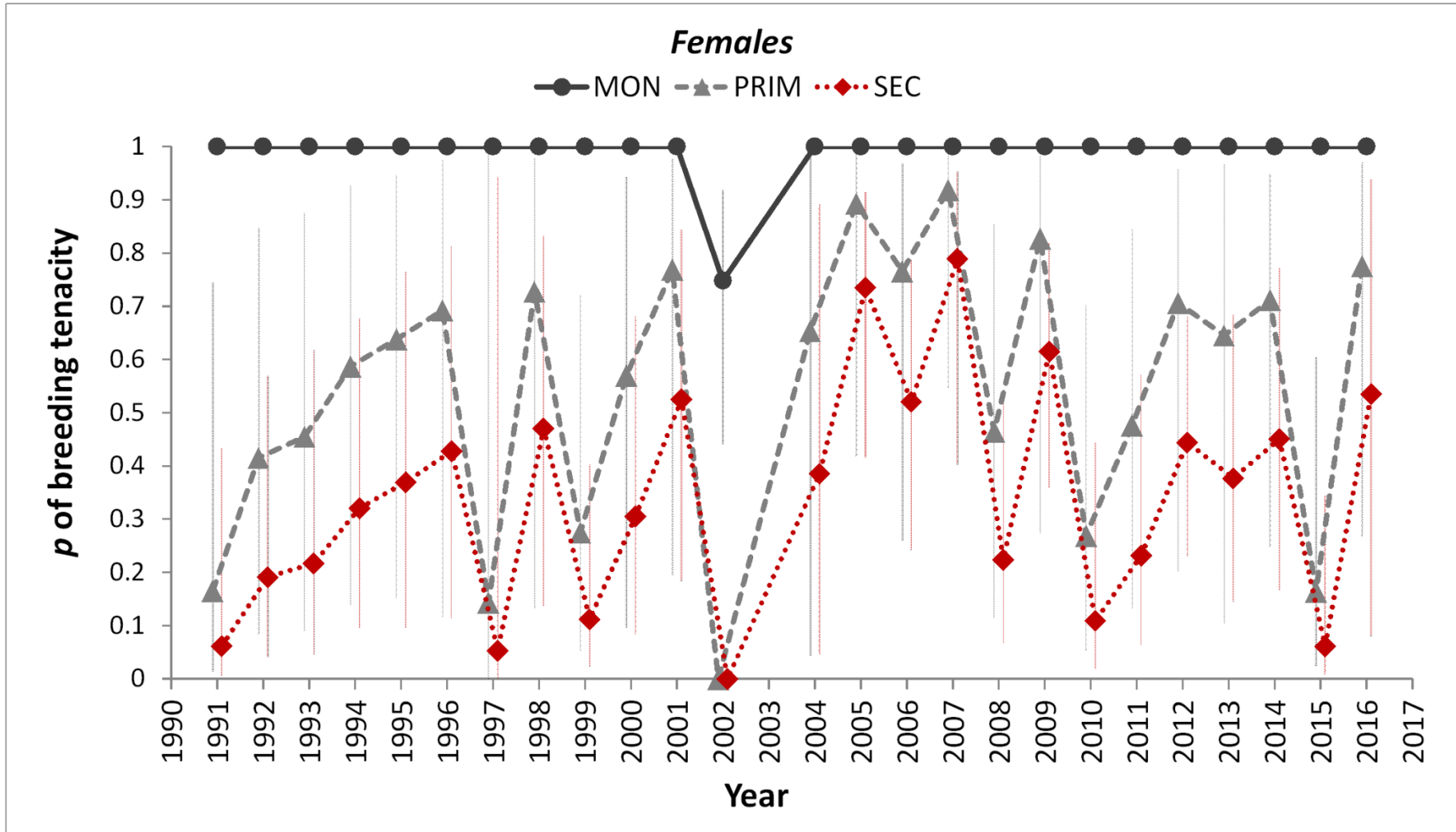


FIGURE 1

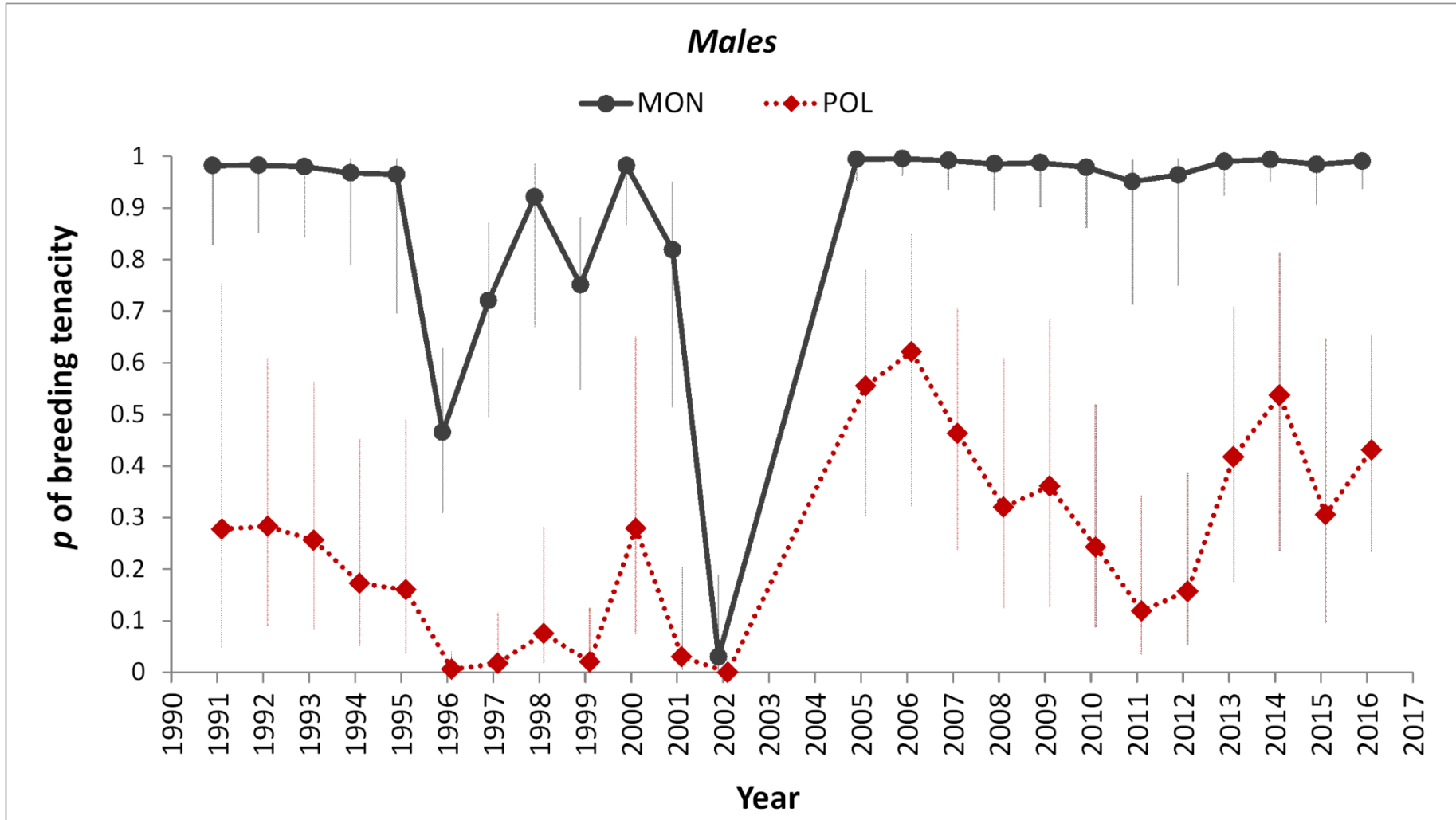


FIGURE 2

SUPPLEMENTARY MATERIAL

APPENDIX S1. Initial State vector and Survival (matrix 1), Transition (matrix 2), Capture/Breeding tenacity (matrix 3) and State assignment (matrix 4) matrices for females. MBF= Monogamous breeder female, PBF= Primary Breeder Female, SBF= Secondary Breeder Female, †= Dead. Events: (0) non-captured, (1) captured as monogamous breeder, (2) captured as primary breeder, (3) captured as secondary breeder and (4) captured of unknown mating status.

$$\text{Initial State} = \begin{pmatrix} \text{MBF} & \text{PBF} & \text{SBF} \\ \pi & \pi & 1-\pi \end{pmatrix} \quad (\text{vector 1a})$$

$$\text{Survival} = \begin{matrix} & \text{MBF} & \text{PBF} & \text{SBF} & \dagger \\ \text{MBF} & \left(\begin{array}{c} \phi \\ 0 \\ 0 \\ 0 \end{array} \right. & \begin{array}{c} 0 \\ \phi \\ 0 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ \phi \\ 0 \end{array} & \begin{array}{c} 1-\phi \\ 1-\phi \\ 1-\phi \\ 1 \end{array} \\ \text{PBF} & & & & \\ \text{SBF} & & & & \\ \dagger & & & & \end{matrix} \quad (\text{matrix 1a})$$

