

Mating strategies in the Rock Sparrow *Petronia petronia*: the role of female quality

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We investigated the breeding phenology and breeding output in relation to female breeding status in the polygamous Rock Sparrow (*Petronia petronia*). The proportion of polygamous males was around 0.38 though it varied over the study periods. We selected 169 clutches of which the pair's breeding status was known. Within these clutches, we compared the breeding biology of females that mate monogamously, females that started breeding early with a polygamous male (primary females) and late breeding females that chose an already mated male (secondary females). Secondary females produced significantly fewer fledglings than monogamous females and females who started breeding early in a polygamous system. Our results showed that primary females and females mated with a monogamous male were heavier than secondary females. No age effect was detected. Overall, our results indicate that a female's decision to mate monogamously or late in a polygamous systems was probably not independent of her phenotype (body condition).

KEY WORDS: individual traits, mating strategy, *Petronia petronia*, Polygyny Threshold Model.

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INTRODUCTION

In several species of passerines, multiple mating strategies may coexist within the same population. In such cases the relative frequency of each strategy is likely to be the outcome of a cost-and-benefit balance involving ecological constraint but also individual quality or condition (OWENS & BENNET 1997). In each strategy, however, males and females may have different costs and benefits. In polygynous systems, the female's breeding cost is increased because males provide less parental care per hatched young. On the other hand males might have less control of paternity (PILASTRO et al. 2002).

In some cases, polygynous females do not incur an apparent cost (LIGHTBODY & WEATHERHEAD 1987, 1988; SEARCY 1988; HARTLEY & SHEPHERD 1994). Here the adaptive explanations are largely related to the Polygyny Threshold Model (PTM) (VERNER 1964, VERNER & WILLSON 1966, ORIANI 1969). This model assumes a cost to females that is compensated for by the male's value or by territory quality (ALTMANN et al. 1977, EMLEN & ORING 1977, BENSCH & HASSELUQUIST 1991). In other cases, the secondary females fledged fewer young than primary or even monogamous females (JOHNSON et al. 1993). For example, female Pied Flycatchers (*Ficedula hypoleuca*) pay a cost for their polygyny when they select a male who already has a mate (LUNDBERG & ALATALO 1992). This is probably due to an asymmetrical investment by the male towards the primary nest. In these cases, territorial polygyny seems an adaptive strategy for males but not for secondary females who would benefit more by choosing unmated males. An adaptive hypothesis to explain mating strategies that appear to be costly is their dependence on the number of mates available (DAVIES 1992, PILASTRO et al. 2001). A costly strategy may also be adaptive if individual quality is highly variable. For example, monogamous females might be of higher intrinsic quality than secondary females. Sometimes females may choose mated males because they are unaware of the presence of primary females. Such a "mistake" in mate choice occurs in those species in which a male defends two spatially distinct territories and attracts each female separately (deception hypothesis, STENMARK et al. 1988). Very few studies have investigated the relationship between ecological constraint, mating strategy and female intrinsic quality (see CARO & BATESON 1986).

The Rock Sparrow (*Petronia petronia*) is a small cavity nesting passerine. It is common in the middle Palearctic, from North Africa to Manchuria, in steppe and desert climates (CRAMP & PERRINS 1994). In Europe its distribution is confined mainly to open and sunny areas in the Mediterranean region of Spain, France, southern Italy and Greece where it usually breeds at low densities in small and loose colonies near human settlements (CRAMP & PERRINS 1994, MINGOZZI & ONRUBIA 1997). Despite this distribution, the ecology and biology of Rock Sparrow are poorly known. Although, some specific traits of the species have received more attention recently (PILASTRO et al. 2001, 2002; TAVECCHIA et al. 2002), complete data on its breeding biology are lacking.

The aim of this paper is to provide detailed information on the breeding biology of the Rock Sparrow using data from a 10 years study. We focus on the pay-offs of different female breeding strategies in terms of reproductive output and on the costs of polygyny for females. In the Rock Sparrow, polygamous females have a time-lag in the onset of breeding. Usually females started breeding monogamously. Some males are later successful in monopolising an alternative nest site and in attracting a second female. We compared the reproductive success of females

paired with an unpaired male, whether monogamously or as early breeding females within a polygamous system (primary females), with that of females that paired with an already mated male (secondary females).