$$\text{State Transition} = \begin{matrix} & \text{MBF} & \text{PBF} & \text{SBF} & \dagger \\ \text{MBF} & \left(\begin{array}{c} 1-\psi \\ \psi \\ \psi \\ 0 \end{array} \right. & \begin{array}{c} \psi \\ 1-\psi \\ \psi \\ 0 \end{array} & \begin{array}{c} \psi \\ \psi \\ 1-\psi \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0 \\ 1 \end{array} \\ \text{PBF} & & & & \\ \text{SBF} & & & & \\ \dagger & & & & \end{matrix} \quad (\text{matrix 2a})$$

$$\text{Capture/ Breeding tenacity} = \begin{matrix} & 0 & \text{MBF} & \text{PBF} & \text{SBF} \\ \text{MBF} & \left(\begin{array}{c} 1-\delta \\ 1-\delta \\ 1-\delta \\ 1 \end{array} \right. & \begin{array}{c} \delta \\ 0 \\ 0 \\ 0 \end{array} & \begin{array}{c} 0 \\ \delta \\ 0 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ \delta \\ 0 \end{array} \\ \text{PBF} & & & & \\ \text{SBF} & & & & \\ \dagger & & & & \end{matrix} \quad (\text{matrix 3a})$$

$$\text{State Assignment} = \begin{matrix} & 0 & 1 & 2 & 3 & 4 \\ \text{0} & \left(\begin{array}{c} 1 \\ 0 \\ 0 \\ 0 \end{array} \right. & \begin{array}{c} 0 \\ \gamma \\ 0 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ \gamma \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0 \\ \gamma \end{array} & \begin{array}{c} 0 \\ 1-\gamma \\ 1-\gamma \\ 1-\gamma \end{array} \\ \text{MBF} & & & & & \\ \text{PBF} & & & & & \\ \text{SBF} & & & & & \end{matrix} \quad (\text{matrix 4a})$$

APPENDIX S2. Initial State vector and Survival (matrix 1), Transition (matrix 2), Capture/Breeding tenacity (matrix 3) and State assignment (matrix 4) matrices for males. MBM= Monogamous breeder male, PBM= Polygamous breeder male, †= Dead. Events: (0) non-captured, (1) captured as monogamous, (2) captured as polygynous, (3) captured of unknown mating status.

$$\text{Initial State} = \begin{pmatrix} \text{MBM} & \text{PBM} \\ \pi & 1-\pi \end{pmatrix} \quad (\text{vector 1b})$$

$$\text{Survival} = \begin{matrix} & \text{MBM} & \text{PBM} & \dagger \\ \text{MBM} & \phi & 0 & 1-\phi \\ \text{PBM} & 0 & \phi & 1-\phi \\ \dagger & 0 & 0 & 1 \end{matrix} \quad (\text{matrix 1b})$$

$$\text{State Transition} = \begin{matrix} & \text{MBM} & \text{PBM} & \dagger \\ \text{MBM} & 1-\psi & \psi & 0 \\ \text{PBM} & \psi & 1-\psi & 0 \\ \dagger & 0 & 0 & 1 \end{matrix} \quad (\text{matrix 2b})$$

$$\text{Capture/Breeding tenacity} = \begin{matrix} & \text{0} & \text{MBM} & \text{PBM} \\ \text{MBM} & 1-\delta & \delta & 0 \\ \text{PBM} & 1-\delta & 0 & \delta \\ \dagger & 1 & 0 & 0 \end{matrix} \quad (\text{matrix 3b})$$

$$\text{State Assignment} = \begin{matrix} & \text{0} & \text{1} & \text{2} & \text{3} \\ \text{0} & 1 & 0 & 0 & 0 \\ \text{MBM} & 0 & \gamma & 0 & 1-\gamma \\ \text{PBM} & 0 & 0 & \gamma & 1-\gamma \end{matrix} \quad (\text{matrix 4b})$$

APPENDIX S3. Goodness-of-fit results

Females

Global TEST, number of groups =2 (Captured as one-year old birds, captured as older than a year birds)

df =122

Quadratic Chi2 =76.1319

->P-level=0.99963

N(0,1) statistic for transient(>0) =-2.5057

->P-level, two-sided test =0.012219

->P-level, one-sided test for transience =0.99389

N(0,1) signed statistic for trap-dependence =-1.2242

->P-level, two-sided test =0.22087

TEST3.SR, group 1 = Captured as one-year old birds

N(0,1) statistic for transient(>0) =-1.4698

P-level, two-sided test =0.1416

P-level, one-sided test for transience =0.9292

TEST3.SR, group 2 = captured as older than a year birds

N(0,1) statistic for transient(>0) =-2.0738

P-level, two-sided test =0.038096

P-level, one-sided test for transience =0.98095

TEST2.CT, group 1 = Captured as one-year old birds

N(0,1) signed statistic for trap-dependence =-0.67792

trap-happiness<0 trap-shyness>0

P-level, two-sided test =0.49782

TEST2.CT, group 2 = captured as older than a year birds

N(0,1) signed statistic for trap-dependence =-1.0719

trap-happiness<0 trap-shyness>0

P-level, two-sided test =0.28377

Males

Global TEST, number of groups =2 (Captured as one-year old birds, captured as older than a year birds)