The possible relationship between choice of mating status and phenotype in females has received little attention (see FORSTMEIER *et al.* 2001). To investigate if intrinsic female qualities may influence a female's mating decision, we tested whether secondary females differ from monogamous or primary females in age or morphology.

STUDY AREA AND METHODS

The study area was located between 1550 and 1800 m a.s.l. in the upper Susa Valley, Cottian Alps. The area is characterized by the presence of high, dry and sunny climatic conditions (MINGOZZI *et al.* 1994). An average of 39 nest boxes (11 × 12 × 50 cm) were set up every spring in three neighbouring villages from 1991. The landscape surrounding these villages was characterised by pastures and mountain meadows. Usually, parents were trapped at the nest when feeding the young. A few individuals (all males) were also trapped at the nest before the onset of reproduction. Trapped birds were measured and marked using aluminium rings and a unique combination of plastic colour rings. Chicks were measured and individually marked with colour rings at an age of about 14 days. Boxes were visited every 3 days, during all stages of the breeding season (MINGOZZI *et al.* 1994) over a period of 10 years (1991-2000). Furthermore, any activity during the reproductive period was monitored with regular 30 min behavioural observations every 5-6 days, in order to determine the pair bond and to record reproductive behaviour (PILASTRO *et al.* 2001). During 1998, 1999 and 2000 we collected 1 hr behavioural observations (every 3 days) at the nest (PILASTRO *et al.* 2002). Individuals were sorted according to breeding strategy only 6 days after fledging. Monogamy was defined if young fledged before the female or the male attracted a second mate. If the male attracted another female before the first female's young were completely independent (6 days after fledging), the first female was assigned primary status. A female was assigned secondary status if the offspring were fed by a male associated with another female. Moreover double-brooded females always started breeding very late in the season (but see PILASTRO *et al.* 2001).

The data analysed in this paper include 211 nests (for the analysis of first and second clutches), for basic biological information, and from these 169 nests in which the pair was known and thus the breeding status assigned. The following morphological characters were measured in females for which the breeding status was known (number in parentheses): wing length ($n = 40$), tarsus length ($n = 26$), tail length ($n = 26$) and body mass ($n = 45$). Body mass was strongly dependent on stage in the breeding cycle of females: during egg laying females were heavier than the females measured outside this period (M. GRIGGIO & A. PILASTRO unpubl. data) as shown in other studies (RICKLEFS & HUSSELL 1984, FORSTMEIER *et al.* 2001). For this reason, we used only females weighed when their offspring had 12-15 days of age. When multiple measures were available for the same female in different years we selected one randomly. We also investigated a possible influence of age by analysing 109 females for which the breeding status was known, divided them into two groups of 1 and > 1 years old, respectively. In 47 cases we were able to assign a breeding status to the same female in 2 consecutive years. This sub-sample was used to investigate breeding status transitions (79 cases recorded) using the Cohen's kappa coefficient (AGRESTI 1996).

When possible, parametric tests were used (t-test), the correspondent non-parametric tests were used when data distribution was unknown (U-Mann-Whitney and Kruskal-Wallis when two or more groups were considered, respectively). Hatching success was defined as the proportion of eggs hatched among those laid and it was analysed as a binomial variable with logit link using linear regressions. Extrabinomial variances were corrected through the estimate of a scale parameter (CRAWLEY 1993). We recall in the "Results" section the statistical

test used for each inference. Throughout the text means \pm SE are given unless specified. All probabilities are from a two-tailed test using 0.05 as the threshold for significance.