df =103

Quadratic Chi2 =72.5682

->P-level=0.99002

N(0,1) statistic for transient(>0) =-0.48922

->P-level, two-sided test =0.62469

->P-level, one-sided test for transience =0.68766

N(0,1) signed statistic for trap-dependence =-0.84183

->P-level, two-sided test =0.39988

TEST3.SR, group 1 = Captured as one-year old birds

N(0,1) statistic for transient(>0) =-0.3316

P-level, two-sided test =0.74019

P-level, one-sided test for transience =0.62991

TEST3.SR, group 2 = captured as older than a year birds

N(0,1) statistic for transient(>0) =-0.35998

P-level, two-sided test =0.71886

P-level, one-sided test for transience =0.64057

TEST2.CT, group 1 = Captured as one-year old birds

N(0,1) signed statistic for trap-dependence =1.1322

trap-happiness<0 trap-shyness>0

P-level, two-sided test =0.25756

TEST2.CT, group 2 = captured as older than a year birds

N(0,1) signed statistic for trap-dependence =-1.7665

trap-happiness<0 trap-shyness>0

P-level, two-sided test =0.077305

TABLE S1. Model selection for Initial State and State Assignment probabilities of females. For each model, we give deviance, number of estimable parameters (np), Quasi-Akaike Information Criterion corrected for small sample sizes (QAIC_c) and the difference in QAIC_c between the current model and best model with the lowest QAIC_c of the current parameter (Δ AIC_c).

No.	IS	S	Model			np	Deviance	QAIC _c	Δ AIC _c
			T	BT (C)	SA				
Model selection for Initial State									
is1	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms + t</i>	245	8652.9451	9185.3141	0.0000
is2	<i>ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms + t</i>	243	8660.3463	9187.9986	2.6845
is3	<i>ms x t</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms + t</i>	293	8608.3741	9255.9701	70.6560
is4	<i>t</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms + t</i>	267	9356.4182	9941.1132	755.7991
Model selection for State Assignment									
sa1	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms + t</i>	195	8699.2536	9115.6578	0.0000
sa2	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>t</i>	193	8746.6625	9158.5113	42.8535
sa3	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms</i>	170	8918.1317	9278.0426	162.3848
sa4	<i>age x ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>i</i>	168	9050.2194	9405.6527	289.9949

Model notation: IS, Initial State; S, Survival, T, Transition, BT(C), Breeding tenacity/capture; SA, State Assignment; *ms*, mating status; *t*, time; *i*, constant.

TABLE S2. Model selection for Initial State and State Assignment probabilities of males. For each model, we give deviance, number of estimable parameters (np), Quasi-Akaike Information Criterion corrected for small sample sizes (QAIC_c) and the difference in QAIC_c between the current model and best model with the lowest QAIC_c of the current parameter (Δ AIC_c).

No.	IS	S	Model			np	Deviance	QAIC _c	Δ AIC _c
			T	BT (C)	SA				
Model selection for Initial State									
is1	<i>age</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms + t</i>	155	5546.7929	5876.6126	0.0000
is2	<i>ms</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms + t</i>	154	5556.8216	5884.3792	7.7666
is3	<i>t</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms + t</i>	177	5518.6277	5989.6873	113.0747
Model selection for State Assignment									
sa1	<i>age</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>t</i>	131	5559.4609	5835.4966	0.0000
sa2	<i>age</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>ms + t</i>	132	5580.9187	5837.4966	2.0000
sa3	<i>age</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>f</i>	108	5743.7082	5969.1750	133.6784
sa4	<i>age</i>	<i>age + [ms x t]</i>	<i>age x ms</i>	<i>ms x t</i>	<i>i</i>	107	5747.2596	5970.5490	135.0524

Model notation: IS, Initial State; S, Survival, T, Transition, BT(C), Breeding tenacity/capture; SA, State Assignment; *ms*, mating status; *t*, time; *i*, constant.

FIGURE S1. Percentage of the accumulated number of successful breeder females of different mating status over the breeding timing period.

For this figure we have accumulated data from laying dates of females recorded from 1990 to 2016. Primary females were the earliest, secondary were the latest and monogamous were intermediate between polygynously-mated females.