RESULTS

Pair formation, egg laying and clutch size

The most common type of mating was monogamy (percentage of monogamous females 61.5%) but this varied among years (61.50 ± 6.65 range: 28.57-86.67 $n = 10$). During this 10 year period an average of 4.6 males per year (0.21 of the entire male population) did not pair despite being successful in establishing the possession of a nest box (0.21 ± 0.024 range: 0.05-0.33). Laying started at the beginning of June but it varied from year to year (TAVERNITI 2000). There was no difference in the onset of laying between monogamous (days from 1st of January = 168.27 $n = 79$) and primary females in a polygynous system (primary females, days from 1st of January = 166.15 $n = 40$; $t_{117} = 1.368$, $P = 0.17$ on log-transformed variable). Secondary females in a polygynous system always started breeding later in the season (days from 1st of January = 183.00 $n = 43$). Overall the average clutch size was 5.46 ($n = 209$) but the first clutch was significantly larger than the second one, 5.6 ($n = 174$) and 4.7 ($n = 35$) eggs, respectively ($t_{207} = 3.82$ $P < 0.001$). However, within the first clutches there was no effect of breeding system, the average clutch size was 5.7 ($n = 79$), 5.8 ($n = 42$) and 5.5 ($n = 44$) for monogamous, primary and secondary females, respectively (Kruskall-Wallis test: $\chi^2 = 1.731$, $P = 0.421$; Table 1).

Hatching and fledging success

Hatching success was calculated as the proportion of eggs that hatched successfully and data were analysed using a binomial error structure and correcting

Table 1.
Breeding parameters according to the breeding status of females.

Female group	M	P1	P2	<i>P</i>
Laying date (from 1st January)	168.27 (79)	166.15 (40)	—	0.17 ¹
Clutch size	5.7 (79)	5.8 (42)	5.5 (44)	0.421 ²
Hatching success	0.82 (79)	0.84 (42)	0.71 (44)	0.12 ¹ (0.04 ¹ when M and P1 were considered together)
Number of fledged	4.04 (79)	4.41 (42)	3.32 (44)	0.09 ² (0.04 ² when comparing P1 and P2 and 0.03 ² when comparing M and P2)

M = monogamous, P1 = primary female of polygynous males, P2 = secondary female of polygynous males. *P* = probability of error in rejecting the null hypothesis of no difference between groups.
¹ Parametric test; ² non-parametric test.

for overdispersion. On average the proportion of eggs hatched was 0.72 ± 0.03 ($n = 209$). Hatching success was 0.76 ± 0.03 and 0.55 ± 0.06 for first and second clutch, respectively, but within the first clutches it changed according to the female status (0.82, 0.84 and 0.71 for monogamous, primary and secondary females, respectively; Table 1). The overall breeding status was not significant ($F_{2,164} = 2.17$, $P = 0.12$), but secondary female hatching success was significantly lower when monogamous and primary females were considered together ($F_{1,164} = 4.24$, $P = 0.041$; Table 1). Fledging probability, conditional to hatching was not significantly affected by female status even when monogamous and primary females were pooled ($F_{1,151} = 0.83$, $P = 0.365$). The nestlings were cared for and fed for about 18 days (18.55 ± 0.11 range: 15-21days $n = 135$). The average number of fledglings was 3.87 ± 0.18 and 1.77 ± 0.37 in first and second clutches, respectively ($n = 209$, U-Mann-Whitney: $P < 0.001$) but second clutches started late in the breeding season (days from 1st of January = 206.09, $n = 33$). The average number of chicks fledged was 4.04, 4.41 and 3.32 in monogamous, primary and secondary female, respectively (Kruskall-Wallis test: $\chi^2_2 = 4.83$, $P = 0.09$; Table 1). Pair-wise comparison suggested a difference between primary and secondary females (U-Mann-Whitney: $P = 0.039$), but not between primary and monogamous female nests (U-Mann-Whitney: $P = 0.72$). As in the previous analysis, when monogamous and primary females were considered together, they had a significantly higher breeding output (U-Mann-Whitney: $P = 0.03$; Table 1). Equivalent results (not showed) were obtained using an ANOVA approach on the log-transformed number of chicks fledged.

Effect of female quality on breeding status

Measurements of tarsus length and tail length revealed no significant differences between monogamous and primary females, nor between monogamous and secondary or between monogamous and primary females together and secondary females (t-test, all $P > 0.05$; Table 2). Secondary females were significantly lighter than monogamous or primary females (t-test, $P < 0.001$; Table 2) while there was no difference in weight between monogamous and primary females (t-test, $P = 0.483$; Table 2). There was also a significant difference in wing length between secondary and monogamous or primary females (t-test, secondary versus monoga-

Table 2.

Morphological data for three groups of females: monogamous females (M), primary (P1) and secondary (P2) females of polygynous males, P -values < 0.05 are in italics, means \pm SE are reported and sample sizes in parentheses.

Female group	Tail length (mm)	Wing length (mm)	Tarsus length (mm)	Body mass (g)
M	52.94 \pm 1.78 (15)	95.06 \pm 2.11 (15)	19.40 \pm 0.55 (17)	33.70 \pm 1.27 (20)
P1	52.66 \pm 1.77 (6)	96.20 \pm 0.95 (9)	19.55 \pm 0.50 (4)	34.07 \pm 1.41 (9)
P2	52.90 \pm 2.01 (5)	96.74 \pm 1.82 (16)	19.56 \pm 0.58 (5)	31.61 \pm 1.82 (16)
Comparisons				
M vs P1	$P = 0.749$	$P = 0.144$	$P = 0.641$	$P = 0.483$
M vs P2	$P = 0.961$	$P = 0.024$	$P = 0.595$	$P < 0.001$
M+P1 vs P2	$P = 0.971$	$P = 0.040$	$P = 0.644$	$P < 0.001$

Table 3.

Female breeding status across seasons: first breeding season (rows) compared with a subsequent breeding season (columns).

	Monogamous	Primary	Secondary
Monogamous	36	14	5
Primary	2	8	5
Secondary	2	2	2

mous $P = 0.024$, secondary versus monogamous and primary $P = 0.040$; Table 2) but not between monogamous and primary females (t-test, $P = 0.144$; Table 2).

The proportion of females ≥ 2 years old was higher among secondary females (0.62, 0.71 and 0.81 in monogamous, primary and secondary females, respectively) but this difference was not significant ($\chi^2 = 3.43$, $P > 0.10$). Forty-seven females were captured more than once, giving a total of 76 transitions between breeding status from year i to year $i+1$. Females tended to stay in the previous breeding status ($k = 0.27 \pm 0.08$ $P = 0.01$; Table 3), but Cohen's kappa coefficient was low showing that some off-diagonal values were higher than expected. This was because a "state-fidelity" was pronounced in monogamous females but less in primary and secondary females.

The probability of moving to the secondary status seemed to increase with age: 0.11, 0.06, 0.24 and 0.33 for females aged 2, 3, 4 and 5 years, respectively. However, the contingency table contained 2 cells with expected values less than 5 and some pooling was necessary. Contrasting results were obtained depending on the pooling (data not shown) and conclusions on the influence of age in the probability of secondary-status cannot be drawn. Overall, our results indicate that a female's decision to mate monogamously or as a secondary female was probably not independent of her phenotype (body condition or morphology).

DISCUSSION

We found that breeding output and female weight differs according to female status. For the same population, a recent study (PILASTRO et al. 2002) shows that polygynous males had a higher annual fledging success than monogamous males but suffered an elevated extrapair paternity rate: a higher proportion of extrapair young was found in their broods than in those of monogamous males. So, corrected for paternity, the fledging success did not differ significantly with male mating status, despite the fact that monogamous males sang at a lower rate and guarded more intensely than polygynous males (PILASTRO et al. 2002).

In females a difference between monogamous, primary and secondary females was clear. The hatching success of secondary females was significantly lower than that of primary or monogamous females when these were pooled (but not when the three statuses were considered in the same analysis). Furthermore there was an effect of female quality, expressed as body mass, that explained the female's breed-

ing status. It is also true that secondary females started laying later in the season than other females. In many other avian populations, reproductive performance decreases during the breeding season (PERRINS 1970). This would occur if food supply and/or weather conditions deteriorated or late-breeding parents reduced their investment because offspring survival declined (HOCHACHKA 1990, SVENSSON 1997, LEPAGE et al. 2000). Another class of hypotheses proposes that timing *per se* may not influence reproduction (WINKLER & ALLEN 1996, NILSSON 2000). The “quality” hypothesis predicts that the correlation between timing and reproduction are both in relation to a third variable: individual quality (e.g. low quality individuals lay fewer eggs late in the season). Recent experimental results suggest that the seasonal decline in clutch size is due to variation in female quality (CHRISTIANS et al. 2001). Also, if it is difficult to distinguish between “condition” and “timing” with a correlative approach, our results are in line with the quality hypothesis (see below).

Generally in this population secondary females received less or no aid from their mates if compared to primary females (M. GRIGGIO & A. PILASTRO unpubl. data). This limited male aid could partially explain the lowered reproductive success of secondary females. Contrary to the prediction by PTM, females seemed not to compensate for this increased cost. Similarly in the House Wren (*Troglodytes aedon*) secondary females produced significantly fewer fledglings than females who chose unmated males (monogamous and primary females) (JOHNSON et al. 1993). In addition we found a correlation between the quality (i.e. condition index) of females and their reproductive success. The deception hypothesis is a non-compensation model, but in our population secondary females were likely to know of the presence of the primary females because there was about a 2-weeks lag between their depositions. Moreover, primary and secondary nests were, in many cases, as close as 25 m from each other (authors’ observations).

PILASTRO et al. (2001) showed that the female Rock Sparrow’s breeding strategy depends on the number of available mates. Likewise, TAVECCHIA et al. (2002) found evidence that the number of females might also influence male mating strategy, suggesting it is the pattern of sex specific dispersal that influences the mating system. But the mean number of available unmated territorial males (i.e. males defending a nest) at the breeding time was about 4-5 individuals. Despite the possible cost, poor quality females bred with mated males when other unmated males were still available. Further studies on sexual selection are needed to clarify this point. Male and female Rock Sparrows possess a yellow patch on the upper breast, which is used in courtship displays and is variable in size among individuals (WILSON 1994). Within sex, patch size does not differ between first year and older birds and does not increase with age within individuals (PILASTRO et al. 2003). Moreover, non-breeding individuals have smaller patches than both breeding males and female birds (PILASTRO et al. 2003). Among females paired to polygynous males, primary females have a larger patch than secondary females. Finally, patch size is positively correlated with body mass in females and there is evidence that this trait is actively selected (GRIGGIO et al. 2003, PILASTRO et al. 2003). This evidence is in line with our results on the morphological characters of females and their reproductive success. From these observations it is reasonable to believe that male and female individual quality (probably expressed also by the size of the yellow patch) is an important variable in mating strategies. Mating with an already mated male is probably an indirect compensation (i.e. genetic quality, sexy son hypothesis; WEATHERHEAD & ROBERTSON 1979). However, without an experimental approach it is impossible to reject the predictions of the PTM hypothesis.

The wide array of mating options, including monogamy and polygyny (this study) and female brood desertion (PILASTRO et al. 2001), extrapair fertilization, intense courtship of brood females (PILASTRO et al. 2003), may all reflect the intense competition for mates. Furthermore, the great variation in male mate guarding and singing rate, attendance and feeding behaviour during brood rearing (PILASTRO et al. 2002), altogether show a complex situation in which individuals appear to be constantly assessing one another and manoeuvring into the best position for breeding opportunities. In our opinion this seemingly favourable strategy is the result of being a marginal population in which there is a limited number of breeding sites and the breeding seasons are variable and short. Our analysis is based on breeding parameters only and status-related fitness should incorporate a survival estimate as well as fecundity. Secondary females might compensate for their lower breeding output by an enhanced survival rate. An analysis of lifetime reproductive success was beyond the purpose of this paper and it is complicated by the fact that the fate of the offspring remains largely unknown (LAMBRECHTS et al. 1999). However, because in short-lived species fitness measures are more sensitive to a change in fecundity rate than in survival (LEBRETON & CLOBERT 1991), the breeding output is the main component of lifetime reproductive success.

Breeding strategies also interact with ecological conditions and the scenario presented here might be further complicated by global climatic changes, i.e. a longer breeding season, and long-term changes in agricultural practices, possibly causing a reduction in suitable habitat (T. MINGOZZI unpubl. data). Unfortunately, studies on populations in a more typical area of the species distribution are lacking. Other studies with manipulative purposes (i.e. detention, quality of individuals, number and quality of nest boxes available) would help to understand the influence of different variables on mating strategies.

In conclusion, our results suggest that the quality of secondary females, in this population of Rock Sparrows, is lower than that of monogamous and primary females, since they produce significantly fewer fledglings than females mated with unmated males. Altogether these results suggest that female (and male) choice, and consequently the breeding strategy, may also depend on characteristics that are specific to the individual, and may be more complicated than indicated by traditional polygyny models, as proposed in the recent work of FORSTMEIER et al. (2001).

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